Journal of Biogeography

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Journal of Biogeography

SYNTHESIS OPEN ACCESS

Global Free-Living Symbiodiniaceae Biodiversity Mirrors Local Environments

Sydney L. Bell[1] | Kate M. Quigley[1,2,3]

[1]James Cook University, Townsville, Queensland, Australia | [2]Minderoo Foundation, Perth, Western Australia, Australia | [3]Oceans Institute, University of Western Australia, Perth, Western Australia, Australia

Correspondence: Sydney L. Bell (sydney.bell@my.jcu.edu.au)

Received: 12 September 2024 | **Revised:** 19 March 2025 | **Accepted:** 26 March 2025

Funding: This work was supported by Australian Research Council, Minderoo Foundation.

Keywords: biogeography | coral reefs | free-living | metacommunity | Symbiodiniaceae | symbiosis

ABSTRACT

Aim: For free-living Symbiodiniaceae, we aim to synthesise current knowledge, identify gaps in our understanding of biogeography and conduct the first quantitative genetic analysis of biogeography at a global scale.

Location: Global.

Taxon: Free-living dinoflagellates of the Family Symbiodiniaceae.

Methods: Publicly available sequences were used to characterise the free-living Symbiodiniaceae community in the environment. Using the genetic ITS2 marker combined with the *DADA2* pipeline, amplicon sequence variants (ASVs) were used to assess Symbiodiniaceae diversity, abundance and distribution patterns from local to global scales.

Results: Relative abundances, community composition and sequence diversity differed significantly between the wider Caribbean and Indo-Pacific, within the Indo-Pacific, and across our three study regions: Great Barrier Reef (GBR), Flower Garden Banks National Marine Sanctuary (FGBNMS) and Moorea in French Polynesia. Symbiodiniaceae community assemblage was most different between the GBR and FGBNMS, with a dominance of *Cladocopium* in the GBR and *Breviolum* in FGBNMS. There was also significant variability within these regions, as shown through a beta dispersion test. The highest diversity indices were found in the GBR, followed by Moorea and FGBNMS.

Main Conclusions: We found free-living Symbiodiniaceae biogeography differed significantly between and within locations at the global scale. Importantly, these global patterns in diversity mirrored local-scale patterns. These free-living biogeographical patterns also followed *in hospite* symbiont community patterns. With most studies of free-living diversity from the Indo-Pacific, we highlight the need for expanded sampling efforts in unexplored regions such as the Indian Ocean. Given the potentially significant role of free-living Symbiodiniaceae in coral acclimation to climate change, identifying and protecting these taxa should be a conservation priority.

1 | Introduction

As one of the most biodiverse marine ecosystems, tropical coral reefs depend on symbiotic relationships to sustain their structure and function. Reef-building corals rely on their endosymbiotic dinoflagellates, Symbiodiniaceae, for energy production, a partnership that has shaped their evolutionary success (Apprill 2020). While much research has focussed on symbiotic Symbiodiniaceae, far less is known about their free-living counterparts, despite their potential role as reservoirs for reef resilience.

Journal of Biogeography, 2025; 52:e15137
https://doi.org/10.1111/jbi.15137

Here, we synthesise current knowledge on Symbiodiniaceae found free-living in the environment and highlight the importance of understanding their distributions, abundance and community composition. Despite their potential role in reef resilience, research on free-living Symbiodiniaceae remains limited, with only 24 studies focussed on their presence in sediment communities. Of these studies, 87.5% have been conducted in the Indo-Pacific, highlighting a significant geographical bias and a gap in our understanding of their global biogeography. We assess their biogeographical patterns, explore the impacts of climate change on the ecology and functioning of this group, and finish by identifying knowledge gaps using a meta-analysis of publicly available data. We close by contextualising this knowledge in the biogeography of Symbiodiniaceae for current coral reef conservation efforts.

1.1 | Symbiodiniaceae Taxonomy, Distributions, and Ecology

The Family Symbiodiniaceae (LaJeunesse et al. 2018) is a diverse group of unicellular, marine dinoflagellates well known for their symbiotic relationship with scleractinian reef-building corals (Droop 1963; McLaughlin and Zahl 1966). Symbiodiniaceae taxonomy has recently undergone a revision, now divided into 15 lineages, 11 of which are formally described genera, likely containing hundreds of species (LaJeunesse et al. 2018, 2022; Pochon and LaJeunesse 2021). This symbiosis is not only prevalent across the coral tree of life but also in many other invertebrate hosts, establishing well-defined ecological niches for many of these dinoflagellates (Knowlton and Rohwer 2003; LaJeunesse et al. 2018; Sampayo et al. 2007). Scleractinian corals specifically have lived in this association with endosymbiotic forms of Symbiodiniaceae for ~240 million years (Muller-Parker et al. 2015; Frankowiak et al. 2016). Symbiodiniaceae could therefore be typified as a keystone Family for coral reefs, providing the necessary organic compounds for their host taxa to thrive in oligotrophic tropical seas (Grover et al. 2008; Burriesci et al. 2012; Davy et al. 2012). Hence, corals' endosymbionts are critical to coral reef survival, utilising the waste products of the coral host (particularly carbon) to enhance coral calcification and reef accretion (Morris et al. 2019; Muscatine and Porter 1977; Pearse and Muscatine 1971). The enduring symbiotic relationships within the marine realm, spanning the hard coral tree of life (Madin et al. 2016; Gault et al. 2021), again emphasises the vital role of Symbiodiniaceae.

Genetically distinct Symbiodiniaceae, hereafter generalised as 'taxa' to acknowledge that the taxonomic revision is still on-going (sensu Davies et al. 2023), possess unique distributions based on several factors. These include differences in host associations, geographic distributions and preferred environmental conditions (LaJeunesse et al. 2004). Competition for resources inside the host and subsequent ecological specialisation likely impact the biogeography, diversification and speciation of most Symbiodiniaceae (LaJeunesse et al. 2014; Lewis et al. 2019; Turnham et al. 2021). This process has led to adaptive radiations and the evolution of symbionts specialised to specific hosts or environments (LaJeunesse et al. 2003; Thornhill et al. 2014).

Ecological specialisation has shaped the distribution and evolution of Symbiodiniaceae and has contributed to their remarkable genetic and functional diversity (LaJeunesse et al. 2018). This diversity, in turn, influences the health of the holobiont, in which the interaction of the coral host and its diverse microbial assemblage make up a collective phenotype (Voolstra and Ziegler 2020). As such, variability in symbiont community composition and diversity, both among and within the coral hosts, influences the overall stress tolerance and subsequent fitness of the coral. Specific symbiont taxa can play a critical role in mitigating bleaching severity and enhancing recovery under stress (Baker et al. 2004; Quigley et al. 2023; Turnham et al. 2023). Additionally, hosting different Symbiodiniaceae taxa can provide enhanced tolerance to high light (Reynolds et al. 2008), increased coral growth rates (Little et al. 2004; Cantin et al. 2009) or enhanced recovery after cold stress (Thornhill et al. 2008). These host–symbiont dynamics underscore the importance of understanding Symbiodiniaceae diversity in the context of coral reef resilience to environmental change.

Advances in genetic sequencing technology (Quigley et al. 2014; Thomas et al. 2014) have revealed the existence of a mostly rare and highly diverse Symbiodiniaceae community within coral hosts and free-living in the environment. Free-living populations, found in habitats such as sediments, water and algal mats, often include a mix of moderately abundant and low-abundance taxa from various genera (Manning and Gates 2008; Pochon et al. 2010; Quigley et al. 2022). *In hospite*, associations of one or a few dominant and abundant taxa and many low-abundance taxa are common (Quigley et al. 2014; Hume et al. 2016; Ziegler et al. 2017). Although rare taxa are by definition at low abundance, they may significantly contribute to host functioning and health, and by extension ecosystem function, particularly under environmental stress (Ziegler et al. 2018). This underscores the potential role of free-living Symbiodiniaceae in maintaining ecosystem resilience, highlighting the need for further exploration into their functional contributions and interactions within diverse environmental niches.

Symbiont community composition can also change over time and in response to disturbances through 'shuffling' (changes in relative abundances, Baker 2003) and 'switching' (uptake of new taxa; Baker 2003; Boulotte et al. 2016). These processes align with the adaptive bleaching hypothesis (ABH; Buddemeier and Fautin 1993) and are thought to enhance holobiont fitness under stress by promoting associations with more tolerant taxa. Therefore, changes to symbiont community composition to more stress-tolerant taxa may be critical for predicting how coral reefs might adapt to climate change-induced stressors.

1.2 | Free-Living Symbiodiniaceae

The Symbiodiniaceae life cycle is complex and follows both a free-living (outside the host) and *in hospite* stage in the host (Bhattacharya et al. 2024; Freudenthal 1962; Trench and Blank 1987). Free-living Symbiodiniaceae can be found within the sediment, water column or on macroalgal surfaces (Manning and Gates 2008; Pochon et al. 2010; Quigley et al. 2022). It is important to note that free-living can also include symbiotic

Symbiodiniaceae expelled from hosts and may include non-symbiotic taxa (Yamashita and Koike 2013; Granados-Cifuentes et al. 2015; Lee et al. 2016).

More than 85% of coral species acquire Symbiodiniaceae from the environment through horizontal transmission (Baird et al. 2009; Quigley et al. 2016). Uptake of Symbiodiniaceae occurs at the egg, larval or juvenile stages (Quigley, Willis, et al. 2017). The remaining ~20% of coral species rely on vertical or mixed-mode transmission where symbiont communities are passed maternally from adults to the eggs or larvae with some environmental acquisition (Baird et al. 2009; Quigley, Willis, et al. 2017). The process of horizontal transmission likely ensures the acquisition of locally adapted Symbiodiniaceae where corals settle, strengthening the associations between hosts and their symbiont community (Douglas and Werren 2016). Additionally, horizontal transmission is hypothesised to be an adaptive strategy for coral larvae to avoid oxidative stress associated with symbiosis in high-light and high-temperature environments (Hartmann et al. 2017). Horizontal transmission is advantageous at present but may create challenges in the establishment of symbiosis under the variable environmental conditions from climate change. For example, there is evidence showing the negative impacts on symbiont infectivity caused by heat stress (Kishimoto et al. 2020; Kitchen et al. 2022). As such, the free-living Symbiodiniaceae pool becomes an increasingly critical source for establishing symbiosis in each new generation, highlighting its importance for coral resilience in the face of climate change.

Generally, Symbiodiniaceae diversity is higher in free-living communities as opposed to in the hosts (Takabayashi et al. 2012; Quigley, Bay, et al. 2017; Ziegler et al. 2018). Sediment communities are also distinct from other habitats such as the water column and macroalgal surfaces (Quigley, Bay, et al. 2017), even though the water column has a greater abundance of exclusively free-living taxa (Littman et al. 2008; Takabayashi et al. 2012; Fujise et al. 2021). Densities of Symbiodiniaceae are higher in the sediment as well, due to characteristics such as relative immobility and negative buoyancy of the cells (Coffroth et al. 2006; Littman et al. 2008; Yacobovitch et al. 2004). The sediment community in particular serves as a diverse reservoir from which corals may acquire Symbiodiniaceae during ontogeny and potentially after bleaching events (Quigley, Bay, et al. 2017; Quigley et al. 2022; Ali et al. 2019; Nitschke et al. 2016; Williamson et al. 2021). Additionally, adult colonies continually re-seed the free-living pool in the sediments as they shed or expel symbionts daily (Yamashita et al. 2011; Nitschke et al. 2016). Coral hosts thereby continuously maintain this environment with high diversity relevant to the coral hosts (Bhattacharya et al. 2024). Horizontal transmission has likely persisted through evolutionary time because it also may benefit Symbiodiniaceae themselves by enabling the increase in relative abundance in the environment and therefore increased likelihood of colonising coral recruits due to their increased expulsion (Scott et al. 2024). Finally, exposure to sediment significantly increases the acquisition of Symbiodiniaceae in larvae compared to if larvae are only exposed to the water column (Adams et al. 2009). Taken together, this highlights the significance of the sediment habitat relative to other environmental sources as a key habitat for free-living Symbiodiniaceae.

It has also been posited that the free-living lifestyle provides four main advantages to Symbiodiniaceae and their subsequent coral hosts under climate change. First, it may be an opportunity for dispersal to new locations and into new hosts (Decelle et al. 2018; Bhattacharya et al. 2024). Second, the free-living stage could provide an opportunity for sexual recombination, increasing beneficial genetic variation and opportunities for adaptation (Figueroa et al. 2021; González-Pech et al. 2021; Thornhill et al. 2017). Third, bleaching may be interpreted as a host-regulated 'turn-over' of symbionts (ABH), where healthy cells can return to a free-living lifestyle and potentially associate with another coral host (Bhattacharya et al. 2024). Lastly, the free-living lifestyle may be characterised by the accumulation of extensive structural elements (GC content and longer introns) that could lead to accelerated evolution and diversification (González-Pech et al. 2021; Shah et al. 2023). These inferences clearly highlight the critical importance of free-living Symbiodiniaceae in the environment.

1.3 | Challenges in Determining Free-Living Symbiodiniaceae Diversity

The taxonomic classification of Symbiodiniaceae was initially slow due to challenges in isolating and differentiating morphological characteristics between potentially different taxa. Advancements in molecular techniques have also enabled classification to move beyond only using morphology by using the estimation of genetic divergence among these symbionts (Davies et al. 2023; Rowan and Powers 1991). This has led to the development of a robust classification system (LaJeunesse et al. 2018), revitalising the study of coral–algal ecological and evolutionary relationships (Nitschke et al. 2020, 2022; Pochon and LaJeunesse 2021; Yorifuji et al. 2021). Additionally, molecular techniques such as sequencing have led to the discovery of increased diversity, where free-living Symbiodiniaceae communities in the sediment appear to be a complex mixture of both transiently and exclusively free-living cells (Quigley, Bay, et al. 2017). Furthermore, in environmental samples, multiple Symbiodiniaceae taxa across multiple genera are present in a single sample. The number and complexity of taxa are challenging because much of the taxonomy remains to be described and critical information about their physiology is unknown. These gaps and complexities in community assemblage structure have contributed to the current limited understanding of free-living Symbiodiniaceae biogeography.

1.4 | Symbiodiniaceae Biogeography

Symbiodiniaceae communities in corals are highly structured by taxa and location (Baker 2003; LaJeunesse et al. 2004; Pochon et al. 2004). It would therefore be expected that free-living communities follow similar habitat partitioning apparent through large-scale patterns in biogeography. In particular, differing biogeographical patterns between the Pacific and Atlantic should be structured by the geographical isolation of the regions beginning in the late Miocene and distinct environmental conditions such as turbidity and temperature (LaJeunesse 2005; LaJeunesse et al. 2010; Rowan et al. 1997). Despite geographic isolation, there still may be rare transmission events between ocean basins—such as the invasion of *Durusdinium trenchii* from the Indo-Pacific into the Caribbean (Pettay et al. 2015). Of the 38 papers that focussed on free-living Symbiodiniaceae (Table S1), we found little mention or analysis of habitat partitioning in sediment communities, in contrast to the frequent mentions of habitat partitioning in papers focussed on symbiont communities in the coral host. Currently, there are only 24 studies on free-living *Symbiodiniaceae* in sediment communities, with 87.5% focusing on the Indo-Pacific region. This significant bias highlights a global gap in our understanding of their biogeography, underscoring the need for more comprehensive research across different ocean basins to better inform conservation and management strategies.

1.5 | Symbiodiniaceae Biogeography Across Small Spatial Scales

In corals, Symbiodiniaceae communities vary across small spatial scales (Cunning et al. 2015; Tonk et al. 2017). Local conditions such as light and temperature drive patterns in association and dominance (Tonk et al. 2017; Wepfer et al. 2020), even across single reef pools (Oliver and Palumbi 2009; Stat et al. 2011; Cunning et al. 2015). Larger 'local' gradients, such as inshore to offshore gradients, also appear to be a strong driver of distributions due to the combination of environmental factors such as light, temperature and nutrients, even over large latitudinal extents (LaJeunesse et al. 2010; Tonk et al. 2017). Therefore, we might expect free-living communities to follow similar rules, where microhabitat differences in environmental factors drive patterns in distributions.

From our survey of the literature, the free-living Symbiodiniaceae in the water column and sediment reservoir also appear to be partitioned across small spatial scales, driven by local environmental conditions. On the GBR, sediments collected from inshore reefs had higher abundances of stress-tolerant *Durusdinium* compared to offshore sediments, but lower abundances of *Symbiodinium* (Cumbo et al. 2013; Quigley, Bay, et al. 2017, 2022). Diversity also differed significantly between inshore and offshore sediments, indicating key biogeographic drivers are operating across this gradient (Quigley, Bay, et al. 2017). Taken together, these biogeographical differences from inshore to offshore are likely driven by higher nutrient levels, more frequent run-off of smaller-sized particles, shallower depths, and less variable light regimes (Tonk et al. 2017; Camp et al. 2018). Additionally, contrasting thermal environments in American Samoa found strong differences in free-living communities between and within pools only meters apart (Cunning et al. 2015). From this, we can conclude that free-living Symbiodiniaceae community composition is likely highly partitioned and varies along small spatial scales, from pools to inshore-to-offshore gradients, just as with *in hospite* communities.

1.6 | Symbiodiniaceae Biogeography Across Large Spatial Scales

Given the lack of analyses over large spatial scales (e.g., ocean basins), we used publicly available sequence data to fill this gap (Table 1). To do this, we analysed sequencing data from the Symbiodiniaceae ITS2 spacer region from samples collected from reef sediments (Table S1). Sequence data were downloaded from NCBI Sequence Read Archive (SRA; http://www.ncbi.nlm.nih.gov/sra). Data consisted of sequences from the Flower Garden Banks National Marine Sanctuary (FGBNMS; Ali et al. 2019), the GBR (Quigley et al. 2022) and Moorea (Grupstra et al. 2021). The FGBNMS study used a different sequencing chemistry (the Roche 454 platform) compared to GBR and Moorea studies (Illumina). The results of this analysis will be discussed alongside regional literature; however, these supporting studies were excluded from the ASV analysis due to unavailable public data, use of different genetic markers, or lack of sediment data (Table S1; Figure S1). We acknowledge that using only 1–2 sites within each region and without more comprehensive geographic coverage of a given region (especially in the Caribbean) is a limitation and may have led to bias. Whilst we are wary to characterise whole regions based on limited geographic sampling, these are the only samples currently available. This highlights that additional global sampling is required, and that with additional sampling, these biogeographical patterns may change.

TABLE 1 | Site and sampling information for sediment samples included in the meta-analysis.

Study site	Sub-sites	Sampling depth (m)	Number of samples
Great Barrier Reef	Inshore, Central	1–6	61
Great Barrier Reef	Inshore, North	1–6	19
Great Barrier Reef	Offshore, Central	1–6	104
Great Barrier Reef	Offshore, North	1–6	18
Moorea	Backreef	1–2	5
Moorea	Forereef	5–10	6
Flower Garden Banks	NA	23	28

Publicly available sequences were processed through demultiplexing, quality inspection, filtering, and variance normalisation, following a protocol and code detailed and reviewed in references (Quigley et al. 2019; Howe-Kerr et al. 2020). After quality and length trimming, we retrieved and analysed 1,846,422 (GBR), 30,251 (FGBNMS), and 90,045 (Moorea) sequence reads from the three datasets. Statistical analyses of the Symbiodiniaceae community were conducted within the R statistical environment (R Core Team 2024) using outputs generated from the 'DADA2' (*v.1.26.0*) pipeline—which created a count table of ASVs. Regardless of using different high-throughput technologies (amplicon or MiSeq), sequences were run through the same 'DADA2'-based analysis pipeline (Figure 1) with modifications for the Symbiodiniaceae ITS2 region (Quigley et al. 2019). The ITS2 region is multicopy

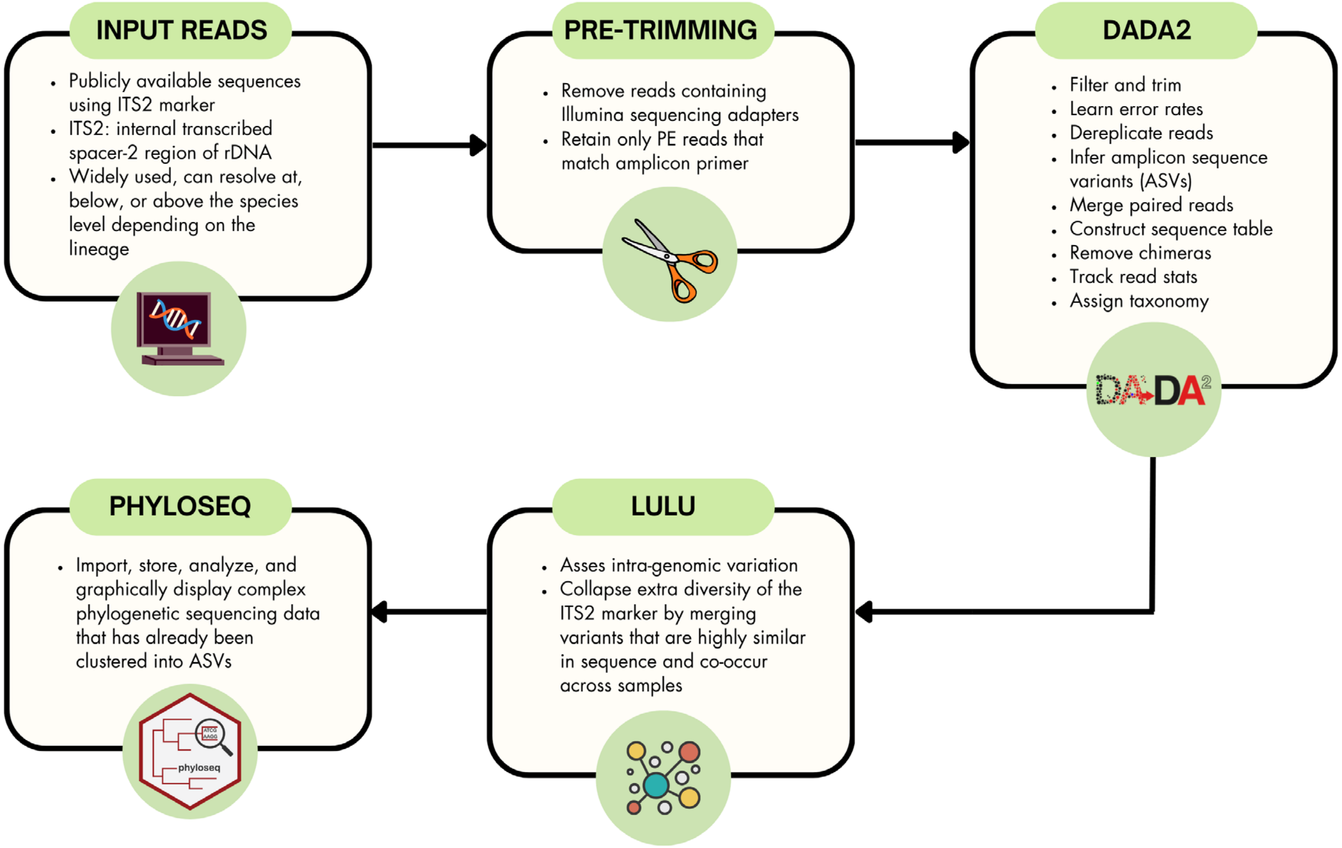

FIGURE 1 | Overview of the analysis pipeline used for processing amplicon sequence data, including quality filtering, error modelling, dereplication, chimera removal, and taxonomic assignment using the DADA2 pipeline (Callahan et al. 2016). The *LULU* algorithm was used as a post-DADA2 clustering curation step following the methodology outlined in Quigley et al. (2019). This approach ensures high-resolution inference of sequence variants from raw sequencing reads.

and susceptible to intragenomic variation, resulting in the detection of multiple sequence variants that are functionally equivalent. To distinguish intragenomic variants from biologically relevant entities, the 'DADA2' pipeline assigns Symbiodiniaceae genotypes from exact amplicon sequence variants (ASVs) using a regression approach (Callahan et al. 2016; Quigley et al. 2019). This method resolves individual base pair differences, resulting in fewer false positives than OTU-based analysis pipelines. Additionally, a post-'DADA2' clustering curation step was applied using the 'LULU' (*v.0.1.0*; Frøslev et al. 2017) algorithm to address intra-genomic variants (thresholds of 90% and 84%; Quigley et al. 2019). The extra diversity of the ITS2 marker is collapsed by merging variants that are highly similar in sequence and co-occur across samples to differentiate between intra- and intergenomic sequence variants (Quigley et al. 2019). Next, 'DESeq2' (*v.1.42.1*; Anders and Huber 2010) was used to adjust counts for differences in read depth (Quigley et al. 2019). Within 'DADA2', Symbiodiniaceae ITS2 taxa were assigned based on BLAST results to a Symbiodiniaceae ITS2 database (Franklin et al. 2012).

A permutational multivariate analysis of variance (PERMANOVA) was used to statically and graphically evaluate differences in Symbiodiniaceae community structure between regions using ordination methods, including Bray–Curtis distance (with 9999 permutations) using the package 'vegan' (*v.2.6–6.1*). PERMANOVAs are sensitive to heterogeneity, therefore the least sensitive PERMANOVA was implemented ('adonis' in *vegan*, Anderson and Walsh 2013; Howe-Kerr et al. 2020). Additionally, the Shannon and Simpson diversity indices (H' and 1-D respectively; 'phyloseq' *v.1.48.0*) were also calculated to assess Symbiodiniaceae diversity in sediment samples. Wilcoxon rank sum tests were used when samples did not have a normal distribution. Finally, the analysis of multivariate homogeneity of group dispersions (variances) was used to assess sequence beta dispersion between regions to assess if any statistical differences exist ('betadisper' *v.2.6–6.1*). It is important to note that sequence alpha and beta diversity below the species level can encompass copy number and intragenomic variability (Davies et al. 2023).

To ensure that methodological differences between studies, including differences in geographical range size and sequencing depth (e.g., 10x more and deeper sequenced samples and larger range size for the GBR relative to the other study regions) did not significantly bias our results, additional analyses and transformations were run. First, to account for differences in read depth across regions, we explored rarefying the data using the 'vegan' package. Second, to account for differences in the number of samples per region, we randomised and then sub-set the GBR data to the smallest number of samples to match those in the other datasets ($n = 25$). Third, the GBR dataset was sub-set to only a single year of collections to match the temporal range of the other

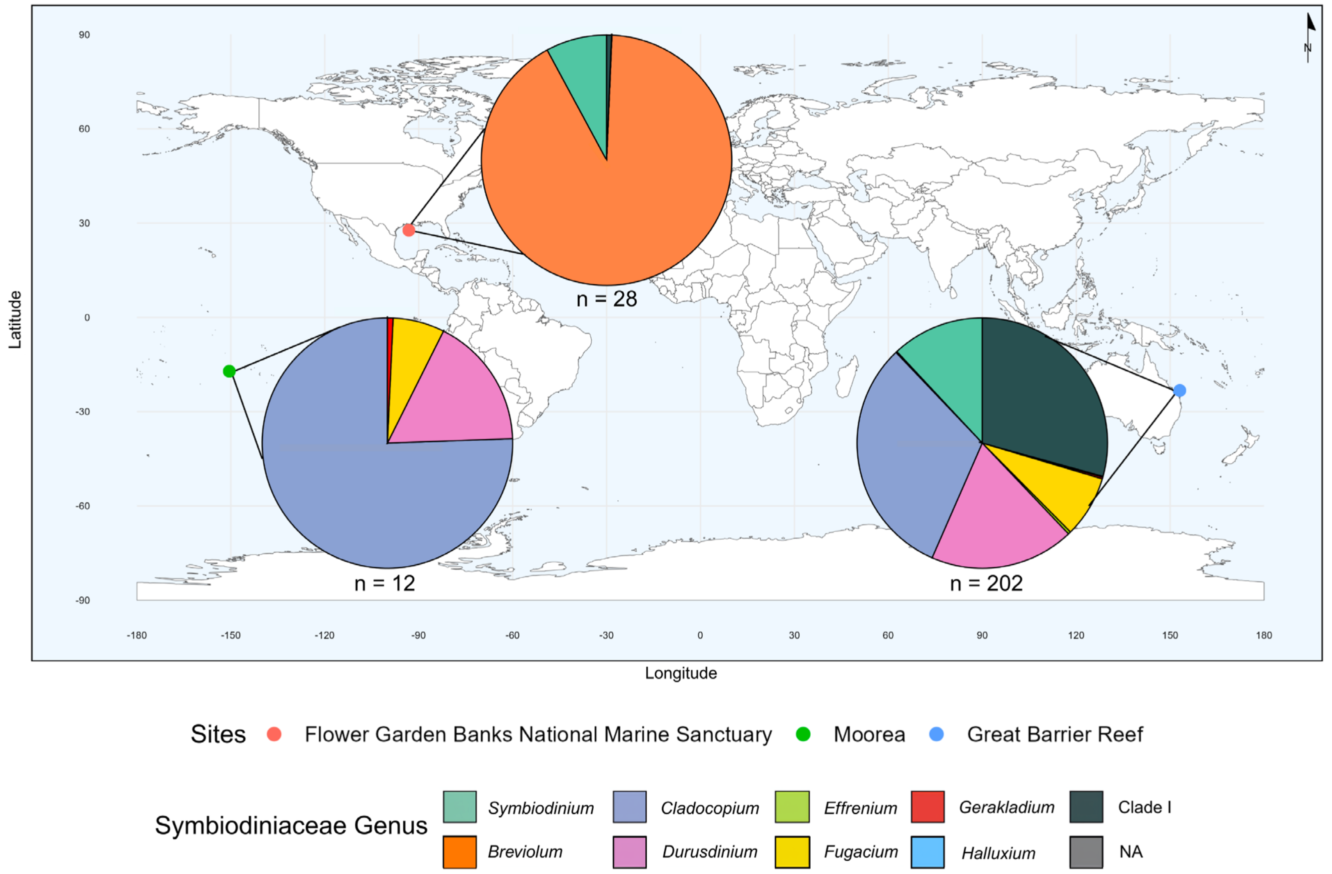

FIGURE 2 | Pie charts indicate the relative abundance of Symbiodiniaceae genera at each study location: FGBNMS, Gulf of Mexico ($n=28$), the GBR, Australia ($n=202$), and Moorea, French Polynesia ($n=12$). Colour indicates Symbiodiniaceae genus or current grouping (a group that has not been formally named as a genus) and the area of the pie slice indicates the proportion of each genus or grouping found within a location.

datasets. Fourth, we subset the larger GBR dataset into smaller range sizes, hereafter referred to as 'sites', such that the spatial size was more comparable to the data from our other study regions (inshore central GBR, offshore central GBR, inshore north GBR, and offshore north GBR). These sites were then analysed separately. Lastly, to account for differences in sampling depth, we grouped the samples by collection depth (Table 1; Table S2). Altogether, we found that the overall conclusions presented using the original datasets with these different transformations remained largely the same. Specifically, across all analyses or transformations we still found significant differences in alpha diversity ($p<1.01\text{e-}15$), beta diversity ($p=0.001$) and community composition ($p=0.001$) across the three regions of interest.

Through this approach, we suggest that large-scale biogeographical patterns exist across two ocean basins, including the Caribbean and Indo-Pacific. These patterns appear to mirror the smaller-scale patterns described above, including taxa potentially partitioning across diverse reefs and latitudes. Across these basins, the greatest difference in abundance and diversity of free-living Symbiodiniaceae occurred between the Caribbean and Indo-Pacific (Figure 2), whereas the FGBNMS were more distinct due to their lower diversity and lower abundance of *Cladocopium*, Clade I, and *Durusdinium*. However, the composition of sequence variants differed significantly between all three reef regions (PERMANOVA; Pseudo-F$=10.592_{2,238}$, $p=0.001$; Figure 3). There were also significant differences in free-living communities between the GBR and FGBNMS (df$=1$, F$=12.623$, $p=0.0001$), the GBR and Moorea (df$=1$, F$=9.0147$, $p=0.0001$), and FGBNMS and Moorea (df$=1$, F$=6.9334$, $p=0.0001$), as shown through pairwise PERMANOVA (9999 permutations). Sequence beta diversity was also significantly different within each region (permutation test for homogeneity of multivariate dispersions, $p=0.001$), where the GBR had the greatest variability compared to Moorea and FGBNMS. Shannon and Simpson diversity indices (H′ and D respectively) also differed significantly across regions (Figure S2). Shannon diversity was significantly higher in the GBR ($H'=2.69\pm0.042$) than in FGBNMS ($H'=1.13\pm0.078$) and Moorea ($H'=1.89\pm0.15$). Similarly, Simpson diversity was also higher in the GBR ($1\text{-}D=0.86\pm0.0069$) compared to FGBNMS ($1\text{-}D=0.75\pm0.035$) and Moorea ($1\text{-}D=0.56\pm0.029$).

Samples across sites and depths from the backreef (1–2 m) and forereef in Moorea (5–10 m) showed no significant differences in ASVs (PERMANOVA pairwise comparisons, Tables S3 and S4). All other comparisons (1–2 m vs. 1–6 m, 1–6 m vs. 5–10 m, 1–6 m vs. 23 m, 1–2 m vs. 23 m and 5–10 m vs. 23 m) were significantly different from each other (PERMANOVA pairwise comparisons Tables S3 and S4). Moreover, Shannon (H'; Figures S3 and S4) and Simpson diversity indices ($1\text{-}D$; Figures S5 and S6) were also significantly different and diverse across sampling sites (H', $\chi^2=114.9$, df$=6$, $p<2.2\text{e-}16$; $1\text{-}D$, $\chi^2=106.3$, df$=6$, $p<2.2\text{e-}16$)

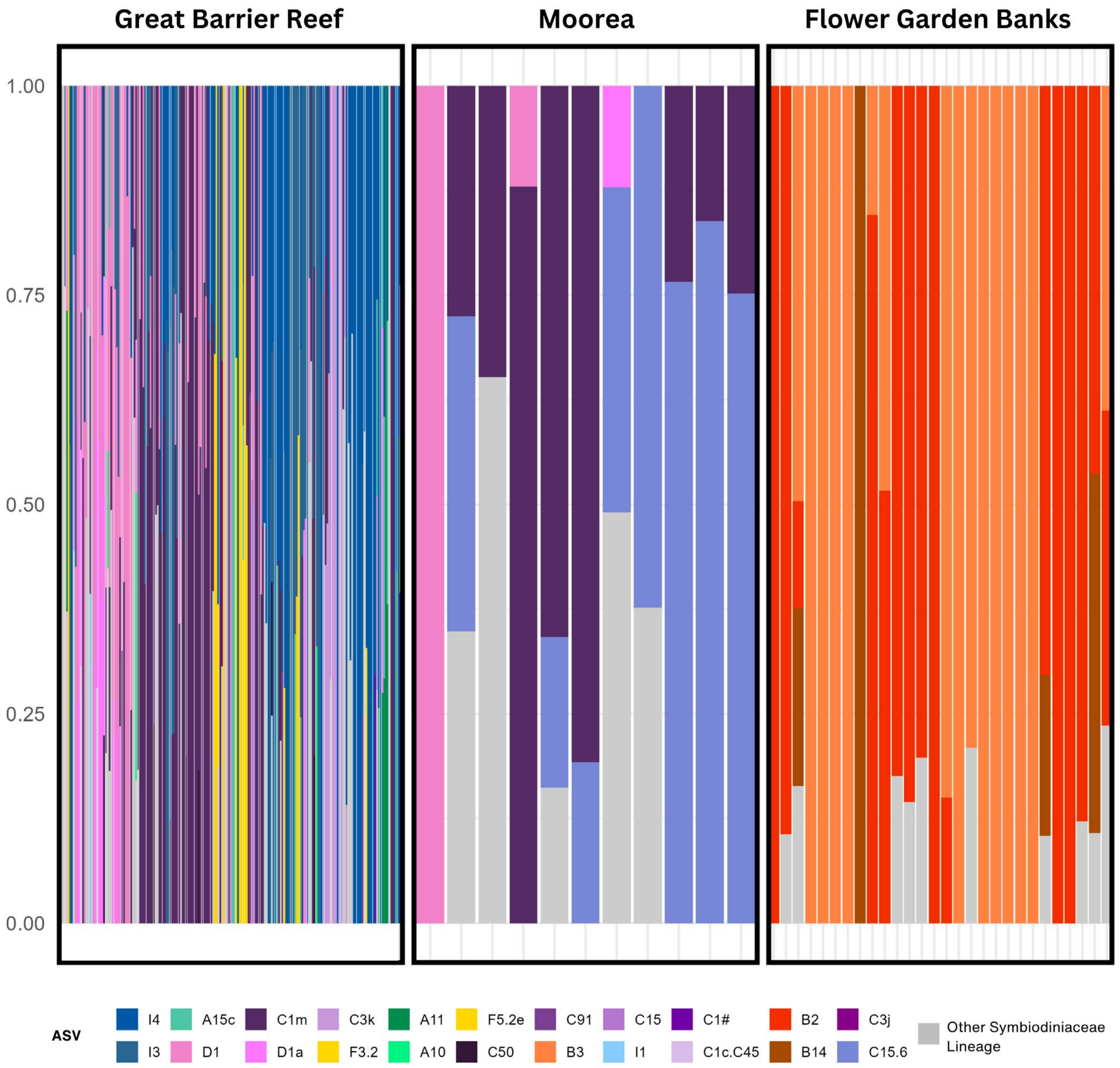

FIGURE 3 | Normalised relative abundances (%) of Symbiodiniaceae communities sequenced from sediment samples collected along reefs from FGBNMS ($n = 28$), the GBR ($n = 202$), and Moorea ($n = 12$). Each bar is a separate sediment sample and is organised based on Bray–Curtis distance. Barplots depict the variance-normalised relative abundance of each ASV. Only the most abundant ($n = 22$) ASVs are displayed in the legend in order of abundance.

and depths (H', $\chi^2 = 78.11$, df = 3, $p < 2.2\text{e-}16$; 1-D, $\chi^2 = 72.93$, df = 3, $p = 1.01\text{e-}15$). Notably, FGBNMS Shannon and Simpson diversity indices were significantly different from all site replicates except upon comparison with the Moorea backreef. The Moorea backreef and forereef were most similar to the inshore central GBR and the offshore north GBR for both Shannon and Simpson. Additionally, all GBR sites were most similar to each other, except for the inshore central GBR, which was significantly different from all other GBR sites.

The composition of sequence variants differed significantly between all sampling sites (PERMANOVA; Pseudo-F = $7.2343_{6,234}$, $p = 0.001$; Table S2) and depths (PERMANOVA; Pseudo-F = $7.2921_{3,237}$, $p = 0.001$; Table S2). When regions were split into sites, 15.6% of variances in community composition, a proxy for beta diversity, could be attributed to sampling location (Table S2). This was in comparison with 8.5% of variances in community composition that could be explained by sampling depth (Table S2). Permutation tests for homogeneity of multivariate dispersions also indicated that variances were significantly different among Symbiodiniaceae communities between all sampling sites ($p = 0.001$; Table S2) and depths ($p = 0.001$; Table S2). When comparing beta diversity tests, depth explained a higher percentage of variances (7.6%; Table S2) compared with sampling site (4.0%; Table S2). Overall, these results encouragingly support our initial results that free-living

Symbiodiniaceae exhibit biogeographical partitioning across broadscale reef basins, even after accounting for differences in sequencing depth or the size of the biogeographical sampling location. However, to more definitively demonstrate biogeographical structure, additional sampling is needed, especially across the broader Caribbean. Until then, these results should only be taken as preliminary.

1.7 | Symbiodiniaceae Distributions Across Biogeographic Regions

1.7.1 | Caribbean

Given these large-scale patterns above, we further investigated diversity within each region by combining the above analysis with trends reported from literature within each region. Free-living *Breviolum* (94.4%) and *Symbiodinium* (5.56%) dominated FGBNMS (Figure 2). Specifically, FGBNMS was dominated by B3 (relative abundance = 46.8%), B2 (*B. psygmophilum*; 41.0%), and B14 (*B. faviinorum*; 6.57%). Within these genera, an additional 92 sequence variants were recorded, suggesting that there may be substantial lineage diversity within free-living *Breviolum* and *Symbiodinium*, although we acknowledge some of these additional variants may be false positives. When compared to previous studies, these trends correspond to the dominance of *Breviolum* and *Symbiodinium* in both the water column and sediments (Manning and Gates 2008; Takabayashi et al. 2012). In Florida, *Breviolum* made up 85.1% of the free-living diversity (Takabayashi et al. 2012)—consistent with FGBNMS. Further, these patterns match *in hospite* patterns (Baker 2003; Goulet et al. 2008; LaJeunesse 2002). These results suggest a tight linkage between free-living and *in hospite Breviolum* populations (Baker 2003; LaJeunesse et al. 2004; Pochon et al. 2004). The biogeographical differences between the Caribbean and the Indo-Pacific can be attributed to the selection of Symbiodiniaceae during the Plio-Pleistocene Northern Hemisphere glaciation (Budd 2000). This selection favoured symbionts that could tolerate cooler sea temperatures (Stanley 1986) and cope with the greater seasonality in upwelling and nutrient distributions (Jackson et al. 1993). As a result, the symbiont communities in the Caribbean more closely resemble those found at higher latitudes in the Indo-Pacific, rather than those at similar latitudes (Baker 2003; Baker et al. 2004).

While our results from FGBNMS align with findings across the wider Caribbean, the analysis is constrained by the limited availability of regional data. FGBNMS is characterised by mesophotic coral reefs, with samples from this study being collected at 23 m (Ali et al. 2019). This depth is notably greater than that of the Moorea samples (at least 2.3 times deeper) and GBR samples (at least 3.8 times deeper). FGBNMS also varies from the wider Caribbean in that it is dominated by boulder corals, lacks branching corals, the number of coral species is about one-third less, and these reefs have some of the highest percentages of coral cover for the region (50%–70%; Kramer 2003; Precht et al. 2005; Schmahl et al. 2008). Lastly, sequences from the FGBNMS originated from aposymbiotic larvae that were exposed to FGBNMS reef sediments (Ali et al. 2019). Therefore, it is likely that the resulting sequences do not represent all the diversity at this sampling site. The uniqueness of FGBNMS highlights the need for future research to include diverse reef systems across the Caribbean and to encompass a broader range of depths for more comparable datasets.

1.7.2 | Indo-Pacific

The free-living Symbiodiniaceae communities in both Moorea and the GBR were dominated by sequence variants from *Cladocopium* (34.7% in GBR; 93.3% in Moorea), followed by Clade I (32.3%) on the GBR and *Durusdinium* (9.15%) in Moorea (Figure 2). The GBR samples showed the greatest diversity (3492 sequence variants), followed by Moorea (143 sequence variants, Figure 3). Specifically, the GBR was dominated by variants C1m (20.3%), I4 (19.6%), and D1 (*D. glynnii*; 15.0%). Moorea had the greatest relative abundance of C15.6 (37.8%), C1m (33.7%), and D1 (*D. glynnii*; 7.6%). These results correspond with literature showing dominance of *Symbiodinium* and *Cladocopium* in free-living communities at local scales (Manning and Gates 2008; Takabayashi et al. 2012; Quigley, Bay, et al. 2017) as well as *in hospite* samples from the Indo-Pacific (Pochon et al. 2006). When coral larvae were exposed to sediment containing Symbiodiniaceae to facilitate the uptake of symbionts, larvae exposed to northern and central GBR sediments contained *C. goreaui* and *C. infistulum*, as well as an unclassified species of *Durusdinium* (Cumbo et al. 2013). Results from our ASV analysis also found *C. goreaui* (C1) and *C. infistulum* (C2) in lower relative abundances, supporting the presence of these taxa in GBR sediments.

Our results suggest that the Indo-Pacific likely has a greater diversity of free-living Symbiodiniaceae when compared to the Caribbean, which also corresponds to previous reports comparing Florida and Hawai'i (Takabayashi et al. 2012). It is important to note that the high diversity in the GBR could be due to deeper sampling of the area. However, when accounting for variable read depth, sample number, and sequencing technology across studies, we found no indication of sampling artefacts on resulting diversity metrics. Ultimately, however, these findings underscore the need for expanded sampling efforts in diverse reef regions beyond the Indo-Pacific.

1.7.3 | Indian Ocean

Although we could not retrieve any samples from this region from the 11 relevant studies due to lack of data, we were able to make inferences from the literature for this region (Table S1). For the majority of the Indian Ocean, the diversity, ecology, and biogeography of free-living Symbiodiniaceae is unknown (Table S1). Work examining *in hospite* communities, however, demonstrates variation along latitudinal and temperature gradients, as well as the presence of novel taxa (Burnett 2002; Baker et al. 2004; McClanahan et al. 2005; Visram and Douglas 2006; Macdonald et al. 2008). *In hospite* abundances in Tanzania and Thailand were correlated with temperature and light intensity gradients, where *Durusdinium* was more abundant in environments associated with high temperatures (LaJeunesse et al. 2010). Northeastern and western Indian Ocean had 70% and 80% less diversity, respectively, compared to *in hospite* communities on the GBR (LaJeunesse et al. 2010). The diversity of Symbiodiniaceae in the environment does correlate to some degree with *in hospite* diversity in corals (~10.6% community overlap, Quigley, Bay, et al. 2017). Studies from other locations also

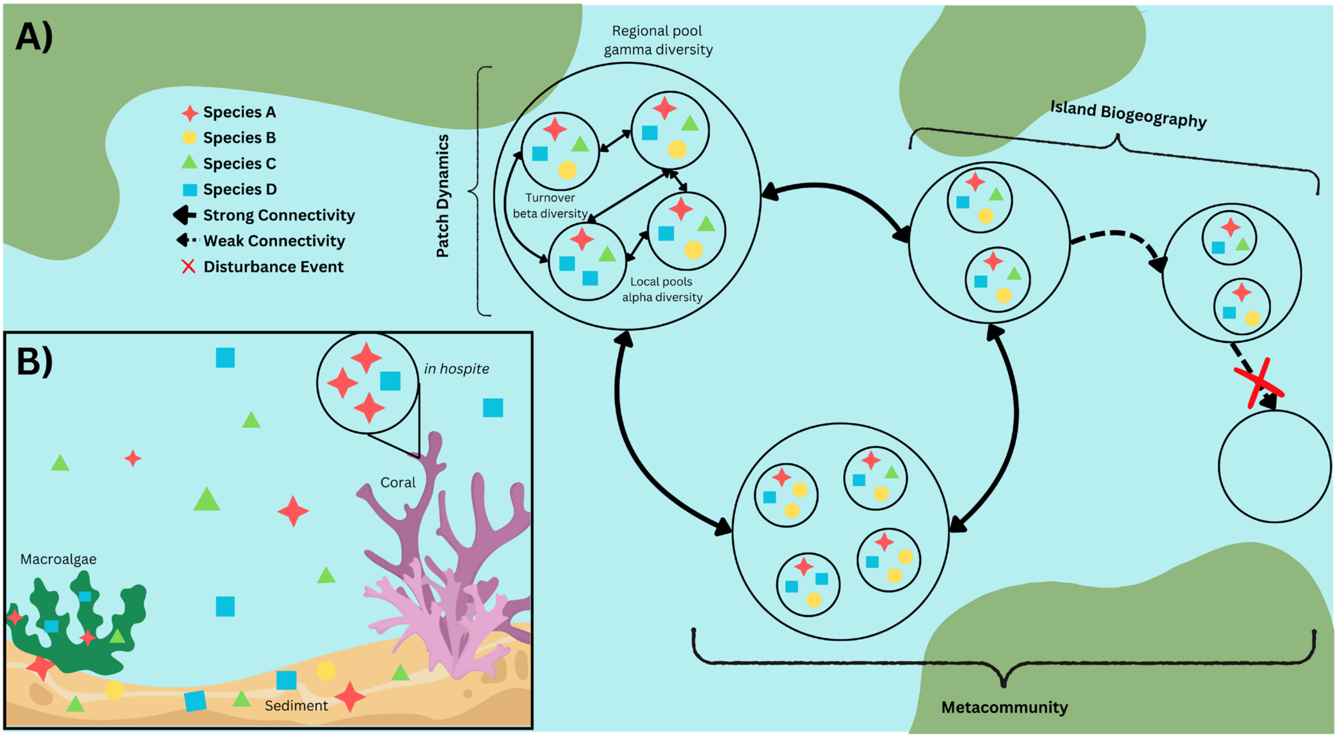

FIGURE 4 | (A) The free-living Symbiodiniaceae community of reef sediment was investigated across regions, and their diversity levels, community structures, and abundances were compared. The major goal is to illustrate the potential roles of stochastic and deterministic processes involved in free-living Symbiodiniaceae assembly. Larger circles indicate the sediment metacommunity, smaller circles indicate the sediment community at each of the sampling locations, and the coloured shapes indicate different Symbiodiniaceae species. For example, smaller circles may represent multiple sampling locations within a reef, while the larger circle may represent the reef as a whole. The figure also incorporates island biogeography principles, illustrating how connectivity and dispersal influence local and regional diversity patterns. (B) Free-living habitats (sediment, water, and macroalgae) and *in hospite* Symbiodiniaceae.

show overlap between *in hospite* and environmental communities (Cunning et al. 2015).

Community composition within the Indian Ocean was also distinct compared with the other ocean basins studied. Interestingly, *Cladocopium thermophilum*, a stress tolerant symbiont, was the dominant taxon found *in hospite* (LaJeunesse et al. 2010). Moreover, approximately 75% of the *Cladocopium* taxa identified were endemic to the region, compared to the Indo-Pacific and GBR (LaJeunesse et al. 2010). *Durusdinium* was also more dominant in sites that were warm, turbid, and experienced greater tidal cycles, suggesting that both regional and local environments within the Indian Ocean influence the relative dominance of *C. thermophilum* and *D. trenchi* (LaJeunesse et al. 2010). These widespread, generalist symbionts were mostly found in coral species that acquire symbionts horizontally from the environment during early development. This dominance implies that free-living communities in the Indian Ocean may also be unique, stress-tolerant generalists. Clearly, studies of free-living Symbiodiniaceae in the Indian Ocean are urgently needed.

1.8 | Implications for Understanding Symbiodiniaceae Biogeography

Our results above highlight the diverse trends in free-living Symbiodiniaceae. We also argue that biogeography paired with the application of metacommunity theory will be essential for understanding current and future trends in Symbiodiniaceae biogeography as the impacts of climate change increase (Figure 4A; Terrell et al. 2023; Leibold 1998; Leibold and Mikkelson 2002; Leibold et al. 2004). For example, metacommunity concepts provide a spatial framework to examine how regional and local environmental processes, like those summarised above, shape the drivers in composition and distribution of free-living communities (Mihaljevic 2012; Chase et al. 2020). Although advances in genomic technology have enhanced species identification in the oceans (Rowan and Powers 1991; Davies et al. 2023), there has thus far been little progress in linking species composition to the processes that maintain diversity and community ecology (Nemergut et al. 2013). For example, metacommunity theory has been used to understand the drivers of Symbiodiniaceae distribution within the coral *Galaxea fascicularis* by examining environmental factors and species interactions (Wepfer et al. 2020). The complexities of symbiont distribution were highlighted by the significant impacts of temperature, depth, and host lineage on communities, as well as latent interactions between symbiont taxa that may indicate facilitative or competitive relationships (Wepfer et al. 2020). Metacommunity theory can simplify these complex systems, aiding in the development of a predictive understanding of both free-living and *in hospite* symbiont biogeography, especially under future stress (Chase et al. 2020).

In addition to metacommunity theory, Symbiodiniaceae biogeography should also consider other spatial ecology concepts such as island biogeography (Figure 4B; Chase et al. 2020; MacArthur and Wilson 2001; Presley and Willig 2022). By combining metacommunity theory with island biogeography, a comprehensive framework can be established that considers multi-scale interactions, spatial dynamics, and the inherent complexity in biodiversity patterns (Pickett et al. 2010; Presley and Willig 2022). Geographic location and distance significantly shape *in hospite* Symbiodiniaceae communities across the Nansei Islands, suggesting spatially driven processes such as drift and potential dispersal limitations of free-living Symbiodiniaceae in the region (Wepfer et al. 2020). Incorporating these concepts will ultimately shed light on the drivers of biogeographical patterns (Mouquet and Loreau 2002). Moreover, it will facilitate the integration of species coexistence theory (Chesson 2000) and concepts like environmental heterogeneity, dispersal, and resource partitioning (Nemergut et al. 2013). Network analysis of Symbiodiniaceae and coral associations around St. John revealed metacommunity-level patterns, distinguishing generalist, host-specialised, and background symbiont taxa, with the latter potentially enhancing host resilience by expanding their fundamental niche (Cunning et al. 2017). This approach will be invaluable for comprehending the complex biogeography and distribution patterns of crucial algal symbionts.

Finally, understanding patterns in Symbiodiniaceae biogeography will have direct conservation benefits. It can aid reef managers in determining refugia potential by identifying areas of important biodiversity or resilience to climate extremes. It can inform the design of protected areas, considering connectivity, species diversity, and vulnerability to climate change (Chase et al. 2020). Although protected areas cannot completely shield organisms from the impact of climate change, they can relieve stress caused by other factors like fishing and run-off (Morelli et al. 2020). Marine protected areas designed with climate change in mind should incorporate free-living Symbiodiniaceae given their importance for coral early life-history stages (Baird et al. 2009; Nitschke et al. 2016; Quigley et al. 2016), high taxonomic and physiological diversity (Takabayashi et al. 2012; Quigley, Bay, et al. 2017; Ziegler et al. 2018), and will be an important contribution to acclimation from climate change disturbances (Quigley et al. 2022; Pettay et al. 2015). Identifying and protecting free-living Symbiodiniaceae should therefore be a critical conservation priority (Mouquet et al. 2013; Socolar et al. 2016).

Author Contributions

S.L.B. and K.M.Q. conceived the ideas. S.L.B. analysed the data. S.L.B. led the writing. K.M.Q. provided edits.

Acknowledgements

This work was supported by the Minderoo Foundation and funding from the Australian Research Council (ARC) DECRA Fellowship to K.M.Q (DE230100284). No fieldwork was conducted as part of this study, and therefore no permits were required. Open access publishing facilitated by James Cook University, as part of the Wiley - James Cook University agreement via the Council of Australian University Librarians.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Available data consisted of sequences from the NCBI Sequence Read Archive: FGBNMS (SRP144167) the GBR (SRP338279) and Moorea (SRP276552).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.