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Barcoding-Inferred Biodiversity of Shallow-Water Indo-Pacific Demosponges

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ABSTRACT

Aim: The Indo-Pacific is the world's largest marine biogeographic region. It is characterised by different degrees of connectivity among its subregions and harbours the majority of demosponge species currently known to science. Comparisons between regional sponge faunas have been undertaken in the past, mostly based on morphological species identification. The Sponge Barcoding Project, in tandem with regional DNA taxonomy campaigns, provides one of the largest DNA-based taxonomic data collections from sponges of the Indo-Pacific. Here, we utilise the barcoding data in the most extensive molecular biodiversity study of sponges to date, which reveals patterns of shallow-water demosponge faunal connectivity, endemism and distribution in the Indo-Pacific with a level of resolution unavailable in prior morphology-based studies.

Location: Demosponge specimens in this study cover 13 marine provinces (MPs) of the Indo-Pacific.

Methods: We classified demosponge barcodes from 1910 sponge samples into 701 molecular operational taxonomic units (MOTUs) using 28S rRNA. MOTU composition of the MPs was compared based on Jaccard and Sørenson dissimilarities and other biodiversity indices.

Results: Our data corroborated high endemism in MPs (up to 84.1% endemic MOTUs). Faunal overlaps are between the Red Sea and the Gulf, which displayed small connectivity with other MPs in the Western Indian Ocean. The Western Indian Ocean is a strong faunistic boundary to the Central Indo-Pacific, to which the Polynesian sponge faunas were comparatively isolated as well.

Main Conclusions: Our data corroborate case studies on sponges that generally reject the presence of cosmopolitan or otherwise widespread sponge species, instead revealing high levels of regional endemism. This is consistent with similar observations and hypotheses in other marine invertebrates, and highlights the need for close regional monitoring to identify biodiversity changes. Connectivity among Indo-Pacific MPs differs for demosponges in many aspects from that of other marine taxa, hypothetically due to their shorter pelagic larval phase.

1 | Introduction

The Indo-Pacific encompasses an expansive region of tropical and subtropical waters, extending from the East African coast, including the Red Sea in the west, to nearly 240 longitudes eastward beyond Easter Island. This vast area represents one of the most biodiverse marine regions globally (e.g., Briggs 1987; van Soest 1994). While the West Pacific is regarded as the marine region with the highest marine diversity worldwide, the Northwestern (Arabia) and Southwestern Indian Oceans constitute additional biodiversity hotspots, harbouring high proportions of endemic taxa (e.g., DiBattista, Roberts, et al. 2016). Due to its extensive size, a comprehensive assessment of Indo-Pacific faunal zonation to understand biogeography and dispersal patterns remains challenging.

The primary drivers of biogeographical differentiation are (1) the large distances of open ocean difficult to cross for species with limited dispersal capabilities, and (2) the oceanic currents determining the predominant directions of offspring distribution. Early studies defined marine biogeographic regions, realms and provinces in the Indo-Pacific based on zoogeographic barriers and endemism, while the subdivision into marine ecoregions aimed to facilitate conservation efforts (Briggs and Bowen 2012; e.g., Spalding et al. 2007). More taxon-based bioregionalisation models have been formulated for reef-fishes (Briggs and Bowen 2012; Kulbicki et al. 2013), corals (e.g., Veron et al. 2015, and very recently McFadden et al. 2025), and other taxa. In this context, molecular studies in particular have highlighted faunal heterogeneity, frequently revealing that species previously thought to be widespread are, in fact, species complexes with allopatric '*mosaic*' distributions (e.g., Reid et al. 2013).

The Indo-Pacific is a biodiversity hotspot for Demospongiae, the largest sponge class that comprises 85% of all described sponge species (Briggs 1987; van Soest 1994). The assessment of overall sponge species richness is challenging (Hooper et al. 2013), and mostly restricted to smaller-scale geographical studies with limited spatial or taxonomic range. While the Western Indian Ocean represents a significant 'peak of species diversity' for several marine phyla (Obura 2016), it remains comparatively unexplored for sponges (van Soest et al. 2012, 2021). Here, our current understanding of demosponge biodiversity is primarily based on species lists (van Soest 1994), and a few comparative studies (e.g., Barnes and Bell 2002). Our knowledge of Western Indian Ocean sponges is smaller compared to other marine taxa, despite the increasing use of molecular markers (e.g., Ngwakum et al. 2021). Better assessments exist for adjacent regions, such as the Red Sea (see Wooster et al. 2019), the Gulf of Oman (e.g., van Soest and Beglinger 2002), and are gaining momentum for the Eastern Arabian Sea (e.g., George et al. 2020), while the Persian Gulf sponge fauna remains underexplored (see Erpenbeck, Gholami, et al. 2020). Comparatively more studies are available from the Malay Archipelago in terms of alpha and beta sponge diversity (e.g., van Soest 1989; Bell and Smith 2004; de Voogd et al. 2006; de Voogd and Cleary 2008), although large parts of the Coral Triangle biodiversity hotspot are yet to be studied. Likewise, several thousand sponge species have been reported from Australian waters, but a large proportion of them are new to science and awaiting description (e.g., Hooper and Ekins 2005; Hooper et al. 2013). Many other regions in the tropical Pacific were studied on a restricted spatial scale only (e.g., Kelly et al. 2003; Núñez Pons et al. 2017), lack comprehensive data (van Soest et al. 2012), or were only recently the subject of broader scale biogeographic analyses (Galitz et al. 2023, 2024). Similarly, most of these studies lack data on cryptobenthic sponges, which represent a considerable portion of the taxonomic diversity on coral reefs (recently studied in Vicente et al. 2022).

Our limited understanding of sponge diversity stands in sharp contrast to their immense ecological importance. Especially on coral reefs, sponges take on key functions in several facets: they protect exposed areas of coral skeletons from boring organisms through overgrowth, stabilise coral fragments in disturbed reefs and thus facilitate reef consolidation, and contribute significantly to reef bioerosion through the activity of excavating sponges (Bell 2008). Of particular importance for the oligotrophic coral reef habitats, is the role of sponges in converting dissolved compounds to particulate matter, and vice versa (e.g., de Goeij et al. 2013). Knowledge of sponge biodiversity and biogeography is indispensable for the recognition of faunal changes. Data on the extent of endemism is key to plan and conduct meaningful biodiversity monitoring, which leads to correctly applied conservation measures, and even the implementation of a 'blue economy' (Glover et al. 2018).

Unfortunately, reliable and comparable assessment of sponge species richness has proven difficult, particularly when using classical (i.e., morphology-based) identification techniques (e.g., van Soest et al. 2012; Hooper et al. 2013). Shortcomings are due to the paucity, homoplasy and plasticity of characters, and challenges in taxonomy and phylogenetic reconstruction (e.g., Cárdenas et al. 2011). Likewise, the lack of an objective species concept for sponges hampers the classification into meaningful units for faunal comparisons. In the last decades, DNA sequence-based methods have provided biodiversity assessment tools that require comparatively little expertise in local faunas, while offering greater objectivity in species identification. The Sponge Barcoding Project was established as a centralised platform to gather molecular taxonomic data on sponge species worldwide, in order to facilitate unambiguous identification methods (Wörheide and Erpenbeck 2007). Here, we utilise sponge barcoding data to investigate patterns of sponge faunal connectivity across the Indo-Pacific. We aim to gain insight into endemism and species distribution in the sponge faunas of marine provinces (MPs) from the Red Sea to eastern Polynesia.

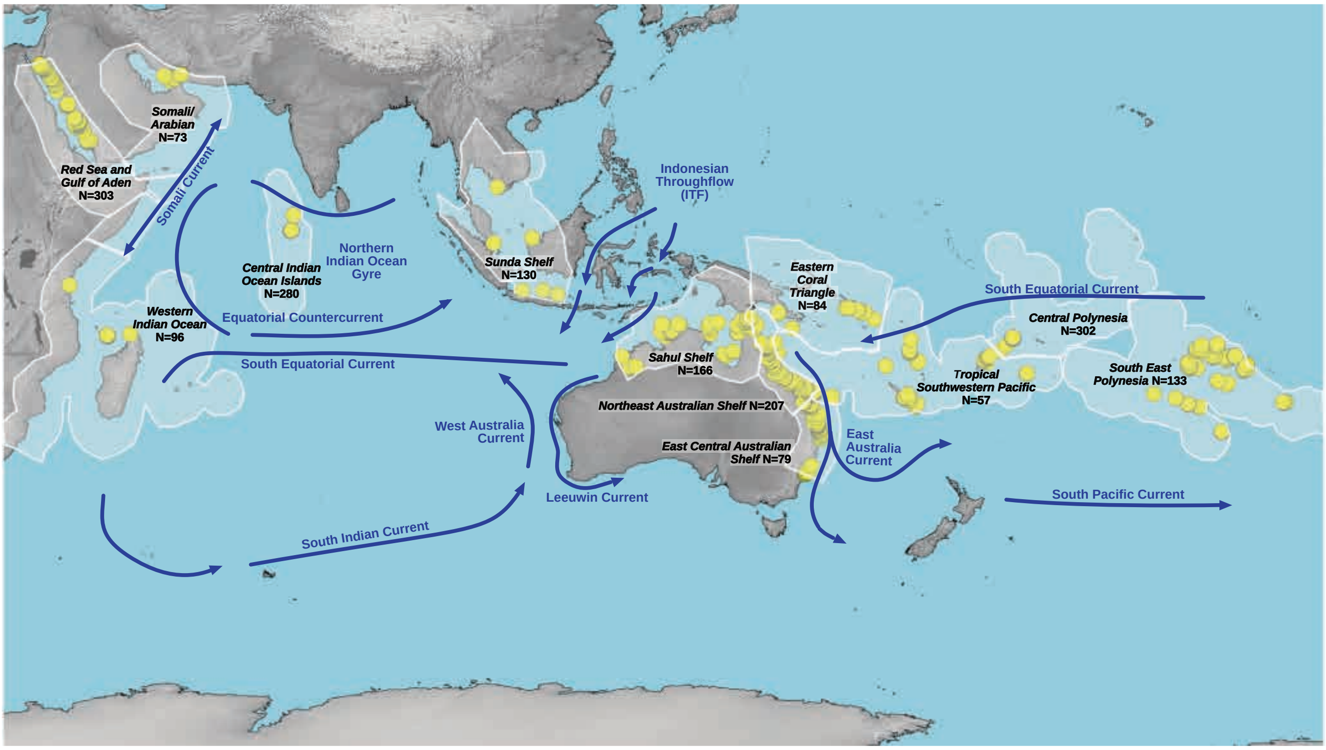


FIGURE 1 | Origin of the samples (yellow dots) within the tropical and subtropical Indo-Pacific MPs (MP boundaries shaded in white). Map generated with SimpleMappr (simplemappr.net).

Additionally, this most extensive molecular biodiversity analysis, to date, seeks to identify dispersal boundaries for sponges in the Indo-Pacific in comparison to other marine taxa.

2 | Material and Methods

2.1 | Origin of Data

The basis of the current analysis is shallow water (mostly SCUBA collected) material from various biodiversity collections spanning from the far Western (Red Sea, Mayotte) to the Eastern (Polynesia) Indo-Pacific. Barcoding data were generated in the course of the Sponge Barcoding Project (Wörheide and Erpenbeck 2007) or during independent, ongoing barcoding studies. All sequences are retrievable from the European Nucleotide Archive (see Appendix S1), metadata of specimens sequenced in the course of the Sponge Barcoding Project are available in the Sponge Barcoding Database (www.spongebarcoding.org).

All specimens were allocated to their respective MPs following Spalding et al. (2007, i.e., 'distinct biotas that have at least some cohesions over evolutionary time frames'). These MPs were used as a geographic baseline for biodiversity comparison. Data from the Red Sea (MP *Red Sea and Gulf of Aden*) originated from biodiversity surveys along the Saudi Arabian coastline conducted 2012–2014 (published in Erpenbeck et al. 2016). Persian Gulf samples (MP *Somali/Arabian*) were collected during several campaigns in Iran using SCUBA diving from 2015 to 2017 (Erpenbeck, Gholami, et al. 2020). Maldives (MP *Central Indian Ocean Islands*) samples were obtained during fieldwork in 2017 and 2022 in Magoodhoo (Fafuu Atoll). Mayotte (MP *Western Indian Ocean*) samples were collected during the ANR-Netbiome project in May 2013, and retrieved from the collections of Naturalis Biodiversity Center (Leiden, the Netherlands). Eastern Indo-Pacific samples originated from French Polynesia (MP *South East Polynesia*) and Wallis Island (MP *Central Polynesia*), and were recently published by Galitz et al. (2023, 2024). Samples from MPs *Northeast Australian Shelf*, *East Central Australian Shelf*, *Tropical Southwestern Pacific*, and most samples from MP *Sahul Shelf* constituted collection material from the Queensland Museum, Brisbane, and the Australian Institute of Marine Science, and were added to the Sponge Barcoding Project (e.g., Vargas et al. 2012), as was comparative material from MP *Southeast Australian Shelf*. Sequence data from Papua New Guinea (MP *Eastern Coral Triangle*) were provided for this project from yet unpublished biodiversity surveys. Material for MP *Sunda Shelf* was assembled from pre-2014 collections (Figure 1).

2.2 | Sequence Generation and Alignment

Analyses were based on the C-region of the nuclear large ribosomal subunit (28S), a ~450 base-pairs (bp) standard marker for sponge DNA barcoding and biodiversity assessments. This fragment has previously been shown to differentiate demosponge species more effectively than the 'Folmer' region of CO1, which is the standard barcoding fragment for many metazoans but is too conservative in demosponges (Erpenbeck et al. 2006, 2016). The high resolving power of 28S, combined with the extensive availability of comparative data from different regions in the Indo-Pacific, makes this marker particularly suitable for the present analysis.

DNA was extracted in the course of different barcoding projects with various methods: the plate extraction method developed for sponge barcoding (Vargas et al. 2012) has been used for the samples from *Northeast Australian Shelf*, *East Central Australian Shelf*, *Tropical Southwestern Pacific* and *South East Polynesia*, CTAB extractions for the samples from *Central Polynesia* (Wallis), and spin columns (NucleoSpin Tissue Kit, Machery & Nagel or Qiagen Blood and Tissue Kit) were used for samples from other marine provinces. Subsequently, for all samples, 28S-C region fragments were amplified and purified, following previously published protocols (Erpenbeck et al. 2016), Both strands of the PCR products were sequenced with a BigDye Terminator v3.1 (Applied Biosystems) following the manufacturer's protocol at the Sequencing Service of the Department Biology, LMU—Genomics Service Unit (Martinsried, Munich, Germany) on an ABI 3730 capillary sequencing machine. Raw sequences were basecalled, trimmed, and assembled in CodonCodeAligner v3.7 (www.codoncode.com) under default settings, and subsequently manually checked. Positions where potential intragenomic polymorphisms (IGPs) were detected as characteristic double peaks in forward and reverse sequences were coded with the respective IUPAC ambiguity codes, which in DECIPHER resulted in their ignorance during sequence length calculation and the subsequent clustering into molecular operational taxonomic units (MOTUs).

2.3 | MOTU Delineation

Sequences were divided with respect to their respective marine provinces *sensu* Spalding et al. (2007) using QGIS 3.10. (QGIS Development QGIS Development Team 2019, http://www.qgis.osgeo.org). Sequences longer than 340 bp were aligned with ClustalW as implemented in the msa package for R (Bodenhofer et al. 2015), which facilitates an unambiguous alignment of sequences with low genetic distances in a data set consisting of highly variable sequences from a broad phylogenetic range. In this approach, the performance of ClustalW was insensitive to differences in sequence length and presence of ambiguity codes. DECIPHER 2.0 (Wright 2016) was used to cluster sequences into the respective MOTUs using the unweighted pair group method with arithmetic mean (UPGMA) algorithm (as applied in Cowman et al. 2017; Hadiyanto et al. 2021), which has been shown to have the best performance in hierarchical cluster analyses (see Kreft and Jetz 2010 for details).

We apply the stringent MOTU cut-off of 0.3%, which has been shown to account for genetic differences detected in several case studies between selected sympatric shallow water demosponge species in the Indo-Pacific (e.g., Erpenbeck et al. 2017; Erpenbeck, Galitz, et al. 2020; Ekins et al. 2023). This cut-off was subsequently used in smaller-spatial biodiversity studies (Galitz et al. 2023, 2024). As this stringency demands high-fidelity of the sequencing, no external sequences without obtainable chromatograms (e.g., NCBI Genbank sequences published by other authors) have been used, as we could not verify the correctness of basecalling. In addition to these precautionary measures, we verified our results in a second analysis, in which MOTUs were restricted to contain at least two sequences (i.e., excluding singletons). This approach was intended to eliminate potential biases arising from undetected sequencing or base-calling errors and should therefore strengthen the robustness of the results, albeit based on a reduced MOTU set.

2.4 | Biodiversity Analyses

We compared MPs in terms of their beta diversity, and the measurement of species composition difference between species assemblages. Rarefaction analyses on species richness and the sampling completeness of the respective marine provinces were conducted with iNEXT online (https://chao.shinyapps.io/iNEXTOnline). Biodiversity analyses were performed with the 'picante' (Kembel et al. 2010) and 'vegan' (Oksanen et al. 2013) packages for R (see Appendix S2 for results). As sampling has been predominantly qualitative, that is without measurement of abundance data, the only visible differences between sites are in species identities.

From the large number of beta-biodiversity indices for absence–presence data, we used the Jaccard index as it is comparatively invulnerable to errors of taxonomy and enumeration, and has relatively low error rates for potential geographic undersampling (see Koleff et al. 2003) as evident from the rarefaction analyses. In parallel, the Sørensen index was calculated; it is closely related to the Jaccard index, but gives double the weight to shared species, thereby reducing the errors caused by false negatives (Hadiyanto et al. 2021; Schroeder and Jenkins 2018). Data and R scripts can be retrieved from https://github.com/PalMuc/Barcoding-inferred-Indo-Pacific-demosponge-biodiversity, archived in Zenodo (https://doi.org/10.5281/zenodo.18740328).

The significance of the beta diversity indices was subsequently verified with PERMANOVA (permutational multivariate analysis of variance) using a custom variation of the *adonis* function of 'vegan' for pairwise comparison of regions, with 999 permutations and false discovery rate (FDR) adjustments taken into account (Anderson 2017). Visualisation of MOTU overlap was conducted using UpSetR (Conway et al. 2017). The cryptobenthic fauna of coral reefs, however, has a different taxonomic composition, and has been disregarded in this analysis for this reason (e.g., Vicente et al. 2022). Likewise, other factors potentially affecting the taxonomic composition, such as temporal variability in sponge coverage percentages are not expected to bias the overall taxonomic pattern as they do not influence the absence/presence pattern as relevant to the current analysis.

3 | Results

A total of 1910 28S sequences from 12 marine provinces were analysed (see Figure 2). iNEXT rarefaction and extrapolation analyses showed high (up to 84%) sample completeness for most MPs (e.g., Central Polynesia, Central Indian Ocean Islands, Red Sea and Gulf of Aden), moderate sample completeness for few (e.g., East Central Australian Shelf, Western Indian Ocean) with *Tropical Southwestern Pacific* displaying the lowest sample completeness (Appendix S2, Figure S2).

The 28S barcoding region is of variable length and had an average of 386 bp in our data set (median 388 bp, maximum 481 bp; short fragments are due to restrictive clipping in the case of

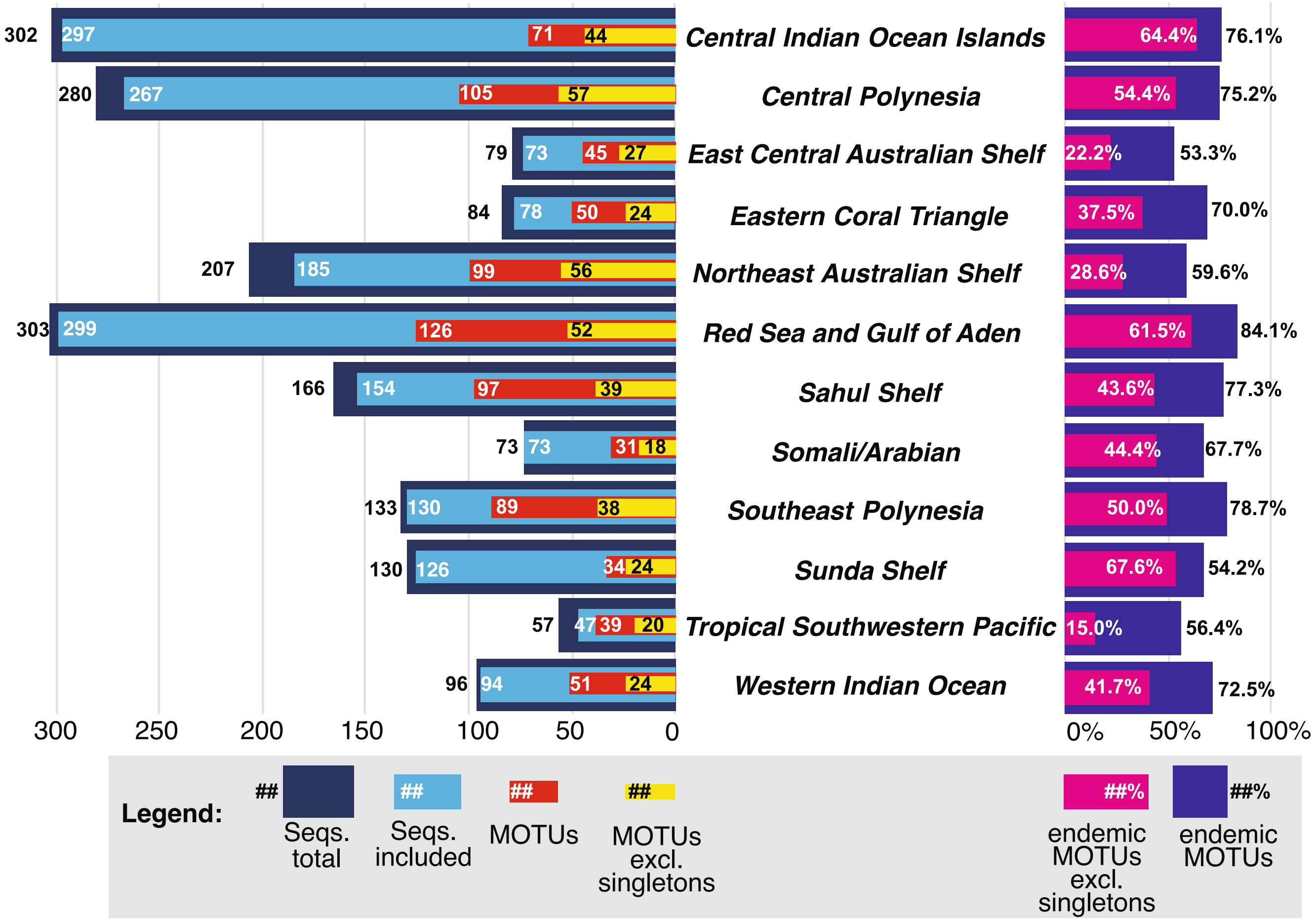


FIGURE 2 | Overview of regional sequence yield, MOTU numbers (left), and endemic MOTU proportion (right) for the marine provinces in the current analysis.

ambiguous basecalling at the 5′ or 3′ terminus). After restriction to a sequence length > 340 bp, the data set comprised 1823 sequences (average 402 bp, median 399 bp). Sequence numbers per region ranged from 306 (MPs *Red Sea and Gulf of Aden*) to 57 (*Tropical Southwestern Pacific*). These sequences fell into 701 MOTUs with the maximum again from MP *Red Sea and Gulf of Aden* (126), and a minimum from MP *Somali/Arabian* (31). A total of 414 MOTUs (59.1%) were singletons, comprising only one specimen in the entire collection. Taxonomically, the 701 MOTUs are dominated by 169 Dictyoceratida (24.1%) and 144 Haplosclerida (20.5%); all other orders were less abundant.

Comparison between MOTU distribution indicated a high percentage of MOTUs (86.3%) restricted to a single marine province (=endemic MOTUs, see Figure 2). Levels of endemism ranged from 53.3% (MP *East Central Australian Shelf*) up to 84.1% (MP *Red Sea and Gulf of Aden*), with an average of 70.43% per MP. Quantification of the shared MOTUs for every MP can be deduced from Figure 3. MOTUs spanning over most MPs were #214 (8 MPs), #79 (7), #176 (5), #231, #180 and #34 (each 4, see Appendix S1 for MP details). All other MOTUs spanned over three or fewer MPs.

Jaccard dissimilarity indices between the marine provinces recover MP pairs without MOTU overlap (=dissimilarity of 100) and those with MOTU overlaps to different degrees (Figure 4). Jaccard dissimilarities were also plotted on a map of the Indo-Pacific (Figure 5). We recovered several distinct MP clusters, three of them with Jackknife support ≥ 60: (i) *Central Polynesia* with *South East Polynesia*; (ii) *Central Indian Ocean Islands* with *Western Indian Ocean* and *Sunda Shelf*; (iii) *Somali/Arabian* with *Red Sea and Gulf of Aden*; (iv) *East Central Australian Shelf* with *Northeast Australian Shelf* and (to a lesser extend) *Tropical Southwestern Pacific*. Analyses based on Sørensen indices revealed congruent results (Appendix S3, Figure S3.2). Analyses excluding singletons consisted of considerably fewer MOTUs (297; 40.9%), but differed only in the Jackknife-unsupported position of the *Sahul Shelf* or the *Eastern Coral Triangle* fauna (Appendix S3, Figures S3.1 and S3.3). This indicates that the main findings are free from bias by potential undetected sequencing errors.

4 | Discussion

4.1 | High Demosponge Endemism due to Limited Dispersal Potential

Our study, the most extensive molecular analysis on shallow water demosponge biodiversity to date, shows a high percentage of non-overlapping MOTUs between the marine provinces, indicating a high degree of endemism within MPs (with up to 84.1% endemic MOTUs) throughout the Indo-Pacific region. This

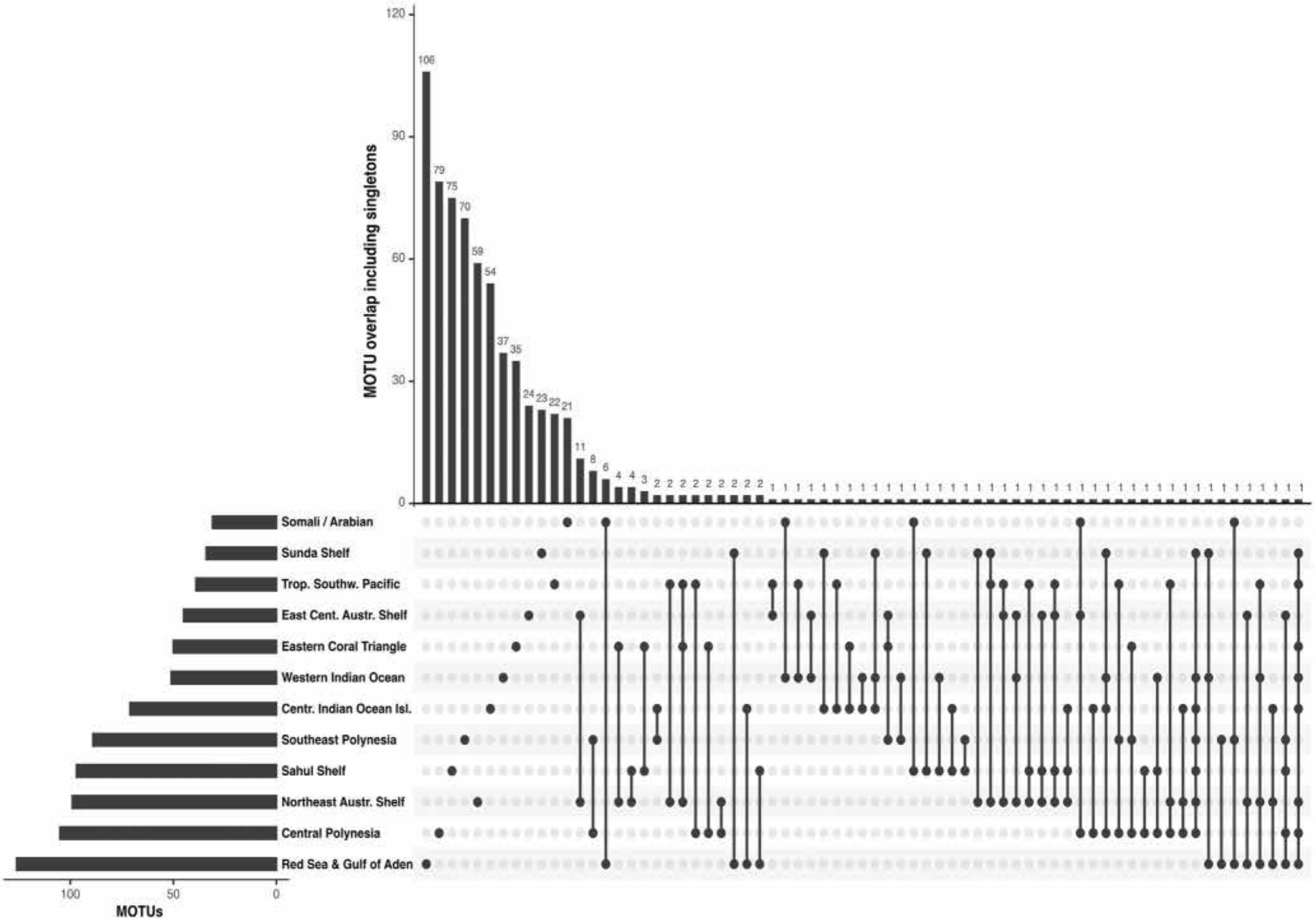
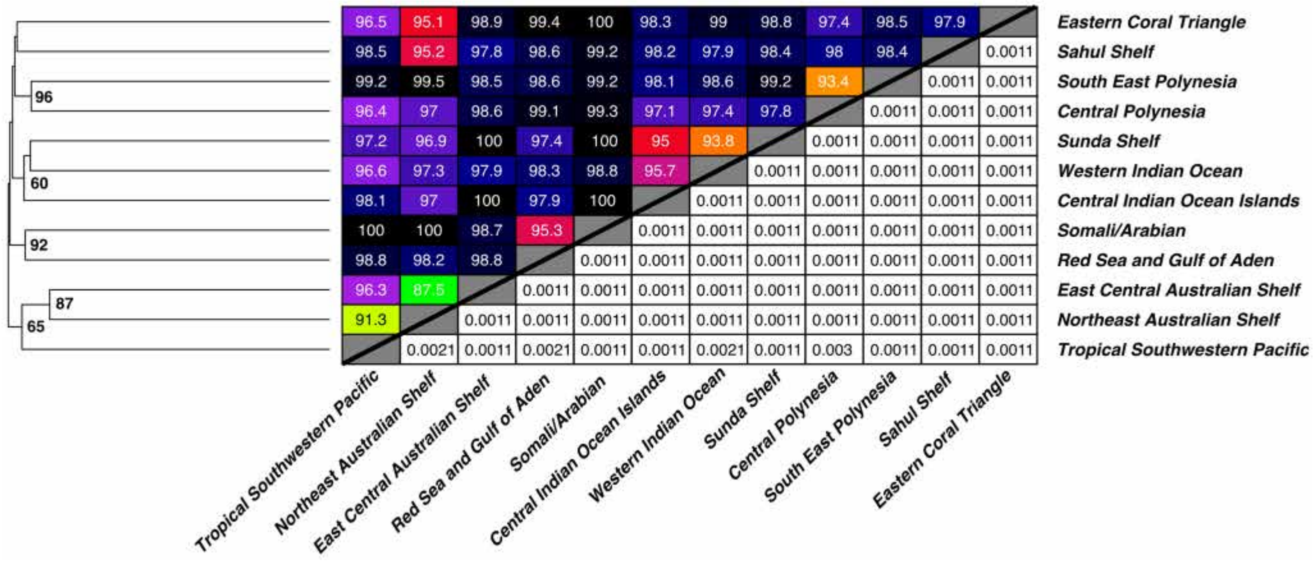


FIGURE 3 | MOTU count including singletons per marine province and overlap between provinces. Histogram on the left: Number of MOTUs per MP. To its right: Black dots without connecting lines represent the number of unique MOTUs in a MP, while dots connected by lines indicate the number of MOTUs present in two or more MPs. Counts of MOTUs for each scenario are depicted as a histogram at the top.



	Tropical Southwestern Pacific	Northeast Australian Shelf	East Central Australian Shelf	Red Sea and Gulf of Aden	Somali/Arabian	Central Indian Ocean Islands	Western Indian Ocean	Sunda Shelf	Central Polynesia	South East Polynesia	Sahul Shelf	Eastern Coral Triangle
Eastern Coral Triangle	96.5	95.1	98.9	99.4	100	98.3	99	98.8	97.4	98.5	97.9	
Sahul Shelf	98.5	95.2	97.8	98.6	99.2	98.2	97.9	98.4	98	98.4		0.0011
South East Polynesia	99.2	99.5	98.5	98.6	99.2	98.1	98.6	99.2	93.4		0.0011	0.0011
Central Polynesia	96.4	97	98.6	99.1	99.3	97.1	97.4	97.8		0.0011	0.0011	0.0011
Sunda Shelf	97.2	96.9	100	97.4	100	95	93.8		0.0011	0.0011	0.0011	0.0011
Western Indian Ocean	96.6	97.3	97.9	98.3	98.8	95.7		0.0011	0.0011	0.0011	0.0011	0.0011
Central Indian Ocean Islands	98.1	97	100	97.9	100		0.0011	0.0011	0.0011	0.0011	0.0011	0.0011
Somali/Arabian	100	100	98.7	95.3		0.0011	0.0011	0.0011	0.0011	0.0011	0.0011	0.0011
Red Sea and Gulf of Aden	98.8	98.2	98.8		0.0011	0.0011	0.0011	0.0011	0.0011	0.0011	0.0011	0.0011
East Central Australian Shelf	96.3	87.5		0.0011	0.0011	0.0011	0.0011	0.0011	0.0011	0.0011	0.0011	0.0011
Northeast Australian Shelf	91.3		0.0011	0.0011	0.0011	0.0011	0.0011	0.0011	0.0011	0.0011	0.0011	0.0011
Tropical Southwestern Pacific		0.0021	0.0011	0.0021	0.0011	0.0011	0.0021	0.0011	0.003	0.0011	0.0011	0.0011

FIGURE 4 | Diagram top left: 28S Jaccard dissimilarities of the studied marine provinces. Cell colour corresponds to the legend depicted in Figure 5 plus black in case of complete dissimilarity (100). Diagram bottom right: False discovery rate (FDR) adjusted *p*-values of respective 28S Jaccard indices generated through pairwise PERMANOVA. The dendrogram on the left depicts faunal similarities between two given regions based on their respective Jaccard dissimilarity indices. Numbers on nodes are for Jackknife support (1000 replicates).

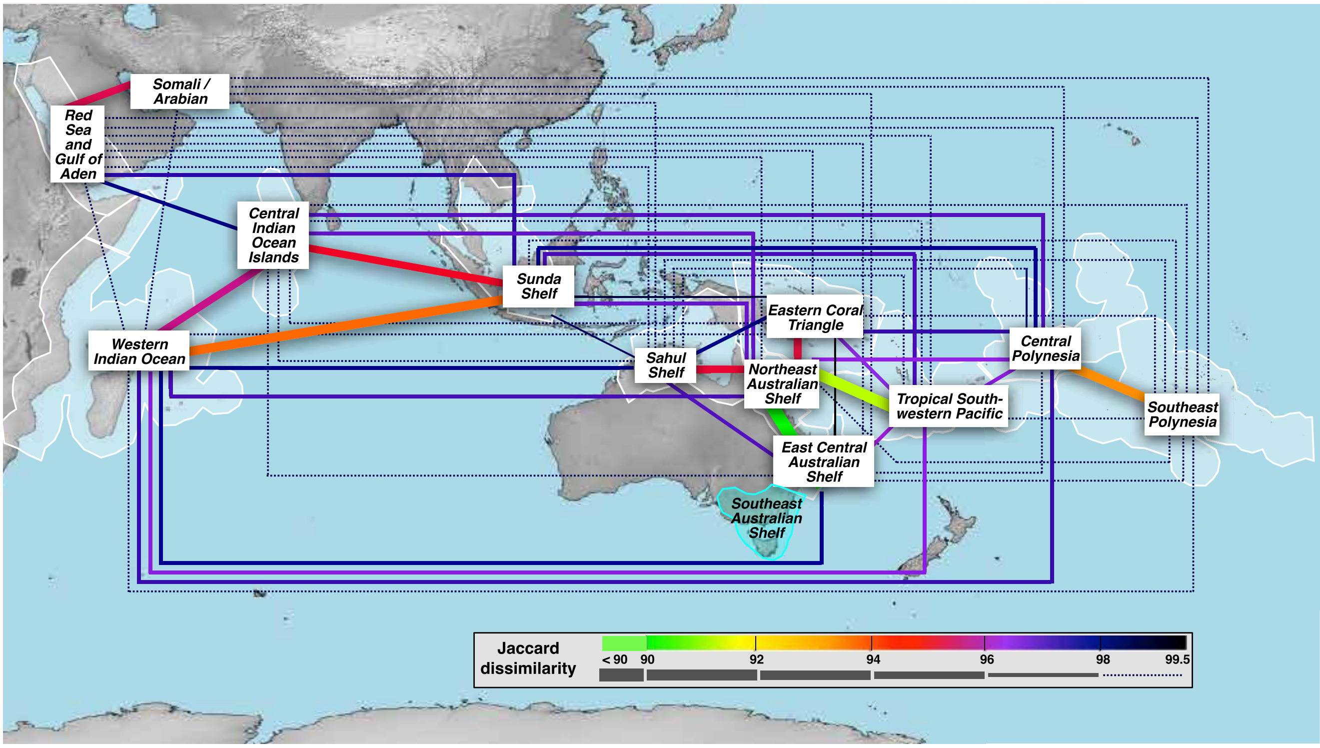


FIGURE 5 | Jaccard dissimilarities between the samples of the twelve Indo-Pacific marine provinces, including singletons. Tropical and subtropical MP areas and boundaries are shaded in white, temperate in light blue. Colour and thickness of the connecting lines between tropical and subtropical marine provinces indicate the degree of dissimilarity between them. Colours are similar to Figure 3. Jaccard dissimilarities of 100 (i.e., no shared MOTUs) are not indicated by a line. Jaccard dissimilarities between 99.5 and 99.9 were not present. Map generated with SimpleMappr (simplemappr.net).

pattern parallels earlier molecular studies that repeatedly rejected the frequent occurrence of widespread sponge (and other) species (e.g., Wörheide, Degnan, et al. 2002; Wörheide, Hooper, and Degnan 2002; Xavier et al. 2010). Our results are therefore consistent with earlier hypotheses, which projected a generally high rate of endemism among other marine invertebrates (e.g., Barnes and Bell 2002; Klautau et al. 1999; Palumbi et al. 1997). In this respect, several genetic studies on sponges and other marine organisms have found genetic structure at large spatial scales, suggesting that long-distance panmixia and dispersal are rare (e.g., Benestan et al. 2021, Wörheide, Hooper, and Degnan 2002; Wörheide et al. 2008), with only few demosponge species currently being discussed as widespread (e.g., Carballo et al. 2013), or even cosmopolitan (e.g., Turner 2020). Nevertheless, our decision to refrain from using sequences from public databases lacking base-calling verification may have reduced the detection of additional widespread MOTUs; however, this conservative approach minimised the risk of falsely identifying endemic MOTUs. Our study identified only a few MOTUs occurring in the western *and* eastern extensions of the analysed Indo-Pacific MPs. The most frequently occurring MOTUs are MOTU 214 (in 8 of the 12 MPs), and MOTU 79 (in 7 MPs, see Figure 1 and Appendix S1). Both MOTUs have previously been identified as *Stylissa carteri* Dendy and '*Hyrtios* cf. *erectus*', with the former including specimens frequently misidentified as *Stylissa massa* Carter, and the latter being a cryptic, but widespread sister lineage of *H. erectus* Keller (Erpenbeck et al. 2017). Our data underline that, in contrast to most other MOTUs, both taxa are abundant in the Indo-Pacific (see de Voogd and Cleary 2008).

Crandall et al. (2019) argued that physical or environmental barriers play a limited role in the broad, spatial genetic differentiation of the Indo-Pacific. Therefore, dispersal capabilities for larvae constitute a significant factor for the biodiversity patterns of demosponges (Maldonado 2006). In most shallow-water demosponge species, the larva is a planktonic, lecithotrophic parenchymella with a short life-span of only a few days, during which it must find and settle onto a suitable substrate for the sessile adult stage. This contrasts with the hoplitomella larvae of some deeper water tetractinellids, which can survive several weeks (see Maldonado 2006). The planktonic parenchymella larva is the predominant larval type in the orders Dictyoceratida and Haplosclerida, which together constitute the taxonomic majority in (sub-) tropical shallow-water habitats as analysed here (Erpenbeck et al. 2016, 2020; Galitz et al. 2023). Benthic crawling larvae as described from a few other demosponge lineages (see Ayling 1980; Bergquist et al. 1970; Borojevic 1967) are unlikely to contribute significantly to the MOTU composition. Here, the absence of suitable stepping stones across the vast oceanic distances reduces distribution success for sponges, resulting in pronounced range fragmentation (see Mora et al. 2012). Other demosponge lineages possess benthic, rather than planktonic larvae, which crawl on the substrate for several days and consequently possess even more limited dispersal capacities (Maldonado 2006). Passive means of transport were conclusively reported in only a few instances, for example by ballast water, hull fouling or attachment to debris (e.g., Elvin et al. 2018). Propagules, clonal fragments or enduring bodies have been described from only a few marine species including sponges (Wörheide et al. 2008), but their exact contributions to demosponge dispersal processes in the Indo-Pacific are not fully known yet.

4.2 | Demosponge Connectivity in the Northwestern Indian Ocean

We found MOTUs overlapping between the Red Sea (MP *Red Sea and Gulf of Aden*) and the Gulf (MP *Somali/Arabian*). Both water bodies constitute northern marginal seas of the Indian Ocean, and have shared physical similarities. Both are semi-enclosed seas in arid regions with scarce freshwater influx and high evaporation (Ludt et al. 2017), potentially favouring settlement and growth of similar demosponge species, as is found for reef-building corals (Obura 2012). However, both seas have only a narrow and particularly shallow connection to the Arabian Sea, hindering the exchange of species already adapted to moderate depths (Ludt et al. 2017). In this respect our data parallel findings from, for example shark populations, which show shared haplotypes between both marine provinces, but unshared in others (Spaet et al. 2015). Likewise, cold upwellings in the northern Arabian Sea form a barrier for temperature-sensitive species and prevent a connection of coral reef stepping-stones to the other marine provinces (e.g., Kemp 1998; DiBattista, Choat, et al. 2016), resulting in the high degree of demosponge endemism as observed previously (Erpenbeck, Gholami, et al. 2020) and in the present study.

4.3 | Low Connectivity Between Northwestern and Western Indian Ocean

The demosponge distributions, as recovered from our molecular analyses, indicated a distinct pattern of considerably few MOTU overlaps between the northwestern Indian Ocean MPs (*Somali/Arabian* and *Red Sea and Gulf of Aden*) and the MPs of the remaining Indian Ocean. The MPs *Central Indian Ocean Islands*, *Western Indian Ocean* and *Sunda Shelf* formed a triangle with a higher internal MOTU overlap isolated from the northwestern Indian Ocean MPs. Our findings matched earlier faunistic analyses on sponges of the Indian Ocean that favoured East—West connectivity of sponge faunas over North–South (e.g., Indonesia to East Africa, see van Soest 1994; van Soest et al. 2012; Erpenbeck et al. 2017). This boundary divides the tectonically inactive western Indian Ocean and the active northern Indian Ocean seas. The cold upwelling currents in the Gulf of Aden and along the Somali coast prevent the formation of shallow-water coral reefs as stepping-stones for sponges along the coast, and there is limited other habitat suitable for larval settlement alongside the Somali coast (e.g., Kemp 1998). The sponge larvae would have to cover vast distances in the open ocean to reach other MPs (e.g., the distance between Socotra near the Gulf of Aden to the Maldives, southwest of India, is ~2000 km). In most cases these distances exceed the survival capabilities of the sponge larvae. For corals, which frequently possess a considerably longer pelagic larval duration than sponges (e.g., Nozawa and Okubo 2011), the northern Indian Ocean Gyre and the reversing Somali Current are important dispersal vectors between the northwestern and the remainder of the Indian Ocean (Obura 2012). These current systems appear less significant for the distribution of sponges.

We observed MOTU overlaps between the MPs *Central Indian Ocean Islands*, *Western Indian Ocean* and *Sunda Shelf*, indicating a degree of connectivity between far western and eastern Indian Ocean MPs. Exchange is facilitated by the stepping stones of the Chagos Archipelago (called 'Chagos Stricture' for corals, see Veron 1995) in combination with the South Equatorial Current and the Equatorial Countercurrent, rather than north-southernly currents. We did not find a division between Western Indo-Pacific and Central Indo-Pacific faunas, contrary to Spalding et al. (2007, based on multiple taxa and biophysical conditions), Kulbicki et al. (2013, reef fish), Briggs and Bowen (2012, based mostly on reef fish), or a similar boundary suggested for corals (Obura 2012, 2016; Veron et al. 2015). In multispecies analyses, no boundary in that region has been found to be significantly different from random distributions either (Crandall et al. 2019). Instead, more demosponge MOTUs of MP *Sunda Shelf* are shared with the *Western Indo-Pacific* realm than with other MPs of its *Central Indo-Pacific* realm. In this respect, demosponge MOTU distribution follows the Indo-Pacific Barrier along the western edge of the Sunda Shelf, which strengthened during low sea-level stands at the Last Glacial Maximum of the Pleistocene (see Crandall et al. 2019).

Several coral reef organisms of the MP *Sunda Shelf* have also been found to conform to the genetically differentiated 'Western Province' of the Indo-Malay Archipelago (to the west of Makassar Strait), which has more resemblance to Indian Ocean faunas than to those of the Central Indo-Malay Archipelago (see Ducret et al. 2022 and references within). These findings are consistent with our observation that MP *Sunda Shelf* demosponges resemble (Western) Indian Ocean faunas more closely than any of the geographically closer MPs further east examined in this study.

4.4 | A Marine 'Wallace's Line' for Demosponges

Our analyses suggest a deep split of demosponge MOTU overlaps between MPs *Sunda Shelf* and *Sahul Shelf* (including all other MPs of the *Central Indo-Pacific* and *Eastern Indo-Pacific* realms), despite their spatial proximity. This separation is congruent with cluster analyses of species lists by van Soest et al. (2012). The Makassar Strait is a remnant of the biogeographic separation of Indian and Pacific Ocean marine populations during the Pleistocene emergence of the Sunda and Sahul shelves (occasionally termed 'marine Wallace's Line', Barber et al. 2000; Reid et al. 2013), and marks a boundary. The current genetic distinctiveness of marine taxa still reflects the historical separation of Indian and Pacific Ocean basins, which was physically far greater during the glacial maxima (Barber et al. 2000). Several currents of the Indonesian Throughflow (ITF) contribute to the present separation. They pass through the Makassar and the Lifamatola Passage, eventually forming the South Equatorial or Leeuwin Current further west, therefore hampering larval and propagule exchange between habitats on both sides of the ITF (e.g., Kochzius and Nuryanto 2008; Reid et al. 2013).

4.5 | High Connectivity Within the Central Indo-Pacific Realm … and Beyond

Our data found a comparatively high overlap of MOTUs between MPs *East Central Australian Shelf*, *Northeast Australian Shelf*, *Sahul Shelf*, *Tropical Southwestern Pacific*, and to a lesser extent, the *Eastern Coral Triangle*. Despite being a biodiversity hotspot, the *Eastern Coral Triangle* was included here in a comparative sponge biodiversity analysis for the first time (see van Soest et al. 2012). The observed MOTU overlaps were a result of both spatial proximity and the presence of numerous stepping stones in this area that are connected by the East Australian Current.

Sponge species richness and taxonomic distributions of Australia have been the subject of several studies (e.g., Hooper and Ekins 2005). These identified a major faunal transition zone at Cape York, which separates the MP *Sahul Shelf* at the Gulf of Carpentaria from the adjacent eastern MPs *Northeast Australian Shelf* (from Torres Strait to the Great Barrier Reef). Hooper and Ekins (2005) discussed this boundary as being ecologically (habitat) related rather than biogeographic. Our present analysis corroborated this boundary, showing a higher Jaccard dissimilarity of MP *Northeast Australian Shelf* to MP *Sahul Shelf* than to MP *Tropical Southwestern Pacific*, which comprises the Coral Sea habitats on the Queensland Plateau and western Pacific Islands adjacent to the Great Barrier Reef.

Our study also observed a high MOTU overlap between MP *Northeast Australian Shelf* and MP *East Central Australian Shelf* to its south, displaying the lowest Jaccard dissimilarity between MPs in our analysis. Both MPs, however, are classified as different marine realms (realm *Central Indo-Pacific* and realm *Temperate Australasia*, respectively; Spalding et al. 2007). We therefore expect a comparatively high Jaccard dissimilarity between these MPs, at least higher than between MPs of the same realm. However, Hooper and Ekins (2005) previously noted that a 'well-recognised biogeographic transition zone' for sponges exists, along with a subsequent hard faunistic boundary to the temperate regions, but located further south of the current *Central Indo-Pacific* realm limits. For this reason, we included the available barcoding data of the more southerly MP *Southeast Australian Shelf*, which is classified in realm *Temperate Australasia*, similarly to MP *East Central Australian Shelf* (Appendix S4, Figure S4.1). We recovered a comparatively strong Jaccard dissimilarity of >0.98 between MP *East Central Australian Shelf* to MP *Southeast Australian Shelf*, while the dissimilarity to MP *Northeastern Australian Shelf* in the north was considerably lower (0.88) and among the lowest dissimilarities observed in this study (Appendix S4, Figure S4.2). The results of our molecular genetic analyses therefore corroborated the findings of Hooper and Ekins (2005), indicating a strong faunistic boundary separating tropical from temperate faunas, located further south than suggested in the realm definitions of Spalding et al. (2007).

4.6 | Eastern Indo-Pacific in 'Splendid Isolation'?

In the Eastern Pacific coral reefs, the abundance of macroscopic epibenthic sponges has been discussed as gradually decreasing in eastward direction due to different primary productivity requirements in the oligotrophic waters (van Soest et al. 2012; Vicente et al. 2022; Wilkinson 1987). Sponge molecular biogeographic connectivity in that region has recently been analysed by Galitz et al. (2023), whose data are incorporated here to compare the *Eastern Indo-Pacific* realm MPs (*Central Polynesia* and *Southeast Polynesia*) with the other Indo-Pacific MPs in the study. Our data revealed that sponge faunas of both MPs of the *Eastern Central Pacific* Realm are more similar to each other than to any MP of the *Central Indo-Pacific* or any other realm. This aligns with the hierarchical classification of Spalding et al. (2007), and corroborates the findings of Galitz et al. (2023) with a larger data set. Nevertheless, MP *Central Polynesia* still shows a considerable degree of MOTU overlap with adjacent MPs of the neighbouring *Central Indo-Pacific* realm, which characterises MP *Central Polynesia* as a 'melting pot of biodiversity' Galitz et al. (2023).

Crandall et al. (2019) identified spatial distance as the predominant factor reducing genetic exchange in the South Pacific, and only to a lesser extent the geologic history—continental and uplifted islands of the Central Indo-Pacific realm and volcanic islands of the Eastern Indo-Pacific realm, respectively. Here, the numerous small gyres of the South Pacific Current facilitate connectivity between demosponge faunas of Fiji and Tonga (MP *Tropical South Pacific*) with Wallis, Futuna and Samoa (MP *Central Polynesia*) across the realm boundaries (see Galitz et al. 2023 for further details). Drivers of genetic exchange within the Eastern Indo-Pacific realm MPs are the South Pacific Current and South Equatorial Current. However, the vast distances (>3000 km), in combination with the short pelagic larval duration of most shallow-water demosponges, hypothetically hamper a higher MOTU overlap between its MP *Central Polynesia* and MP *Southeast Polynesia*.

In conclusion, our data comprises the to date most comprehensive molecular biogeographic analysis on shallow-water Indo-Pacific demosponges. It corroborates earlier case studies that reveal high levels of regional endemism and generally reject the presence of cosmopolitan or otherwise widespread sponge species. It documents relatively limited faunal connectivity between marine provinces, which is consistent with similar observations and hypotheses in other marine invertebrates. The fragmented distribution of demosponges is province-specific and is likely attributed to their low dispersal potential and the influence of oceanographic and historical barriers. Conservation and blue economy approaches therefore need to consider that sponge diversity is richer and more spatially constrained than previously recognised.

Author Contributions

Dirk Erpenbeck: conceptualization, data curation, formal analysis, funding acquisition, investigation, project administration, resources, supervision, visualization, writing – original draft, writing – review and editing. **Adrian Galitz:** data curation, formal analysis, investigation, writing – review and editing. **Michael L. Berumen:** resources, writing – review and editing. **Gabriele Büttner:** investigation, writing – review and editing. **Cécile Debitus:** funding acquisition, resources, writing – review and editing. **Moritz Dirnberger:** investigation, writing – review and editing. **Merrick Ekins:** investigation, resources, writing – review and editing. **Kathryn Hall:** resources, writing – review and editing. **Leonard Namuth:** investigation, writing – review and editing. **Sylvain Petek:** funding acquisition, resources, writing – review and editing. **Neda Rahnamae:** formal analysis, investigation, writing – review and editing. **Maggie M. Reddy:** investigation, resources, writing – review and editing. **Daniela Rettenberger:** investigation, writing – review and editing. **Stefanie R. Ries:** investigation, writing – review and editing. **Simone Schätzle:** investigation, writing – review and editing. **Christine H. L. Schönberg:** resources, writing – review and editing. **Edwin Setiawan:** investigation, resources, writing – review and editing. **Joëlle van der Sprong:** resources, writing – review and editing. **Olivier P. Thomas:** funding acquisition, resources, writing – review and editing. **Vani Tirumalasetty:** investigation, writing – review and editing. **Nicole J. de Voogd:** resources, writing – review and editing. **Oliver Voigt:** resources, writing – review and editing. **John N. A. Hooper:** funding acquisition, resources, writing – review and editing. **Gert Wörheide:** funding acquisition, project administration, resources, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All sequence data can be accessed from the European Nucleotide Archive at https://www.ebi.ac.uk/ena/browser/home. Previously unpublished data is submitted under accession numbers OZ210097–OZ210308. Data and R scripts can be retrieved from https://github.com/PalMuc/Barcoding-inferred-Indo-Pacific-demosponge-biodiversity, archived in Zenodo (https://doi.org/10.5281/zenodo.18740328).

References

Anderson, M. J. 2017. "Permutational Multivariate Analysis of Variance (PERMANOVA)." In *Wiley StatsRef: Statistics Reference Online*, edited by N. Balakrishnan, T. Colton, B. Everitt, W. Piegorsch, F. Ruggeri, and J. L. Teugels. https://doi.org/10.1002/9781118445112.stat07841.

Ayling, A. L. 1980. "Patterns of Sexuality, Asexual Reproduction and Recruitment in Some Subtidal Marine Demospongiae." *Biological Bulletin* 158, no. 3: 271–282.

Barber, P. H., S. R. Palumbi, M. V. Erdmann, and M. K. Moosa. 2000. "Biogeography. A Marine Wallace's Line?" *Nature* 406, no. 6797: 692–693. https://doi.org/10.1038/35021135.

Barnes, D. K. A., and J. J. Bell. 2002. "Coastal Sponge Communities of the West Indian Ocean: Taxonomic Affinities, Richness and Diversity." *African Journal of Ecology* 40, no. 4: 337–349.

Bell, J. J. 2008. "The Functional Roles of Marine Sponges." *Estuarine, Coastal and Shelf Science* 79, no. 3: 341–353. https://doi.org/10.1016/j.ecss.2008.05.002.

Bell, J. J., and D. Smith. 2004. "Ecology of Sponge Assemblages (Porifera) in the Wakatobi Region, South-East Sulawesi, Indonesia: Richness and Abundance." *Journal of the Marine Biological Association of the United Kingdom* 84: 581–591.

Benestan, L., K. Fietz, N. Loiseau, et al. 2021. "Restricted Dispersal in a Sea of Gene Flow." *Proceedings of the Royal Society B: Biological Sciences* 288, no. 1951: 20210458. https://doi.org/10.1098/rspb.2021.0458.

Bergquist, P. R., M. E. Sinclair, and J. J. Hogg. 1970. "Adaptation to Intertidal Existence: Reproductive Cycles and Larval Behaviour in Demospongiae." In *Biology of the Porifera*, edited by W. G. Fry, 247–271. Zoological Society of London Symposia, Academic Press.

Bodenhofer, U., E. Bonatesta, C. Horejš-Kainrath, and S. Hochreiter. 2015. "Msa: An R Package for Multiple Sequence Alignment." *Bioinformatics* 31, no. 24: 3997–3999. https://doi.org/10.1093/bioinformatics/btv494.

Borojevic, R. 1967. "La ponte et le développement de *Polymastia robusta*." *Cahiers de Biologie Marine* 8, no. 1: 1–6.

Briggs, J. C. 1987. *Biogeography and Plate Tectonics*. Elsevier Science.

Briggs, J. C., and B. W. Bowen. 2012. "A Realignment of Marine Biogeographic Provinces With Particular Reference to Fish Distributions: Marine Biogeographic Provinces." *Journal of Biogeography* 39, no. 1: 12–30. https://doi.org/10.1111/j.1365-2699.2011.02613.x.

Carballo, J. L., J. M. Aguilar-Camacho, I. S. Knapp, and J. J. Bell. 2013. "Wide Distributional Range of Marine Sponges Along the Pacific Ocean." *Marine Biology Research* 9, no. 8: 768–775. https://doi.org/10.1080/17451000.2013.765581.

Cárdenas, P., J. R. Xavier, J. Reveillaud, C. Schander, and H. T. Rapp. 2011. "Molecular Phylogeny of the Astrophorida (Porifera, Demospongiae)

Reveals an Unexpected High Level of Spicule Homoplasy." *PLoS One* 6, no. 4: e18318. https://doi.org/10.1371/journal.pone.0018318.

Conway, J. R., A. Lex, and N. Gehlenborg. 2017. "UpSetR: An R Package for the Visualization of Intersecting Sets and Their Properties." *Bioinformatics* 33, no. 18: 2938–2940. https://doi.org/10.1093/bioinformatics/btx364.

Cowman, P. F., V. Parravicini, M. Kulbicki, and S. R. Floeter. 2017. "The Biogeography of Tropical Reef Fishes: Endemism and Provinciality Through Time." *Biological Reviews of the Cambridge Philosophical Society* 92, no. 4: 2112–2130. https://doi.org/10.1111/brv.12323.

Crandall, E. D., C. Riginos, C. E. Bird, et al. 2019. "The Molecular Biogeography of the Indo-Pacific: Testing Hypotheses With Multispecies Genetic Patterns." *Global Ecology and Biogeography* 28, no. 7: 943–960. https://doi.org/10.1111/geb.12905.

de Goeij, J. M., D. Van Oevelen, M. J. A. Vermeij, et al. 2013. "Surviving in a Marine Desert: The Sponge Loop Retains Resources Within Coral Reefs." *Science* 342, no. 6154: 108–110. https://doi.org/10.1126/science.1241981.

de Voogd, N. J., and D. F. R. Cleary. 2008. "An Analysis of Sponge Diversity and Distribution at Three Taxonomic Levels in the Thousand Islands/Jakarta Bay Reef Complex, West-Java, Indonesia." *Marine Ecology* 29, no. 2: 205–215. https://doi.org/10.1111/j.1439-0485.2008.00238.x.

de Voogd, N. J., D. F. R. Cleary, B. W. Hoeksema, A. Noor, and R. W. M. van Soest. 2006. "Sponge Beta Diversity in the Spermonde Archipelago, SW Sulawesi, Indonesia." *Marine Ecology Progress Series* 309: 131–142. https://doi.org/10.3354/meps309131.

DiBattista, J. D., H. J. Choat, M. R. Gaither, et al. 2016. "On the Origin of Endemic Species in the Red Sea." *Journal of Biogeography* 43, no. 1: 13–30. https://doi.org/10.1111/jbi.12631.

DiBattista, J. D., M. B. Roberts, J. Bouwmeester, et al. 2016. "A Review of Contemporary Patterns of Endemism for Shallow Water Reef Fauna in the Red Sea." *Journal of Biogeography* 43, no. 3: 423–439. https://doi.org/10.1111/jbi.12649.

Ducret, H., J. Timm, M. Rodríguez-Moreno, F. Huyghe, and M. Kochzius. 2022. "Strong Genetic Structure and Limited Connectivity Among Populations of Clark's Anemonefish (*Amphiprion clarkii*) in the Centre of Marine Biodiversity." *Coral Reefs* 41, no. 3: 599–609. https://doi.org/10.1007/s00338-021-02205-8.

Ekins, M., D. Erpenbeck, C. Debitus, et al. 2023. "Revision of the Genus *Fascaplysinopsis*, the Type Species *Fascaplysinopsis reticulata* (Hentschel, 1912) (Porifera, Dictyoceratida, Thorectidae) and Descriptions of Two New Genera and Seven New Species." *Zootaxa* 5346, no. 3: 201–241. https://doi.org/10.11646/zootaxa.5346.3.1.

Elvin, D. W., J. T. Carlton, J. B. Geller, J. W. Chapman, and J. A. Miller. 2018. "Porifera (Sponges) From Japanese Tsunami Marine Debris Arriving in the Hawaiian Islands and on the Pacific Coast of North America." *Aquatic Invasions* 13, no. 1: 31–41.

Erpenbeck, D., R. Aryasari, S. Benning, et al. 2017. "Diversity of Two Widespread Indo-Pacific Demosponge Species Revisited." *Marine Biodiversity* 47, no. 4: 1035–1043. https://doi.org/10.1007/s12526-017-0783-3.

Erpenbeck, D., A. Galitz, M. Ekins, et al. 2020. "Soft Sponges With Tricky Tree: On the Phylogeny of Dictyoceratid Sponges." *Journal of Zoological Systematics and Evolutionary Research* 58, no. 1: 27–40. https://doi.org/10.1111/jzs.12351.

Erpenbeck, D., A. Gholami, M. A. Hesni, et al. 2020. "Molecular Biodiversity of Iranian Shallow Water Sponges." *Systematics and Biodiversity* 18, no. 2: 192–202. https://doi.org/10.1080/14772000.2020.1737978.

Erpenbeck, D., J. N. A. Hooper, and G. Wörheide. 2006. "CO1 Phylogenies in Diploblasts and the 'Barcoding of Life'—Are We Sequencing a Suboptimal Partition?" *Molecular Ecology Notes* 6, no. 2: 550–553. https://doi.org/10.1111/j.1471-8286.2005.01259.x.

Erpenbeck, D., O. Voigt, A. M. Al-Aidaroos, et al. 2016. "Molecular Biodiversity of Red Sea Demosponges." *Marine Pollution Bulletin* 105, no. 2: 507–514. https://doi.org/10.1016/j.marpolbul.2015.12.004.

Galitz, A., M. Ekins, E. Folcher, et al. 2023. "Poriferans Rift Apart: Molecular Demosponge Biodiversity in Central and French Polynesia and Comparison With Adjacent Marine Provinces of the Central Indo-Pacific." *Biodiversity and Conservation* 32: 2469–2494. https://doi.org/10.1007/s10531-023-02613-y.

Galitz, A., M. Ekins, M. M. Reddy, et al. 2024. "Molecular Genetic Biodiversity Assessment of the Wallis Island Sponge Fauna in the Tropical Pacific." *Journal of the Marine Biological Association of the United Kingdom* 104: e56. https://doi.org/10.1017/s0025315424000432.

George, A. M., R. W. M. van Soest, R. D. Sluka, and S. Lazarus. 2020. "A Checklist of Marine Sponges (Porifera) of Peninsula India." *Zootaxa* 4885, no. 2: 277–300. https://doi.org/10.11646/zootaxa.4885.2.10.

Glover, A. G., H. Wiklund, C. Chen, and T. G. Dahlgren. 2018. "Managing a Sustainable Deep-Sea 'Blue Economy' Requires Knowledge of What Actually Lives There." *eLife* 7: e41319. https://doi.org/10.7554/elife.41319.

Hadiyanto, H., R. K. Hovey, C. J. Glasby, J. Prince, and R. Correia. 2021. "Marine Ecoregions and Subecoregions Within Indo-West Australian Waters: A Statistical Approach Based on Species Distributions." *Journal of Biogeography* 48, no. 9: 2246–2257. https://doi.org/10.1111/jbi.14147.

Hooper, J. N. A., and M. Ekins. 2005. *Collation and Validation of Museum Collection Databases Related to the Distribution of Marine Sponges in Northern Australia (Contract National Oceans Office C2004/020)*, 1–235. Department of Sustainability, Environment, Water, Population and Communities.

Hooper, J. N. A., K. A. Hall, M. Ekins, D. Erpenbeck, G. Wörheide, and G. Jolley-Rogers. 2013. "Managing and Sharing the Escalating Number of Sponge 'Unknowns': The SpongeMaps Project." *Integrative and Comparative Biology* 53, no. 3: 473–481. https://doi.org/10.1093/icb/ict038.

Kelly, M., J. N. A. Hooper, V. Paul, G. Paulay, R. W. M. van Soest, and W. de Weerdt. 2003. "Taxonomic Inventory of the Sponges (Porifera) of the Mariana Islands." *Micronesica* 35–36: 100–120.

Kembel, S. W., P. D. Cowan, M. R. Helmus, et al. 2010. "Picante: R Tools for Integrating Phylogenies and Ecology." *Bioinformatics* 26, no. 11: 1463–1464. https://doi.org/10.1093/bioinformatics/btq166.

Kemp, J. 1998. "Zoogeography of the Coral Reef Fishes of the Socotra Archipelago." *Journal of Biogeography* 25, no. 5: 919–933.

Klautau, M., C. A. M. Russo, C. Lazoski, N. Boury-Esnault, J. P. Thorpe, and A. M. Sole-Cava. 1999. "Does Cosmopolitanism Result From Overconservative Systematics? A Case Study Using the Marine Sponge *Chondrilla nucula*." *Evolution; International Journal of Organic Evolution* 53, no. 5: 1414–1422.

Kochzius, M., and A. Nuryanto. 2008. "Strong Genetic Population Structure in the Boring Giant Clam, *Tridacna crocea*, Across the Indo-Malay Archipelago: Implications Related to Evolutionary Processes and Connectivity." *Molecular Ecology* 17, no. 17: 3775–3787. https://doi.org/10.1111/j.1365-294X.2008.03803.x.

Koleff, P., K. J. Gaston, and J. J. Lennon. 2003. "Measuring Beta Diversity for Presence–Absence Data." *Journal of Animal Ecology* 72, no. 3: 367–382. https://doi.org/10.1046/j.1365-2656.2003.00710.x.

Kreft, H., and W. Jetz. 2010. "A Framework for Delineating Biogeographical Regions Based on Species Distributions." *Journal of Biogeography* 37, no. 11: 2029–2053. https://doi.org/10.1111/j.1365-2699.2010.02375.x.

Kulbicki, M., V. Parravicini, D. R. Bellwood, et al. 2013. “Global Biogeography of Reef Fishes: A Hierarchical Quantitative Delineation of Regions.” *PLoS One* 8, no. 12: e81847. https://doi.org/10.1371/journal.pone.0081847.

Ludt, W. B., L. Morgan, J. Bishop, and P. Chakrabarty. 2017. “A Quantitative and Statistical Biological Comparison of Three Semi-Enclosed Seas: The Red Sea, the Persian (Arabian) Gulf, and the Gulf of California.” *Marine Biodiversity* 48, no. 4: 2119–2124. https://doi.org/10.1007/s12526-017-0740-1.

Maldonado, M. 2006. “The Ecology of the Sponge Larva.” *Canadian Journal of Zoology* 84: 175–194.

McFadden, C. S., K. L. Erickson, A. Lane, et al. 2025. “Biodiversity and Biogeography of Zooxanthellate Soft Corals Across the Indo-Pacific.” *Scientific Reports* 15, no. 1. https://doi.org/10.1038/s41598-025-98790-7.

Mora, C., E. A. Treml, J. Roberts, K. Crosby, D. Roy, and D. P. Tittensor. 2012. “High Connectivity Among Habitats Precludes the Relationship Between Dispersal and Range Size in Tropical Reef Fishes.” *Ecography* 35, no. 1: 89–96. https://doi.org/10.1111/j.1600-0587.2011.06874.x.

Ngwakum, B. B., R. P. Payne, P. R. Teske, L. Janson, S. E. Kerwath, and T. Samaai. 2021. “Hundreds of New DNA Barcodes for South African Sponges.” *Systematics and Biodiversity* 19: 747–769.

Nozawa, Y., and N. Okubo. 2011. “Survival Dynamics of Reef Coral Larvae With Special Consideration of Larval Size and the Genus *Acropora*.” *Biological Bulletin* 220, no. 1: 15–22. https://doi.org/10.1086/BBLv220n1p15.

Núñez Pons, L., B. Calcinai, and R. D. Gates. 2017. “Who's There?—First Morphological and DNA Barcoding Catalogue of the Shallow Hawai'ian Sponge Fauna.” *PLoS One* 12, no. 12: e0189357. https://doi.org/10.1371/journal.pone.0189357.

Obura, D. 2012. “The Diversity and Biogeography of Western Indian Ocean Reef-Building Corals.” *PLoS One* 7, no. 9: e45013. https://doi.org/10.1371/journal.pone.0045013.

Obura, D. O. 2016. “An Indian Ocean Centre of Origin Revisited: Palaeogene and Neogene Influences Defining a Biogeographic Realm.” *Journal of Biogeography* 43, no. 2: 229–242. https://doi.org/10.1111/jbi.12656.

Oksanen, J., F. G. Blanchet, and R. Kindt. 2013. “Package ‘Vegan’.” Community Ecology. https://doi.org/10.32614/CRAN.package.vegan.

Palumbi, S. R., G. Grabowsky, T. F. Duda Jr., L. Geyer, and N. Tachino. 1997. “Speciation and Population Genetic Structure in Tropical Pacific Sea Urchins.” *Evolution; International Journal of Organic Evolution* 51, no. 5: 1506–1517.

Reid, D. G., M. Claremont, L. Smith, M. Shamoto, M. Glaubrecht, and T. Ozawa. 2013. “Mosaics in the Mangroves: Allopatric Diversification of Tree-Climbing Mudwhelks (Gastropoda: Potamididae: Cerithidea) in the Indo-West Pacific.” *Biological Journal of the Linnean Society* 110, no. 3: 564–580. https://doi.org/10.1111/bij.12151.

Schroeder, P. J., and D. G. Jenkins. 2018. “How Robust Are Popular Beta Diversity Indices to Sampling Error?” *Ecosphere* 9, no. 2: e02100. https://doi.org/10.1002/ecs2.2100.

Spaet, J. L. Y., R. W. Jabado, A. C. Henderson, A. B. M. Moore, and M. L. Berumen. 2015. “Population Genetics of Four Heavily Exploited Shark Species Around the Arabian Peninsula.” *Ecology and Evolution* 5, no. 12: 2317–2332. https://doi.org/10.1002/ece3.1515.

Spalding, M. D., H. E. Fox, G. R. Allen, et al. 2007. “Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas.” *Bioscience* 57, no. 7: 573–583. https://doi.org/10.1641/B570707.

Turner, T. 2020. “The Marine Sponge *Hymeniacidon perlevis* Is a Globally-Distributed Exotic Species.” *Aquatic Invasions* 15, no. 4: 542–561. https://doi.org/10.3391/ai.2020.15.4.01.

van Soest, R. W. M. 1989. “The Indonesian Sponge Fauna: A Status Report.” *Netherlands Journal of Sea Research* 23, no. 2: 223–230.

van Soest, R. W. M. 1994. “Demosponge Distribution Patterns.” In *Sponges in Time and Space*, edited by R. W. M. van Soest, T. M. G. van Kempen, and J.-C. Braekman, 213–224. Balkema.

van Soest, R. W. M., R. Aryasari, and N. J. De Voogd. 2021. “*Mycale* Species of the Tropical Indo-West Pacific (Porifera, Demospongiae, Poecilosclerida).” *Zootaxa* 4912, no. 1: 1–212. https://doi.org/10.11646/zootaxa.4912.1.1.

van Soest, R., and E. J. Beglinger. 2002. “A New Species of *Biemna* (Porifera, Poecilosclerida) From the Sultanate of Oman.” *Beaufortia* 52, no. 2: 15–24.

van Soest, R. W. M., N. Boury-Esnault, J. Vacelet, et al. 2012. “Global Diversity of Sponges (Porifera).” *PLoS One* 7, no. 4: e35105. https://doi.org/10.1371/journal.pone.0035105.

Vargas, S., A. Schuster, K. Sacher, et al. 2012. “Barcoding Sponges: An Overview Based on Comprehensive Sampling.” *PLoS One* 7, no. 7: e39345. https://doi.org/10.1371/journal.pone.0039345.

Veron, J. E. N. 1995. *Corals in Space and Time: The Biogeography and Evolution of the Scleractinia*. Cornell University Press.

Veron, J., M. Stafford-Smith, L. DeVantier, and E. Turak. 2015. “Overview of Distribution Patterns of Zooxanthellate Scleractinia.” *Frontiers in Marine Science* 1: 81. https://doi.org/10.3389/fmars.2014.00081.

Vicente, J., M. K. Webb, G. Paulay, et al. 2022. “Unveiling Hidden Sponge Biodiversity Within the Hawaiian Reef Cryptofauna.” *Coral Reefs* 41: 727–742. https://doi.org/10.1007/s00338-021-02109-7.

Wilkinson, C. R. 1987. “Interocean Differences in Size and Nutrition of Coral Reef Sponge Populations.” *Science* 236: 1654–1657.

Wooster, M. K., O. Voigt, D. Erpenbeck, G. Wörheide, and M. L. Berumen. 2019. “Sponges of the Red Sea.” In *Coral Reefs of the Red Sea*, edited by C. R. Voolstra and M. L. Berumen, 91–122. Springer International Publishing. https://doi.org/10.1007/978-3-030-05802-9_6.

Wörheide, G., B. M. Degnan, J. N. A. Hooper, and J. Reitner. 2002. “Phylogeography and Taxonomy of the Indo-Pacific Reef Cave Dwelling Coralline Demosponge *Astrosclera* ‘*Willeyana*’: New Data From Nuclear Internal Transcribed Spacer Sequences.” In *Proceecdings of the 9th International Coral Reef Symposium*, 339–346.

Wörheide, G., L. S. Epp, and L. Macis. 2008. “Deep Genetic Divergences Among Indo-Pacific Populations of the Coral Reef Sponge *Leucetta chagosensis* (Leucettidae): Founder Effects, Vicariance, or Both?” *BMC Evolutionary Biology* 8: 24. https://doi.org/10.1186/1471-2148-8-24.

Wörheide, G., and D. Erpenbeck. 2007. “DNA Taxonomy of Sponges—Progress and Perspectives.” *Journal of the Marine Biological Association of the United Kingdom* 87: 1629–1633.

Wörheide, G., J. N. A. Hooper, and B. M. Degnan. 2002. “Phylogeography of Western Pacific *Leucetta ‘Chagosensis’* (Porifera: Calcarea) From Ribosomal DNA Sequences: Implications for Population History and Conservation of the Great Barrier Reef World Heritage Area (Australia).” *Molecular Ecology* 11: 1753–1768. https://doi.org/10.1046/j.1365-294x.2002.01570.x.

Wright, E. S. 2016. “Using DECIPHER v2. 0 to Analyze Big Biological Sequence Data in R.” *R Journal* 8, no. 1: 352–359. https://doi.org/10.32614/RJ-2016-025.

Xavier, J. R., P. G. Rachello-Dolmen, F. Parra-Velandia, C. H. L. Schönberg, J. A. J. Breeuwer, and R. W. M. van Soest. 2010. “Molecular Evidence of Cryptic Speciation in the ‘Cosmopolitan’ Excavating Sponge *Cliona celata* (Porifera, Clionaidae).” *Molecular Phylogenetics and Evolution* 56, no. 1: 13–20. https://doi.org/10.1016/j.ympev.2010.03.030.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Worksheet 'Sample and MOTU List': List of samples included in the present analysis with location information, source or ENA accession number respectively and resulting MOTU. Worksheet 'Sequence and MOTU counts': Overview of MP sequence yield and MOTU numbers in the current analysis. Worksheet 'MOTU > 3 MPs': List of the MOTUs with > 3 marine provinces. **Appendix S2:** Left panels: Rarefaction, extrapolation of biodiversity and sample completeness for each marine province analysed in the present MS. **Appendix S3:** Jaccard and Sørensen dissimilarity for sponges of the studied marine provinces. **Appendix S4:** Analyses of faunistic boundaries for sponges from the Central Indo Pacific and Temperate Australasia realm around Australia.