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Molecular operational taxonomic units reveal restricted geographic ranges and regional endemism in the Indo-Pacific octocoral family Xeniidae

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Abstract

Aim: To quantify taxon diversity, biogeographic distributions and patterns of community assembly in xeniid octocorals using molecular operational taxonomic units (MOTUs).

Location: Red Sea, Indian and western Pacific Oceans.

Taxon: Xeniidae, a family of reef-dwelling octocorals (Anthozoa, Octocorallia).

Methods: Xeniids collected at 13 locations were sequenced at three barcode loci, and assigned to MOTUs defined by minimum genetic distance thresholds. Taxon richness (number of MOTUs) and endemicity (per cent of MOTUs found at a single location) were quantified. Patterns of β-diversity (species turnover) and phylogenetic β-diversity (lineage turnover) among geographical regions were visualized using hierarchical clustering, non-metric multidimensional scaling (NMDS) plots and distance-decay relationships. Community assembly was investigated by comparing the mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) separating species in each assemblage to values generated for null communities.

Results: A genetic distance threshold of 0.3% discriminated 67 MOTUs, with taxon richness ranging from 2–18 MOTUs per site. Out of the 67 MOTUs, 48 (72%) were found at only a single location, and only two spanned both the western Indian and Pacific Oceans. Species turnover among sites was high, but phylogenetic β-diversity was lower than β-diversity and differed significantly from null models of community assembly at only two sites. β-diversity and phylogenetic β-diversity both increased significantly with geographic distance, and sites clustered into three distinct biogeographic regions (Red Sea and western Indian Ocean; Western Australia; western Pacific Ocean and Great Barrier Reef, Australia). All five major clades of xeniids were represented in each region.

Main conclusions: A genetic approach to biodiversity estimation suggests that most xeniid taxa are regional endemics whose geographic distribution is likely governed by dispersal limitation. This conclusion contrasts with published records of certain morphospecies occurrences, which imply that they have broad geographic ranges. So far,

the distribution of xeniid biodiversity mirrors that of scleractinian corals, with species richness highest in the Coral Triangle, but endemicity peaking in peripheral areas.

KEYWORDS
biodiversity, community assembly, dispersal limitation, DNA barcoding, endemicity, MOTU, octocorals, Xeniidae

1 | INTRODUCTION

Identification and subsequent protection of biodiversity hotspots characterized by high species richness and endemicity form the basis of conservation strategies in both marine and terrestrial habitats (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000; Roberts et al., 2002). Centres of biodiversity defined by high species richness, however, are not always coincident with centres of endemicity (Hughes, Bellwood, & Connelly, 2002) or centres of evolutionary diversification (Huang, Goldberg, Chou, & Roy, 2018). Our current understanding of the global distribution of biodiversity in the marine environment is based largely on studies of vertebrates (Allen, 2008), scleractinian corals (Huang et al., 2018; Hughes et al., 2002) and some conspicuous, mobile invertebrates (molluscs, crustaceans) (Edgar et al., 2017; Roberts et al., 2002). These taxonomic groups are well-studied, many species are known even to amateurs, and their geographic ranges have been well established. The vast majority of marine organisms, however, remain undescribed and uncharacterized (Appeltans et al., 2012; Knowlton et al., 2010; Mora, Tittensor, Adl, Simpson, & Worm, 2011), and a lack of taxonomic and geographic records precludes a more general understanding of global patterns of marine biodiversity.

Determination of species ranges requires the ability to recognize species boundaries and to accurately discriminate taxa. For many marine organisms, including the anthozoan cnidarians that are the foundation species of both shallow- and deep-water reef communities (Roberts, Wheeler, & Freiwald, 2006), morphology is often a poor indicator of species boundaries. Recent studies of coral systematics and phylogeography include cases in which well-known morphospecies believed to occupy broad geographic ranges have subsequently been discovered to be comprised of cryptic species complexes of range-restricted, regional endemics (e.g. Keshavmurthy et al., 2013). Conversely, molecular genetic studies of some morphologically unique taxa considered to represent range-restricted endemics—in some cases proposed for listing as endangered species—have exposed them to be nothing more than ecomorphs of common, geographically widespread species (Forsman et al., 2010; Paz-García, Hellberg, García-de-Léon, & Balart, 2015). In groups such as these in which morphological variation is poorly understood or cryptic species are common, molecular approaches to biodiversity estimation have been shown to greatly facilitate the documentation of marine biodiversity and its geographical distribution (e.g. LeRay & Knowlton, 2016 and references therein).

The anthozoan subclass Octocorallia, a group that includes many of the most visible, ecologically dominant and structurally important sessile macro-organisms found on shallow, tropical reefs and in the deep sea (Buhl-Mortensen et al., 2010; Roberts et al., 2006), exemplifies the challenges of biodiversity estimation in the marine environment. The inadequacy of early taxonomic descriptions, a dearth of modern taxonomic work on the group (Cairns, 2007), and poorly understood, environmentally plastic morphological traits (Gutiérrez-Rodríguez, Barbeitos, Sánchez, & Lasker, 2009; Prada, Schizas, & Yoshioka, 2008; West, 1997; West, Harvell, & Walls, 1993) make species-level identification difficult—or even impossible—for many of the >3,000 described taxa of octocorals (Bridge et al., 2012; Fabricius & Alderslade, 2001; McFadden, Brown, Brayton, Hunt, & van Ofwegen, 2014). This situation hinders efforts to understand geographical ranges, species diversity and community structure. Recent studies have suggested, however, that molecular approaches can facilitate the quantification of octocoral biodiversity, and may begin to allow us to document biogeographical distributions of taxa that currently cannot be assigned Latin binomials (McFadden, Reynolds, & Janes, 2014; McFadden, Brown, et al., 2014; McFadden et al., 2017; Pante, France, Gey, Cruaud, & Samadi, 2015).

Species belonging to the family Xeniidae are among the most common and conspicuous octocorals found in shallow-water reef communities throughout the Indo-Pacific (Benayahu & Loya, 1981; Dinesen, 1983; Fabricius, 1997, 1998). Interest in this family has been increasing with reports that they may be capable of rapidly recolonizing recently disturbed reefs, thereby either inhibiting (Fabricius, 1998; Fox, Pet, Dahuri, & Caldwell, 2003; Tilot, Leujak, Ormond, Ashworth, & Mabrouk, 2008; Wood & Dipper, 2008) or perhaps facilitating (Fox et al., 2003) the subsequent recruitment and recovery of reef-building scleractinian corals. Xeniids also have the potential to become invasive when introduced to new environments, as documented on South American reefs overgrown by introduced xeniids that are presumed to have arrived via the aquarium trade (Mantellato, Silva, Louzada, McFadden, & Creed, 2018; Ruiz Allais, Halàsz, McFadden, Amaro, & Benayahu, 2014). Study of the biogeography and ecology of xeniids is impeded, however, by the challenges of identifying species—sometimes even genera—with the result that studies that have reported their impacts on reef communities often identify them to the wrong genera or only to family (Tilot et al., 2008; Wood & Dipper, 2008). These challenges

arise in part because much of the early literature on the group is poorly illustrated and species descriptions may not correctly describe the type specimens on which they are based, making it difficult to put names on morphospecies without direct comparison to the original type material (Benayahu, van Ofwegen, & McFadden, 2018; Halàsz, 2016; Halàsz, McFadden, Aharonovich, Toonen, & Benayahu, 2013). In addition, recent taxonomic studies have suggested that morphological features of polyps and sclerites that have traditionally been used to diagnose and distinguish species of xeniids from one another are often unreliable and incongruent with genetically determined species boundaries (Benayahu, van Ofwegen, & McFadden, 2018; Halàsz, Reynolds, McFadden, Toonen, & Benayahu, 2014; Halàsz et al., 2013; McFadden, Brown, et al., 2014; McFadden et al., 2017). Although scanning electron microscopy has identified new morphological characters (e.g. the crystalline microstructure of skeletal elements; Alderslade, 2001; Aharanovich & Benayahu, 2011) that help to discriminate genera reliably (Benayahu, van Ofwegen, & McFadden, 2018), identification of new morphological characters to discriminate species—especially ones that can be observed in the field—is an ongoing challenge (Halàsz et al., 2014; McFadden et al., 2017).

Although approximately 138 species of xeniids belonging to 19 genera are listed currently in the World Register of Marine Species (WoRMS Editorial Board, 2016), the true number remains unknown, and recent molecular genetic studies have suggested that some genera may be comprised of fewer species than have been described based on morphology (Halàsz et al., 2014; McFadden et al., 2017). Geographical ranges of species as reflected in the classical taxonomic literature may also be highly speculative. Many species have not been recorded since their original description and are known only from their type localities, while others have been reported from locations that span the entire Indo-Pacific, from the Red Sea to the Great Barrier Reef. For example, Reinicke (1997) listed 29 species of xeniids with confirmed records in the Red Sea, nine of which have type localities in the western Pacific. Similarly, 10 or more of the species that have been recorded from Madagascar and other islands in the western Indian Ocean have type localities in Indonesia, the Philippines or the Great Barrier Reef (Tixier-Durivault, 1966; Verseveldt, 1971). All of the xeniids whose reproductive biology has been studied, however, brood their larvae (Benayahu, 1991; Kahng, Benayahu, & Lasker, 2011), a mode of reproduction that is generally associated with limited dispersal and restricted geographical ranges (Jablonski, 1986; Jablonski & Lutz, 1983). This raises the intriguing question of whether some xeniid octocorals have wide geographic ranges despite their mode of reproduction, or if the wide geographic ranges that have been reported for many species are simply a result of erroneous taxonomy.

In order to answer such questions about the diversity, biogeography and ecology of xeniid octocorals, we applied a molecular taxonomic approach to species delimitation, defining species as molecular operational taxonomic units (MOTUs) based on previously determined genetic distance thresholds (McFadden, Reynolds, et al., 2014; McFadden et al., 2017). By mapping the distribution of MOTUs across the Indo-Pacific and quantifying the β-diversity (turnover) of MOTUs and phylogenetic lineages with geographic distance, we test the hypothesis that xeniids have restricted geographic ranges, as predicted by their brooding mode of reproduction.

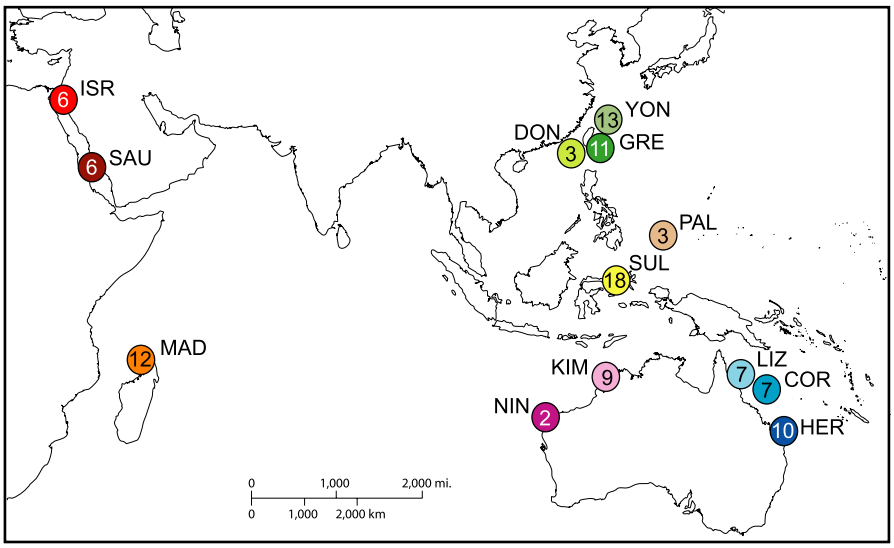

FIGURE 1 Map of the Indian and western Pacific Oceans showing sites at which biodiversity of xeniid octocorals was surveyed. Numbers in circles are taxon richness estimates (S = number of molecular operational taxonomic units (MOTUs) based on 0.3% genetic distance threshold). ISR: Eilat, Israel; SAU: Saudi Arabia, central Red Sea; MAD: Nosy Bé, Madagascar; NIN: Ningaloo Reef, Western Australia; KIM: Kimberley, Western Australia; SUL: Lembeh Strait, Sulawesi, Indonesia; PAL: Republic of Palau; DON: Dongsha Atoll, Taiwan; GRE: Green (Ludao) Island, Taiwan; YON: Yonaguni Island, Ryukyu Archipelago, Japan; LIZ: Lizard Island, Queensland, Australia; COR: Coral Sea Islands Territory, Australia; HER: Heron Island, Queensland, Australia [Colour figure can be viewed at wileyonlinelibrary.com]

2 | MATERIALS AND METHODS

2.1 | Collection

Xeniid octocorals were collected during comprehensive biodiversity surveys conducted from 2009–2016 at 13 geographical locations spanning the Indo-West Pacific (Figure 1). Results of five of these surveys have been published previously (Red Sea, Israel: McFadden et al., 2011, 2017; Halàsz et al., 2014; Red Sea, Saudi Arabia: Haverkort-Yeh et al., 2013; Palau: McFadden, Brown, et al., 2014; Sulawesi, Indonesia: McFadden, Reynolds, et al., 2014; Dongsha Atoll, Taiwan: Benayahu, van Ofwegen, Dai, et al., 2018). Any xeniids that were encountered by divers using SCUBA were collected and preserved in 70% EtOH. Collections were made haphazardly without attempting to quantify relative abundance. Effort varied among locations, mostly dependent on time constraints and weather conditions, ranging from a low of four dives (over 4 days) at Yonaguni Island to a high of 49 dives (over 28 days) at Ningaloo (mean = 20.5 dives per location ± 14.3 *SD*). Tissue subsamples for DNA were preserved in either 95% EtOH or salt-saturated dimethyl sulfoxide (DMSO) buffer. Voucher material for all specimens has been deposited at the California Academy of Sciences (CASIZ) (Indonesia, Palau), the Smithsonian Institute (USNM) (Saudi Arabia), the Queensland Museum (QM) (Australia) and the Steinhardt Museum of Natural History, Tel Aviv University, Israel (SMNH) (Israel, Madagascar, Taiwan, Japan) (see Table S1 in Appendix S1).

2.2 | DNA sequencing and analysis

DNA was extracted from preserved tissues using the DNEasy Blood & Tissue Kit (Qiagen Inc). Fragments of two mitochondrial (*mtMutS*, *COI+igr1*) and one nuclear ribosomal (*28S*) gene regions were amplified by PCR and sequenced using previously published primers and protocols (McFadden, Reynolds, et al., 2014). These three gene regions in combination have been used as a molecular barcode for species delimitation in previous studies of xeniids (Halàsz et al., 2014; Janes, McFadden, & Chanmethakul, 2014; McFadden, Reynolds, et al., 2014) as well as other octocoral taxa (McFadden, Brown, et al., 2014), and have been estimated to discriminate 75%–90% of identified morphospecies.

Sequences were aligned using the L-INS-i method in MAFFT (Katoh, Kuma, Toh, & Miyata, 2005). As there was no evidence for incongruence between mitochondrial and nuclear data, all three gene regions were then concatenated into a single genetic barcode. Duplicate genotypes were removed from the dataset such that all further analyses were conducted using no more than two representatives of each unique multilocus genotype from each location (n = 170). Pairwise genetic distances (Kimura 2-parameter) among concatenated sequences were calculated using the DNADist program in PHYLIP 3.69 (Felsenstein, 2005). Although use of the Kimura 2-parameter model of evolution for genetic barcoding studies has been criticized (Srivathsan & Meier, 2012), simulations have suggested that it performs adequately when genetic divergence among sequences is low, as it is here (Barley & Thomson, 2016). MOTHUR 1.29 (Schloss et al., 2009) was used to delimit MOTUs based on genetic distance thresholds of 0.1%–0.5% (McFadden, Brown, et al., 2014; McFadden, Reynolds, et al., 2014). To visualize relationships among MOTUs, phylogenetic trees were constructed using both neighbor-joining (Kimura 2-parameter substitution model, 1,000 bootstrap replicates) (MEGA 5; Tamura et al., 2011) and maximum likelihood methods (PHYML, GTR+I+G model of evolution, 100 bootstrap replicates; Guindon & Gascuel, 2003).

2.3 | Biodiversity analyses

To quantify β-diversity (species turnover), Sørenson's index, a measure of similarity/dissimilarity that gives greater weight to species shared between sites, was calculated between pairs of sites from the presence/absence matrix. In addition, we estimated phylogenetic β-diversity between pairs of sites using the PhyloSor index (Bryant et al., 2008), a measure of the proportion of branch lengths in a phylogeny that are shared among sites. Sørenson's dissimilarity (β_{SOR}) and phylogenetic dissimilarity ($Phylo\beta_{SOR}$ = 1−PhyloSor) were each further partitioned into additive components reflecting the contributions of turnover (β_{SIM}, $Phylo\beta_{SIM}$) versus nestedness (β_{NES}, $Phylo\beta_{NES}$), where nestedness accounts for differences in α-diversity among sites (i.e. differences in β-diversity simply due to one site having a strict subset of the species found at another site) ('betapart', Baselga, 2012; R Core Development Team, 2012). Baselga's (2012) multiple-site dissimilarity measure was used to summarize these same indices across all sites.

Patterns of β-diversity and phylogenetic β-diversity among geographical regions were visualized using hierarchical clustering and non-metric multidimensional scaling (NMDS) plots of the Sørenson's and PhyloSor indices as well as the turnover components of dissimilarity, β_{SIM} and $Phylo\beta_{SIM}$ (PRIMER-E; Clarke & Gorley, 2015). Great-circle ("crow's-flight") distances between pairs of sites were approximated from geographical coordinates using the haversine formula (https://www.movable-type.co.uk/scripts/ latlong.html), and Mantel tests ('ecodist', Goslee & Urban, 2007, R Core Development Team, 2012) were conducted to determine if there was a significant relationship between species turnover (β_{SIM}) or lineage turnover ($Phylo\beta_{SIM}$) and ln(geographic distance). Distance–decay relationships were visualized by plotting β_{SIM} and $Phylo\beta_{SIM}$ as functions of ln(distance).

Patterns of community assembly were investigated by calculating the mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) separating species in each assemblage ('picante', Kembel et al., 2010; R Core Development Team, 2012). Standardized effect sizes (SES) for each measure were determined by comparing observed values to those generated for null communities assembled by randomizing labels across tips in the tree while holding constant the occurrence frequency and richness of MOTUs at each site (independent swap algorithm, Gotelli, 2000; runs = 999).

3 | RESULTS

3.1 | Delimitation of MOTUs

Complete or partial sequences were obtained for a total of 386 xeniid specimens, representing 142 unique multilocus barcodes; no more than two representatives of each unique genotype from each geographic location were included in subsequent analyses (n = 170) (see Table S1 in Appendix S1). Application of genetic distance thresholds ranging from 0.5%–0.1% discriminated 50–100 MOTUs respectively (Table 1). Taxon richness (S = number of MOTUs) was highest at Sulawesi (S = 16–19) followed closely by Yonaguni Island (S = 13–17) and Madagascar (S = 12–16) (Table 2, Figure 1). Taxon richness was lowest at Palau (S = 3), Dongsha Atoll (S = 3) and Ningaloo (S = 2). Percentages of MOTUs considered to be regional endemics (MOTUs found at only a single location) ranged from 58% to 79% (Table 1). There was no apparent relationship between the estimated taxon richness (number of MOTUs sampled) and the effort expended per location (Figure 2).

Previous studies that have compared morphological versus molecular species identification methods in xeniids and other octocorals have found the highest concordance between morphospecies IDs and MOTUs at a genetic distance threshold of 0.3% (McFadden, Brown, et al., 2014; McFadden, Reynolds, et al., 2014). In the present study, that value discriminated 67 MOTUs of xeniids, 48 (72%) of which were found at only a single location (Table 2, Figure 3). Endemism was highest at Madagascar, which had nine MOTUs (75%) found nowhere else, and lowest at Dongsha Atoll, which had no endemic MOTUs (Figure 3). Of the 19 MOTUs that were found at more than one location, three were shared only by the two locations in the Red Sea, one was shared only between the Red Sea and Madagascar, one only between the two sites in Western Australia, and two only among sites on the Great Barrier Reef (Table 3; Figure 3). Eight MOTUs were shared only among locations in the western Pacific, and two were shared between Western Australia and Sulawesi. Only two of 67 MOTUs were found in both the Pacific and western Indian Oceans. The most widespread of these (MOTU 01) was found at every location with the exception of the two sites in Western Australia (Figure 3).

TABLE 1 Number of molecular operational taxonomic units (MOTUs) of xeniid octocorals detected at 13 sites spanning the Indo-Pacific. Four different pairwise genetic distance (K2p) thresholds were used to define MOTUs. Values for 0.3% threshold (shaded) were used for all additional analyses

	Genetic distance threshold			
MOTUs	0.1%	0.2%	0.3%	0.5%
Total no. (S)	100	81	67	50
No. found at >1 site	21	20	19	21
No. endemic to a site (E)	79	61	48	29
% endemicity	79	75	72	58

Applying lower (less conservative) genetic distance thresholds (0.1%–0.2%) increased both the number of MOTUs as well as the proportion of endemic MOTUs at each site, but had relatively little effect on the estimated number of MOTUs shared among sites (19 at a threshold of 0.3% vs. 21 at 0.1%) (Table 2). Application of the most conservative 0.5% genetic distance threshold decreased both the total number of MOTUs and number of endemic MOTUs (Table 2). Compared to the 0.3% threshold, however, estimates of numbers of MOTUs remained unchanged at seven of 13 locations, and decreased by only one or two at the other six sites. The numbers of MOTUs shared among sites increased only slightly—from 19 to 21—when the 0.5% threshold was used, but the total number of taxa shared between the western Indian and Pacific Oceans increased from two to four.

3.2 | Phylogenetic analyses

Both maximum likelihood (Figure 3; Figure S1 in Appendix S2) and neighbor-joining (Figure S2 in Appendix S2) phylogenetic analyses of MOTUs (0.3% threshold) revealed five well-supported and reciprocally monophyletic clades, all of which have been identified in previous studies (Benayahu, van Ofwegen, & McFadden, 2018; McFadden, Reynolds, et al., 2014). Within these clades morphologically-defined genera were both paraphyletic and polyphyletic (McFadden, Reynolds, et al., 2014). Clade 1 includes specimens identified morphologically to genera *Caementabunda* and *Conglomeratusclera*; Clade 2: *Anthelia* and *Fasciclia*; Clade 3: *Sympodium*; Clade 4: *Sansibia*, *Xenia* (clade X3 of McFadden, Reynolds, et al., 2014) and *Yamazatum*; Clade 5: *Asterospicularia*, *Heteroxenia*, *Ovabunda* and *Xenia* (clades X1 and X2 of McFadden, Reynolds, et al., 2014) (see Table S1 in Appendix S1). All five of these major clades were represented in both the Pacific and Indian Oceans. Strikingly, clades 1 and 4 were not found in the Red Sea. Clades 2, 3 and 5 included strongly supported subclades each consisting of 2–4 MOTUs that were endemic to the Indian Ocean and Red Sea, and were well separated genetically from Pacific taxa (Figure 3).

3.3 | Diversity analyses

As expected based on the small number of MOTUs shared among locations (Figure 3, Table 3), β-diversity was high. Dissimilarity summarized across all sites (multiple-site dissimilarity; Baselga, 2012) was β_{SOR} = 0.929, with turnover rather than nestedness accounting for most of the β-diversity (β_{SIM} = 0.889, β_{NES} = 0.040). Pairwise β-diversity values were also high (Figure 4a), with the only notable exception being the two Red Sea populations (Israel–Saudi Arabia, β_{SOR} = 0.167). In the case of the two populations from Taiwan (Dongsha Atoll–Green Island), nestedness accounted for 100% of the observed β-diversity (β_{SOR} = 0.571, β_{SIM} = 0) because all three of the MOTUs found at Dongsha Atoll were also found at the more species-rich Green Island site. There was a significant positive relationship between turnover and geographical distance, with less overlap in species composition (i.e. greater turnover) between

TABLE 2 Taxon richness (S = number of MOTUs) and number of endemic taxa (E) of xeniid octocorals at 13 Indo-Pacific locations estimated using genetic distance thresholds from 0.1%–0.5%. Results presented in Figure 2 and Table 3 are based on 0.3% threshold (shaded). [Red Sea] treats Israel and Saudi Arabia as one location

	Genetic distance threshold (K2p)											
	0.1%			0.2%			0.3%			0.5%		
Location	S	E	%E	S	E	%E	S	E	%E	S	E	%E
Israel (ISR)	9	4	44	7	1	14	6	1	17	4	0	0
Saudi Arabia (SAU)	9	4	44	8	2	25	6	1	17	5	0	0
[Red Sea]	13	12	92	9	8	89	7	5	71	5	2	40
Madagascar (MAD)	16	13	81	14	12	86	12	9	75	12	6	50
Sulawesi (SUL)	19	14	74	18	9	50	18	9	50	16	6	38
Green Island (GRE)	15	7	47	13	6	46	11	3	27	11	2	18
Yonaguni Island (YON)	17	9	53	13	7	54	13	6	46	13	4	31
Dongsha (DON)	3	1	33	3	1	33	3	0	0	3	0	0
Palau (PAL)	3	2	67	3	2	67	3	2	67	3	1	33
Ningaloo (NIN)	2	1	50	2	1	50	2	1	50	2	1	50
Kimberley (KIM)	11	9	82	9	7	78	9	6	67	8	2	25
Lizard Island (LIZ)	9	3	33	9	4	44	7	3	29	6	1	17
Coral Sea (COR)	7	5	71	7	3	43	7	2	43	7	2	29
Heron Island (HER)	11	7	64	11	6	55	10	5	50	9	4	44

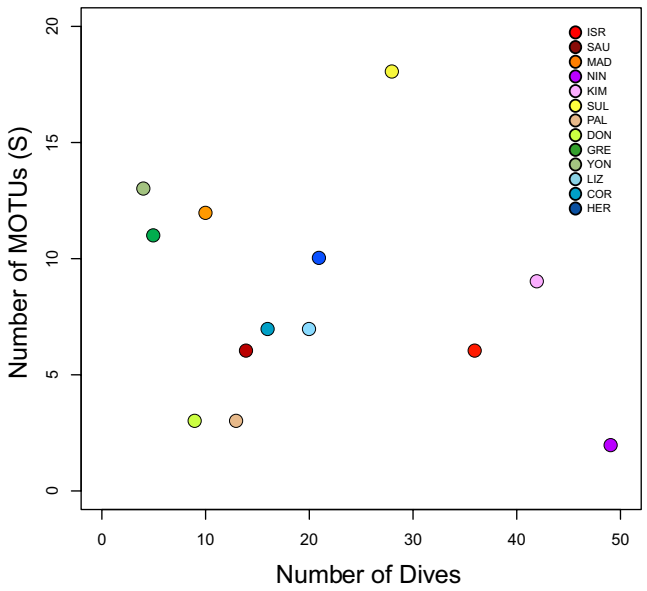

FIGURE 2 Number of molecular operational taxonomic units (MOTUs) (0.3% genetic distance threshold) of xeniid octocorals detected per location as a function of collection effort (number of dives). Coloured circles indicate geographic locations and correspond to Figure 1 [Colour figure can be viewed at wileyonlinelibrary.com]

distant sites (Mantel test, β_{SOR}: $r = 0.448$, one-tailed $p = 0.003$; β_{SIM}: $r = 0.506$, one-tailed $p = 0.004$) (Figure 4a).

Phylogenetic β-diversity (turnover of lineages) was lower than compositional β-diversity (turnover of MOTUs), indicating a high degree of phylogenetic similarity among sites despite the lack of shared taxa (Figure 4a,b). The multiple-site phylogenetic dissimilarity (Baselga, 2012) was Phyloβ_{SOR} = 0.731, with nestedness contributing a higher fraction of the phylogenetic β-diversity (Phyloβ_{SIM} = 0.594, Phyloβ_{NES} = 0.136). There was a significant positive relationship between lineage turnover (Phyloβ_{SIM}) and geographic distance between sites (Mantel test, $r = 0.334$, one-tailed $p = 0.006$) (Figure 4b), but not between Phyloβ_{SOR} and distance ($r = 0.206$, one-tailed $p = 0.067$). Phylogenetic diversity (PD) (Faith, 1992) was strongly correlated with richness, with greater PD present at sites with more MOTUs (Table 4, Figure 5).

Neither the MPD_{OBS} between MOTUs nor the $MNTD_{OBS}$ separating them differed significantly from null models of community assembly at any sites with the exceptions of MPD at Kimberley and Sulawesi (Table 4). At both of these sites the MPD among species was significantly less than expected, suggesting that the species composition includes taxa that are more closely related to one another than expected by chance. A majority of the MOTUs that were

TABLE 3 Numbers of xeniid octocoral molecular operational taxonomic units (MOTUs) (0.3% genetic distance threshold) shared among 13 locations surveyed across the Indo-Pacific. Shaded cells on diagonal indicate MOTUs endemic to a location. S: taxon richness (total number of MOTUs per location). %E: percentage of MOTUs endemic to a location. Location abbreviations: ISR Israel (Red Sea); SAU Saudi Arabia (Red Sea); MAD Madagascar; SUL Sulawesi, Indonesia; GRE Green Island, Taiwan; YON Yonaguni Island, Japan; DON Dongsha Atoll, Taiwan; PAL Palau; NIN Ningaloo Reef, W. Australia; KIM Kimberley, W. Australia; LIZ Lizard Island, Australia; COR Coral Sea Islands Territory, Australia; HER Heron Island, Australia

Site	ISR	SAU	MAD	SUL	GRE	YON	DON	PAL	NIN	KIM	LIZ	COR	HER	%E
ISR	1													17
SAU	5	1												17
MAD	2	2	9											75
SUL	1	1	2	9										50
GRE	1	1	2	5	3									27
YON	1	1	2	5	6	6								46
DON	1	1	1	2	3	1	0							0
PAL	1	1	1	1	1	1	1	2						67
NIN	0	0	0	0	0	0	0	0	1					50
KIM	0	0	0	2	0	0	0	0	1	6				67
LIZ	1	1	1	2	3	3	1	1	0	0	2			29
COR	1	1	1	2	3	3	1	1	0	0	4	3		43
HER	1	1	1	3	3	3	1	1	0	0	4	3	5	50
S	6	6	12	18	11	13	3	3	2	9	7	7	10	72

found at these two sites belonged to clade 5 and to the otherwise relatively uncommon clade 4, while clade 3 was absent from both sites (Figure 3).

Results of hierarchical clustering (see Figure S3 in Appendix S2) and NMDS plots of compositional β-diversity (Sørenson's index of similarity) were identical and grouped sites into four main clusters (Figure 6a). The two Western Australia (eastern Indian Ocean) sites clustered together, well separated from other sites, a difference driven largely by the absence of MOTU01 and shared presence of MOTU08 at those two sites. At a similarity of 20%, all of the remaining sites were grouped into three clusters, consisting of (a) the western Indian Ocean and Red Sea sites, (b) the Great Barrier Reef and three of the western Pacific sites (Sulawesi, Green Island, Yonaguni Island), and (c) the two remaining western Pacific sites—Palau and Dongsha Atoll—both of which had low diversity.

Hierarchical clustering (see Figure S4 in Appendix S2) and NMDS plots of phylogenetic β-diversity (PhyloSor) both recovered relationships among sites that were slightly different from those of compositional β-diversity, suggesting that Heron Island is more closely affiliated phylogenetically with the western Pacific sites [SUL–GRE–YON] than with the other Great Barrier Reef populations, and separating Palau and Ningaloo from all other sites (Figure 6b). Palau and Ningaloo both had low diversity, but harboured several MOTUs belonging to relatively uncommon phylogenetic lineages that were shared with few other locations (Figure 3). Although Dongsha Atoll had similarly low diversity, all of the MOTUs found there were shared with Green Island and other locations.

4 | DISCUSSION

Biogeographic analyses of MOTUs suggest that geographic ranges of xeniid octocorals may be far more restricted than has been assumed previously based on records of Latin binomials derived from taxonomy. Only two of the 67 MOTUs found at sites we surveyed had ranges that spanned both the western Indian and western Pacific Oceans, and only one of those geographically widespread MOTUs also occurred in the Red Sea. This result suggests that those morphospecies that have been reported to occur across broad geographic ranges need to be re-examined, and that widespread, commonly encountered morphospecies are likely to comprise complexes of morphologically cryptic, regionally endemic species. These include three morphospecies whose type locality is the Red Sea but that

FIGURE 3 Maximum likelihood phylogeny of multi-locus (*mtMutS+COI+28S*) barcodes from xeniid octocorals collected in 13 regional biodiversity surveys. Nodes have been collapsed to show only molecular operational taxonomic units (MOTUs) separated by >0.3% genetic distance; numbers at nodes are bootstrap support values (>50%, shown for major clades only). Coloured circles at branch tips indicate geographic location(s) at which each MOTU was collected (colours correspond to Figure 1). Numbered grey circles identify major clades of xeniids (see text). IN: Red Sea–Indian Ocean clade [Colour figure can be viewed at wileyonlinelibrary.com]

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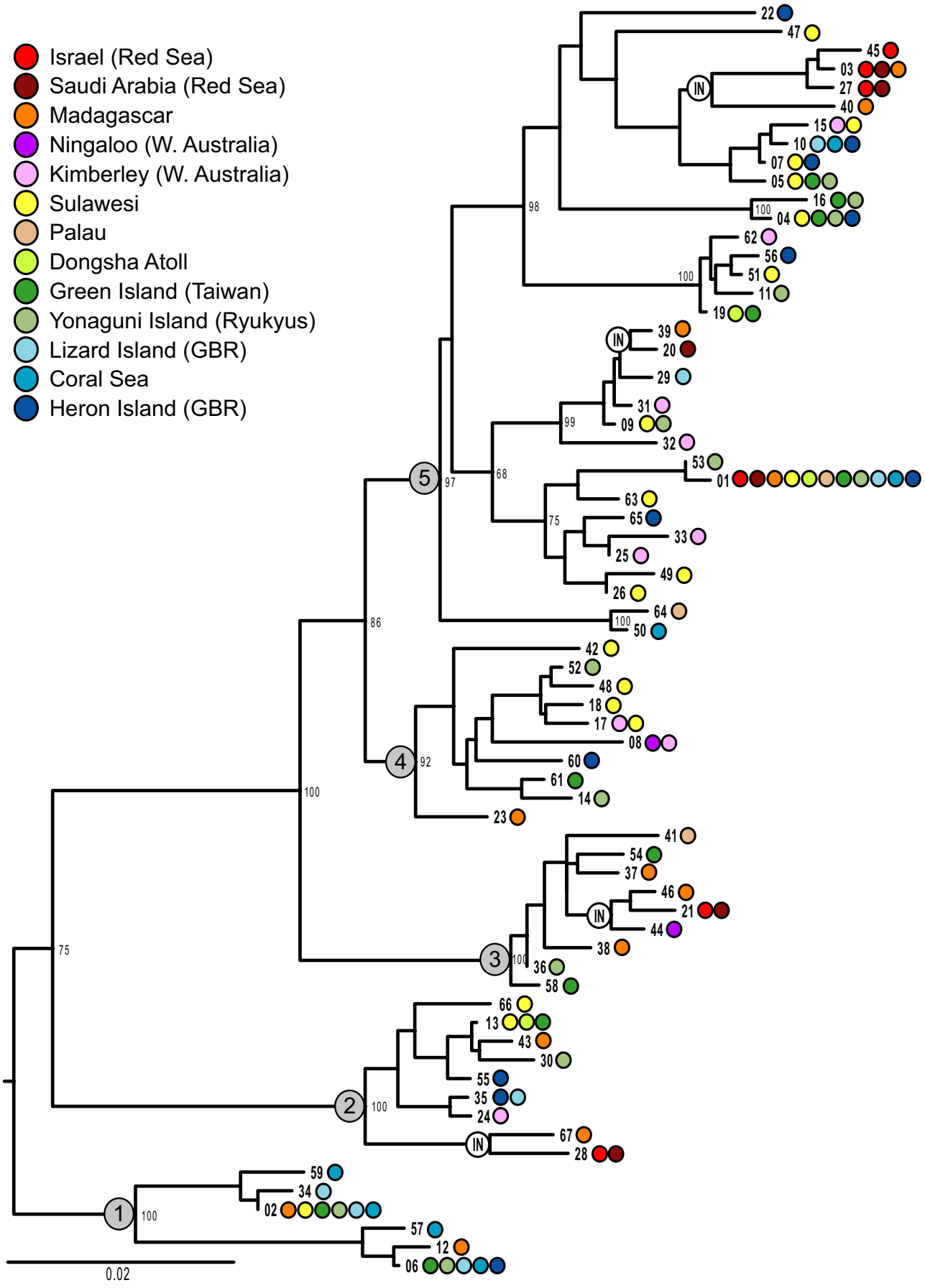

have subsequently been reported from throughout the Indo-Pacific: *Anthelia glauca* Lamarck, 1816, *Sympodium caeruleum* Ehrenberg, 1834, and *Xenia umbellata* Lamarck, 1816 (e.g. Benayahu, Shlagman, & Schleyer, 2003; McFadden, Reynolds, et al., 2014; Roxas, 1933; Schenk, 1896; Utinomi, 1977; Verseveldt, 1971, 1977). Our analysis included specimens that had previously been assigned to each of those three species based on classical taxonomic identification (Haverkort-Yeh et al., 2013; McFadden et al., 2011; McFadden, Brown, et al., 2014; McFadden, Reynolds, et al., 2014). Specimens assigned to *A. glauca* (MOTU 28), to *S. caeruleum* (MOTU 21) and to *X. umbellata* (MOTU 27) that were collected from the two Red Sea sites, however, belonged to MOTUs that were found only in the Red Sea and were genetically well separated from all other MOTUs that had been identified as those same morphospecies (Figure 3, Table S1 in Appendix S1). Although *S. caeruleum* has been widely considered to be the only valid species in the genus *Sympodium*, a 0.3% genetic distance threshold delineated nine distinct MOTUs within that clade (clade 3), several of which were distributed sympatrically (Figure 3). This result strongly suggests that *S. caeruleum* is a cryptic species complex, and that additional species of *Sympodium* need to be formally described. Specimens of *A. glauca* and *X. umbellata* collected from anywhere other than the Red Sea also need to be re-examined and potentially assigned to new taxa.

In stark contrast to these Red Sea endemics, the MOTU that included *Heteroxenia fuscescens* (Ehrenberg, 1834) (MOTU 01), also originally described from the Red Sea, was the most widely distributed MOTU we encountered, present at 11 of 13 locations (absent only from the two sites in Western Australia). The broad geographic distribution inferred for this species holds even when the much less conservative genetic distance threshold of 0.1% is used to delimit species. *Heteroxenia fuscescens* was the only xeniid species for which the molecular evidence suggested a truly pan-Indo-Pacific distribution. All xeniids studied so far are brooders whose planula larvae spend little or no time in the planktonic stage (Kahng et al., 2011; and references therein). Nonetheless, the planulae of *H. fuscescens* and some other species have demonstrated the ability to survive and remain competent to metamorphose for longer than a month in the laboratory when denied access to appropriate settlement cues, suggesting that long-distance dispersal could occur (Ben-David-Zaslow & Benayahu, 1996, 1998; Yacobovitch, Weis, & Benayahu, 2003). It is currently unknown why the geographic range of H. fuscescens is apparently so much greater than that of other brooding xeniids. Unlike most other xeniids, however, *H. fuscescens* is hermaphroditic and planulates throughout the year (Benayahu, 1991), reproductive traits that perhaps adapt it well to establish itself in new areas if a rare, long-range larval dispersal event occurs. *H. fuscescens* is also unusual among xeniids in producing azooxanthellate planulae that acquire symbionts horizontally from the environment at early metamorphosis (Benayahu, Achituv, & Berner, 1989). Acquisition of zooxanthellae from the external environment could increase the survival and fitness of *H. fuscescens* larvae that disperse to new environments if they acquire a strain of symbiont that is well adapted to the local regime (Byler, Carmi-Veal, Fine, & Goulet, 2013).

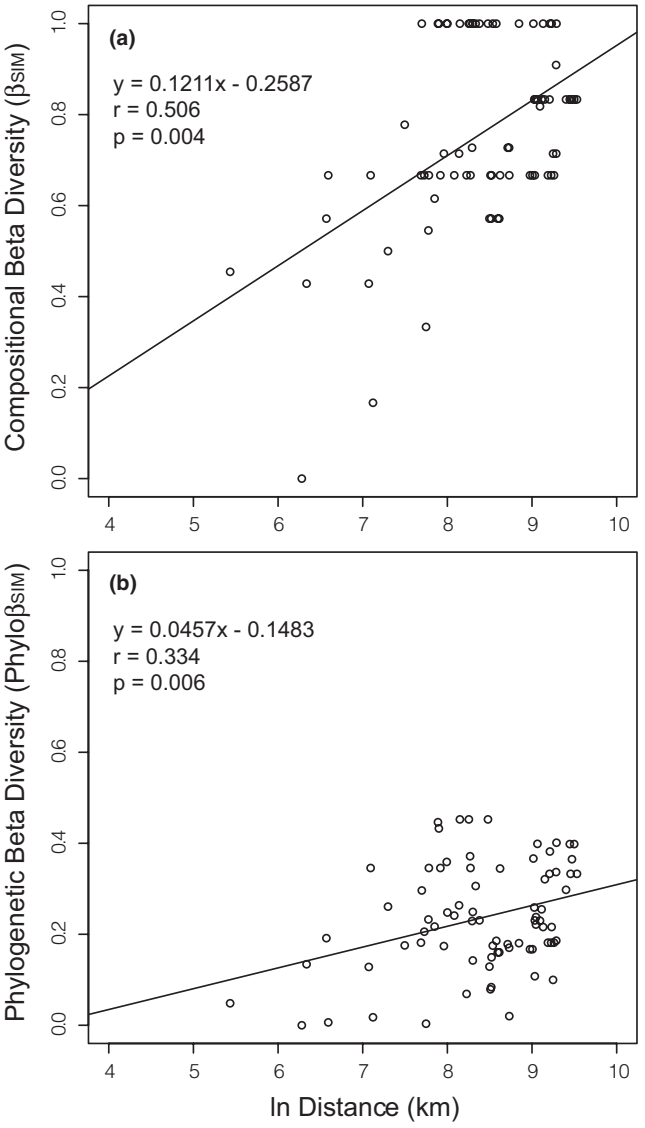

FIGURE 4 Pairwise values for (a) compositional β-diversity (β_{SIM} = turnover) and (b) phylogenetic β-diversity ($Phylo\beta_{SIM}$) of xeniid octocoral assemblages as a function of geographic distance between sites

4.1 | Limitations of threshold-based species delimitation

The use of simple genetic distance measures to delimit species is fraught with problems, especially in groups of organisms for which clear barcode gaps are lacking (Meyer & Paulay, 2005). Use of single- or multilocus molecular barcodes either to identify or to discover species has been particularly problematic in anthozoan cnidarians as a result of their very low rates of mitochondrial gene evolution, with congeneric morphospecies often sharing identical barcode sequences (Huang, Meier, Todd, & Chou, 2008; McFadden et al., 2011; Shearer & Coffroth, 2008). The ability to test the efficacy of multilocus barcodes for species delimitation in octocorals has been further hampered by a poor understanding of interspecific and intraspecific morphological variation in

TABLE 4 Measures of phylogenetic diversity among molecular operational taxonomic units (MOTUs) (0.3% genetic distance threshold) of xeniid octocorals collected at 13 locations spanning the Indo-West Pacific. S = taxon (MOTU) richness; PD = Faith's (1992) phylogenetic diversity; MPD_{obs} = observed mean pairwise distance among MOTUs; $MNTD_{obs}$ = observed mean nearest taxon distance among MOTUs; SES_{MPD} = standardized effect size for MPD compared to values generated for null communities (runs = 999); SES_{MNTD} = standardized effect size for MNTD compared to values generated for null communities (runs = 999). *: $p < 0.05$

Site	S	PD	MPD_{obs}	SES_{MPD}	$MNTD_{obs}$	SES_{MNTD}
ISR	6	0.214	0.0707	0.496	0.0405	0.284
SAU	6	0.225	0.0727	0.743	0.0404	0.215
MAD	12	0.307	0.0729	1.220	0.0262	0.351
NIN	2	0.118	0.0589	−0.234	0.0589	−0.221
KIM	9	0.231	0.0522	−1.882*	0.0275	−0.436
SUL	18	0.307	0.0555	−1.951*	0.0172	−0.223
GRE	11	0.289	0.0681	0.404	0.0303	0.712
YON	13	0.308	0.0639	−0.303	0.0261	0.650
DON	3	0.155	0.0791	0.749	0.0623	0.619
PAL	3	0.145	0.0580	−0.453	0.0493	−0.194
LIZ	7	0.220	0.0718	0.681	0.0310	−0.611
COR	7	0.192	0.0666	0.127	0.0224	−1.521

this group. In cases where genetic distance-based assessments of species boundaries are in disagreement with morphospecies identifications, it often cannot be determined if the molecular markers are inadequate for species delimitation, if interpretations of morphological characters and ranges of intraspecific morphological variation are flawed, or both. Nonetheless, studies in a number of different octocoral taxa have suggested that threshold- or character-based barcodes typically can discriminate 80% or more of morphospecies, and allow species identification to be narrowed to a small number of sister taxa (Baco & Cairns, 2012; Benayahu, van Ofwegen, Dai, et al., 2018; McFadden et al., 2011; McFadden, Brown, et al., 2014).

In previous studies based on the same multilocus barcode used here, application of a 0.3% genetic distance threshold yielded the highest concordance between morphospecies identifications and MOTUs (McFadden, Brown, et al., 2014; McFadden, Reynolds, et al., 2014). Results of the present study suggest that that threshold value may be somewhat conservative. Among specimens from the Red Sea (Israel and Saudi Arabia) assigned morphologically to the genus *Ovabunda* (see Table S1 in Appendix S1), the 0.3% threshold delimited two MOTUs (03, 45) while an even more conservative 0.5% threshold lumped species belonging to two morphologically distinct genera, *Ovabunda* and *Xenia*, into a single MOTU. A recent species delimitation study based on several single-copy nuclear genes and hundreds of single-nucleotide polymorphisms derived from restriction site-associated DNA sequencing clearly differentiated *Ovabunda* from *Xenia*, and provided strong support for four species of *Ovabunda* among the specimens included here (McFadden et al., 2017), the same number suggested by application of a 0.2% genetic distance threshold. The least conservative threshold we applied, 0.1%, overestimated the diversity, suggesting eight *Ovabunda* species. Although the 0.2% genetic distance threshold came closest to estimating what appears to be the actual diversity of this particular clade, every clade has its own history of genetic diversification and speciation, and it is unlikely that a single threshold value will ever be applicable across all clades (Hickerson, Meyer, & Moritz, 2006; Meyer & Paulay, 2005).

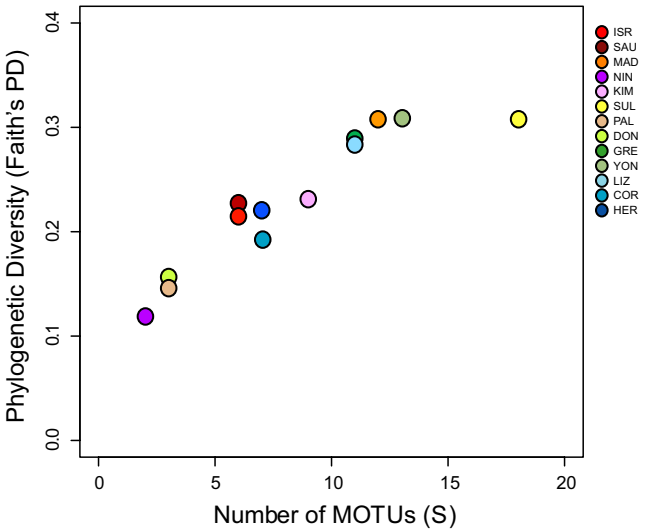

FIGURE 5 Relationship between phylogenetic diversity (Faith's PD) and richness (number of MOTUs, 0.3% genetic distance threshold) of xeniid octocoral assemblages at 13 locations in the Indian and western Pacific Oceans. Coloured circles indicate geographic locations and correspond to Figure 1 [Colour figure can be viewed at wileyonlinelibrary.com]

4.2 | Biogeography and community assembly

Whether or not the MOTUs we have defined here represent species, they are at least genetically differentiated populations from which we can begin to understand the biogeographic distribution of genetic variation and the processes that generate biodiversity. Although our sampling of locations across the Indo-Pacific is relatively sparse so far, the biogeographic pattern that is emerging for xeniids is in general agreement with that shown for scleractinian corals (Huang et al., 2018; Hughes et al., 2002), namely that

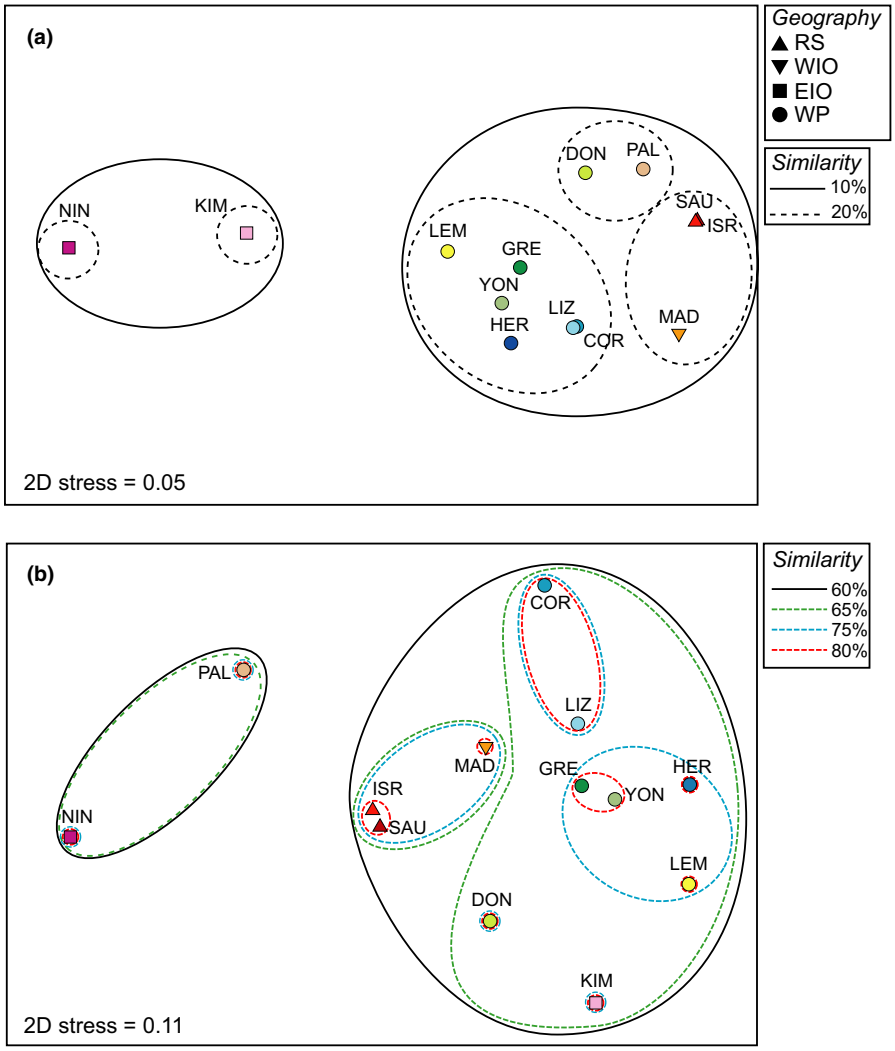

FIGURE 6 Non-metric multidimensional scaling (NMDS) plots of (a) compositional β-diversity (Sørenson's index of similarity) and (b) phylogenetic β-diversity (PhyloSor) of xeniid octocoral assemblages at 13 locations in the Indo-West Pacific. Coloured circles indicate geographic locations and correspond to Figure 1. Triangles: Red Sea and W. Indian Ocean; squares: E. Indian Ocean (Western Australia); circles: W. Pacific Ocean and Great Barrier Reef [Colour figure can be viewed at wileyonlinelibrary.com]

although species richness is highest in the Coral Triangle (represented here by Sulawesi), endemicity peaks in isolated, peripheral regions such as the Red Sea (e.g. DiBattista et al., 2015, 2016), Madagascar and Western Australia (Roberts et al., 2002) (Table 2). Analyses based on the estimated ages of scleractinian lineages suggest that this pattern can be explained by a combination of higher speciation rates and lower extinction rates in peripheral populations, coupled with range expansion into the centre of diversity (Huang et al., 2018). In the absence of any fossil record or estimates of lineage ages for the group, whether or not these same dynamics might explain the observed distribution of xeniid biodiversity cannot currently be tested.

The high turnover in species composition (β-diversity) and high endemicity we observed among xeniid communities may reflect the action of evolutionary processes (e.g. in situ diversification with dispersal limitation) or ecological factors that differ among locations (e.g. environmental filters) (Graham & Fine, 2008). Our sampling design does not allow us to address the role of environmental filtering explicitly, as we did not intend to sample across any known environmental gradients. However, the significant distance decay relationships we observed for both β-diversity and phylogenetic β-diversity (Figure 4) suggest that dispersal limitation may play a role in generating the biogeographic patterns observed among xeniids, at least at the scale over which we have sampled. Moreover, PD within communities did not differ from the expectations of a null model of community assembly (Table 4), indicating that the taxon composition at most sites was comprised of a random assemblage with no over- or under-representation of particular clades. Combined, these observations support the role of neutral (stochastic) processes in the generation of xeniid assemblages, that is, assemblages consist of random taxa that are ecologically equivalent. Neutral theory posits further that ecologically equivalent species are most likely to evolve in species-rich communities that are dispersal and recruitment limited (Hubbell, 2006), as appears to be the case here. The occurrence of all major phylogenetic lineages of xeniids within each distinct biogeographic region (western Indian Ocean–Red Sea, eastern Indian Ocean, western Pacific–Great Barrier Reef) also suggests that there has been no differential extinction among clades to eliminate deep lineages from particular regions.

The geographic scale over which the composition of xeniid assemblages varies is in some cases surprisingly small. For example, Green I. (Taiwan) and Yonaguni Island (Japan) are only 250 km apart, yet fewer than half of the MOTUs found at these two sites were

shared between them, and six of the 13 MOTUs found at Yonaguni were endemic to that location (Table 3). This difference suggests either that (a) environmental conditions differ significantly between these two islands and they support different assemblages of xeniids as a result, or (b) there is limited dispersal between them despite their relative proximity. Regardless of the processes responsible, the fact that geographically proximate sites support such different species assemblages emphasizes the importance of small-scale biogeographic distributions to our understanding and management of biodiversity in Indo-Pacific coral reef communities.

5 | CONCLUSIONS

In macroinvertebrates such as the conspicuous and ecologically important octocorals, morphological variation is often difficult to interpret and may not reflect species boundaries. As a result, inferring species occurrences and ranges from traditional taxonomic records of morphospecies may lead to erroneous conclusions about patterns of biodiversity, and impede understanding of their underlying causes. Based on the taxonomic literature for xeniid octocorals, some species would appear to be broadly distributed throughout the Indo-Pacific, with geographic ranges spanning the Great Barrier Reef to the Red Sea (e.g. McFadden, Reynolds, et al., 2014; Roxas, 1933; Schenk, 1896; Utinomi, 1977; Verseveldt, 1977). The relatively crude genetic proxy for species we have used here suggests instead a different pattern, in which most xeniids are narrow-range endemics and very few occupy broad geographic ranges. The large number of MOTUs we found at only a single location (likely to be regional or local endemics) and the high turnover in MOTU composition among sites also suggest that the diversity of this family is likely to be considerably higher than currently estimated based on the number of morphospecies. Similar genetics-based biogeographic studies of the many other coral reef invertebrates whose taxonomy is as or more poorly known than that of octocorals are necessary for further understanding of the patterns and processes underlying diversification of coral reef fauna, and the impacts of ongoing environmental change on the distribution of that biodiversity (e.g. LeRay & Knowlton, 2016).

Molecular approaches such as those applied here to octocorals and elsewhere to other groups (e.g. Huang et al., 2018; LeRay & Knowlton, 2016; Pante et al., 2015; Plaisance, Caley, Brainerd, & Knowlton, 2011) can illuminate patterns of biodiversity and their generation that may be obscured by the application of traditional morphology-based identification in taxonomically challenging groups such as octocorals. Nonetheless, most of our current knowledge of species' ranges and biogeographic patterns is based on taxonomic records from the past two centuries of exploration. To verify and re-evaluate the identity of specimens now recognized to belong to morphologically cryptic taxa—or groups within which species concepts have simply been altered by the application of modern morphological or molecular methods—it will be necessary to thoroughly re-examine specimens curated in natural history collections. Development of technologies to sequence ancient and highly degraded DNA from museum specimens and to reinterpret relevant morphological features using advanced imaging techniques (e.g. high-resolution microscopy, micro-CT scanners, etc.) is facilitating our ability to revisit historical species identifications and to revise the biogeographical information that arises from them (e.g. Benayahu, van Ofwegen, & McFadden, 2018). For groups such as xeniid octocorals for which it is challenging to assign Latin binomials reliably to most species, obtaining DNA sequence data from existing types and other historical material will facilitate the association of morphospecies names with MOTUs. In addition, identification of morphological character sets that are congruent with MOTUs may allow newly collected material to be matched to historical vouchers. For records that exist solely in the literature, however—whether because physical vouchers have been lost or were never taken—it may never be possible to verify the identity of species that were recorded or to reconcile names with the species concepts that are emerging from today's modern integrative taxonomic approaches. In those cases, the occurrence of species at particular geographic locations can only be confirmed by new collections.

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DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.5r59p06

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BIOSKETCH

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SUPPORTING INFORMATION

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

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