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Mar Biodiv (2015) 45:157–168
DOI 10.1007/s12526-014-0236-1

SENCKENBERG

ORIGINAL PAPER

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Received: 14 November 2013 / Revised: 29 April 2014 / Accepted: 29 April 2014 / Published online: 17 May 2014

Abstract The South China Sea in the Central Indo-Pacific is a large marine region that spans an area of more than 3 million km^2 bounded by the coastlines of ten Asian nation states and contains numerous small islands. Although it abuts the western border of the Coral Triangle, the designated centre of maximum marine biodiversity, the South China Sea has received much less scientific and conservation attention. In particular, a consolidated estimate of the region's scleractinian reef coral diversity has yet to emerge. To address this issue, we assemble a comprehensive species distribution data set that comprises 16 reef areas spread across the entire South China Sea. Despite containing less than 17 % of the reef area as compared to the Coral Triangle, this region hosts 571 known species of reef corals, a richness that is comparable to the Coral Triangle's based on a standardised nomenclatural scheme. Similarity profile analysis and non-metric multidimensional scaling demonstrate that most areas are compositionally distinct from one another and are structured according

Electronic supplementary material The online version of this article (doi:10.1007/s12526-014-0236-1) contains supplementary material, which is available to authorized users.

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to latitude but not longitude. More broadly, this study underscores the remarkable and unexpected diversity of reef corals in the South China Sea.

Keywords Coral reefs · Coral Triangle · Indo-Pacific · Latitudinal gradient · Scleractinia · Species richness

Introduction

The South China Sea (SCS) is a region in the Central Indo-Pacific marine realm (Spalding et al. 2007) covering an area of more than 3 million km^2 (Morton and Blackmore 2001; UNEP 2004). Its southwestern sector is situated on the shallow Sunda Shelf, while the central and northeastern areas consist of a deep basin reaching just over 5 km below sea level (Morton and Blackmore 2001; Xu and Malanotte-Rizzoli 2013). The coastlines of the surrounding major land masses and over 200 small islands within it (Ng and Tan 2000) provide suitable conditions for the growth and development of coral reefs (UNEP 2004). These include features such as Reed Bank, an extensive 100-km long barrier reef reaching 20 m below the surface that runs parallel to the Philippine island of Palawan (Taylor and Hayes 1983).

Many of the coral reefs fringing the major land masses are threatened by coastal development and overexploitation (McManus 1997; Kimura et al. 2008; Tun et al. 2008; Burke et al. 2011), while those of less inhabited island clusters such as the Spratly and Paracel islands are probably under less threat (but see McManus 1994; McManus and Meñez 1997). Initiatives are underway to protect healthy reefs and restore degraded ones (Pitcher et al. 2000; Aliño 2001; Ablan et al. 2002; Chou et al. 2009; Pernetta 2009; McManus et al. 2010; Vo et al. 2013), but thorough understanding of species richness patterns is an imperative for solving this biodiversity crisis. In recent years, the SCS has been receiving less conservation attention than the adjacent Coral Triangle (Clifton 2009; Burke et al. 2012; Napitupulu et al. 2012), mainly because spatial analyses generally show the latter to contain the world's highest numbers of reef corals, fishes and several other taxa (Allen and Werner 2002; Carpenter and Springer 2005; Hoeksema 2007; Allen 2008; Veron et al. 2009; Sanciangco et al. 2013). Not surprisingly, reef areas in the eastern SCS that are also part of the Coral Triangle, such as El Nido, have been on high priority for conservation action (Hodgson and Dixon 2000; Flower et al. 2013).

Many hurdles stand in the way of accurate diversity estimates for the SCS, including its areal vastness, its span of ten nation states, as well as overlapping territorial claims and conflicts (McManus 1994; Djalal 2000; Ng and Tan 2000; Talaue-McManus 2000; Morton and Blackmore 2001). Nevertheless, biodiversity studies have been carried out for many marine groups, including annelids (Paxton and Chou 2000), molluscs (Norman and Lu 2000; Sachidhanandam et al. 2000; Tan 2000), crustaceans (Jones et al. 2000; Komai 2000; Lowry 2000; Moosa 2000; Rahayu 2000), echinoderms (Lane et al. 2000), sponges (Hooper et al. 2000) and fish (Randall and Lim 2000), most of which document considerable proportions of global richness. For example, over 3,000 species of fish are known from the SCS (Randall and Lim 2000), a richness comparable to that of the Coral Triangle, estimated to be 3,000–4,000 (Burke et al. 2012).

Surprisingly, the diversity of scleractinian reef corals across the entire SCS is, as yet, unknown. UNEP (2004) estimates that the SCS supports about 20 % of Southeast Asia's reefs and more than half of its coral species. Species richness is reported to vary widely, from 12 to 351, across 50 locations with hotspots at Nha Trang (Vietnam) and El Nido (Palawan). Unfortunately, the UNEP report does not provide any species-level inventories for further analysis. The Coral Geographic database contributed by Veron et al. (2009, 2011) provides species records for the offshore reefs of the South China Sea ecoregion, and separately for the Gulf of Thailand, southern Vietnam, northern Vietnam, Hainan, Hong Kong and Taiwan, totalling 487 species. However, these do not take into account records from the southwestern and Philippines sectors of the SCS as well as numerous studies at the local scale (Table 1). As a result, the actual coral diversity of this region remains unclear.

These are exciting times for coral biodiversity research. Modern developments in phylogenetics have led to a multitude of taxonomic revisions, in many instances based on specimens collected from the SCS (Fukami et al. 2008; Huang et al. 2009a, 2011a, 2014; Stefani et al. 2011; Lin et al. 2011, 2012a, b; Benzoni et al. 2012a, 2014; Pichon et al. 2012; Keshavmurthy et al. 2013). New species are also being discovered (e.g., Latypov 2006; Hoeksema 2009, 2014; Licuanan and Aliño 2009; Benzoni et al. 2014) and new distribution records documented (e.g., Hoeksema 2009; Hoeksema and Koh 2009; Hoeksema et al. 2010). This study takes advantage of these developments by reviewing coral species records associated with various areas within the SCS (from published and grey literature), incorporating newly described species, and assembling a distributional data set based on current taxonomy. Such an approach can yield critical insights on biogeography and conservation, particularly for regions that until recently have been understudied for corals (e.g., Pichon 2007; Pichon and Benzoni 2007; Wafar et al. 2011; Obura 2012a, b). Therefore, we expect the data and analyses to further our understanding of the biodiversity in this large marine region.

Materials and methods

We consolidated species records of scleractinian reef corals from literature for various areas in the SCS (Table 1).

Table 1 South China Sea reef areas examined in this study

Code	Area	Richness	Sources
SG	Singapore	255	Huang et al. 2009b
MY	West Malaysia (Middle Rocks and eastern Peninsular Malaysia)	398	Harborne et al. 2000; Fenner 2001; Harding et al. 2003; Affendi et al. 2005, 2007; Yusuf and Affendi 2009; Affendi and Rosman 2012
TH	Thailand	264	Srithunya et al. 1981; Jiravat 1985; Sakai et al. 1986; Chou et al. 1991; Yeemin et al. 1994; Yeemin 2001, 2002, 2003; Putchim et al. 2002; Chankong 2006; Saenghaisuk and Yeemin 2009; Kongjandtre et al. 2010, 2012; Hoeksema et al. 2012; Wallace et al. 2012b
VN1	southwestern Vietnam	251	Latypov 1986, 2006, 2011; Vo and Hodgson 1997
VN2	southern Vietnam	398	Vo and Hodgson 1997; Vo and Phan 1997; Vo 1998; Vo et al. 2004; 1 Latypov 2006, 2011, 2012, 2013; Hoeksema et al. 2010; Phan 2012
VN3	central Vietnam	252	Vo and Hodgson 1997; Latypov 2006, 2011; Phan and Vo 2010; Vo and Nguyen 2010
VN4	northern Vietnam	176	Vo and Hodgson 1997; Latypov 2006, 2011
PA	Paracel Islands (Paracel Islands and Macclesfield Bank)	201	Wells 1935; Hoeksema 1989; Huang et al. 2006, 2011b; Shen et al. 2013
CN1	southern China (Weizhou, northwest Hainan, Sanya and Xuwen)	102	Huang et al. 2009c, 2011c, 2012b; Chen et al. 2010
CN2	southeastern China (Wanshan Islands, Hong Kong and Dongshan)	95	Ang et al. 2003; Huang et al. 2012a, c
BN	Brunei	391	Turak and DeVantier 2011
SA	western Sabah (Labuan, Pulau Tiga and Kota Kinabalu)	248	Nyanti and Johnston 1992; Waheed et al. 2012; Hoeksema 2014; Awang and Chan 2014; Waheed and Hoeksema 2014
SP	Spratly Islands	333	Dai and Fan 1996; Nguyen and Dang 2008; Latypov 2011; Huang et al. 2012d
PL	northern Palawan (El Nido)	398	Turak and DeVantier 2010
LZ	western Luzon (Batangas, Bolinao and Anda)	433	Licuanan 2009; DeVantier LM and Turak E, unpublished data
TW	Taiwan (Taiwan and Pratas Islands)	316	Dai 1991; Chen 1999; Li et al. 2000; Dai and Horng 2009a, b

Supraspecific taxonomy was based primarily on the species concepts of Veron (2000), with recent updates by Wallace et al. (2007), Dai and Horng (2009a, b), Licuanan (2009), Gittenberger et al. (2011), Benzoni et al. (2012a, b), Budd et al. (2012) and Huang et al. (2014). Species records were also standardised according to the synonymies defined by various workers (Yabe and Sugiyama 1932; Scheer and Pillai 1974; Veron et al. 1977; Veron and Pichon 1976, 1980, 1982; Veron and Wallace 1984; Sheppard 1987; Hoeksema 1989; Veron and Hodgson 1989; Wallace 1999; Veron 2000, 2002; Ditlev 2003; Dai and Horng 2009b; Benzoni et al. 2010; Arrigoni et al. 2012; Wallace et al. 2012a). The full data set and detailed list of synonyms are available as a supplementary Online Resource.

To explore the structure of reef coral diversity in the SCS, we first carried out a similarity profile analysis (SIMPROF; Clarke et al. 2008) on the presence/absence data. On the basis of the Bray-Curtis similarity index (Bray and Curtis 1957) computed among sites, we used the R package *clustsig* (Whitaker and Christman 2010) to generate 1,000 expected and simulated profiles each to test for the number of hierarchical clusters linking all the areas. No a priori groups were assumed.

Non-metric multidimensional scaling (NMDS; Kruskal 1964a, b; Minchin 1987) was then performed using the Bray-Curtis distances, allowing up to 10,000 random starts to find stable solutions. This was separately done in two and three dimensions. We also investigated the role of geographic location in structuring species distribution by fitting the areas' mid-point latitude and longitude as vectors onto the NMDS plots. Significance of the vectors was assessed using 10,000 random permutations. Ordination analyses were carried out in the R package *vegan* (Oksanen et al. 2013).

Finally, we computed sea surface and reef areas that are encompassed by the SCS and the adjacent (and marginally overlapping) Coral Triangle using base data published by Burke et al. (2011), in which reef locations were compiled as gridded data at a resolution of 500 m. Map projection was carried out following the original study—cylindrical equal-area projection by Lambert (1772) with central meridian at 160°W.

Results

The data set assembled here spans the entire geographic range of the SCS, from the lowest latitude reefs of Singapore to the northern and easternmost communities of Dongshan (south-eastern China) and Taiwan (Fig. 1). Species records cover

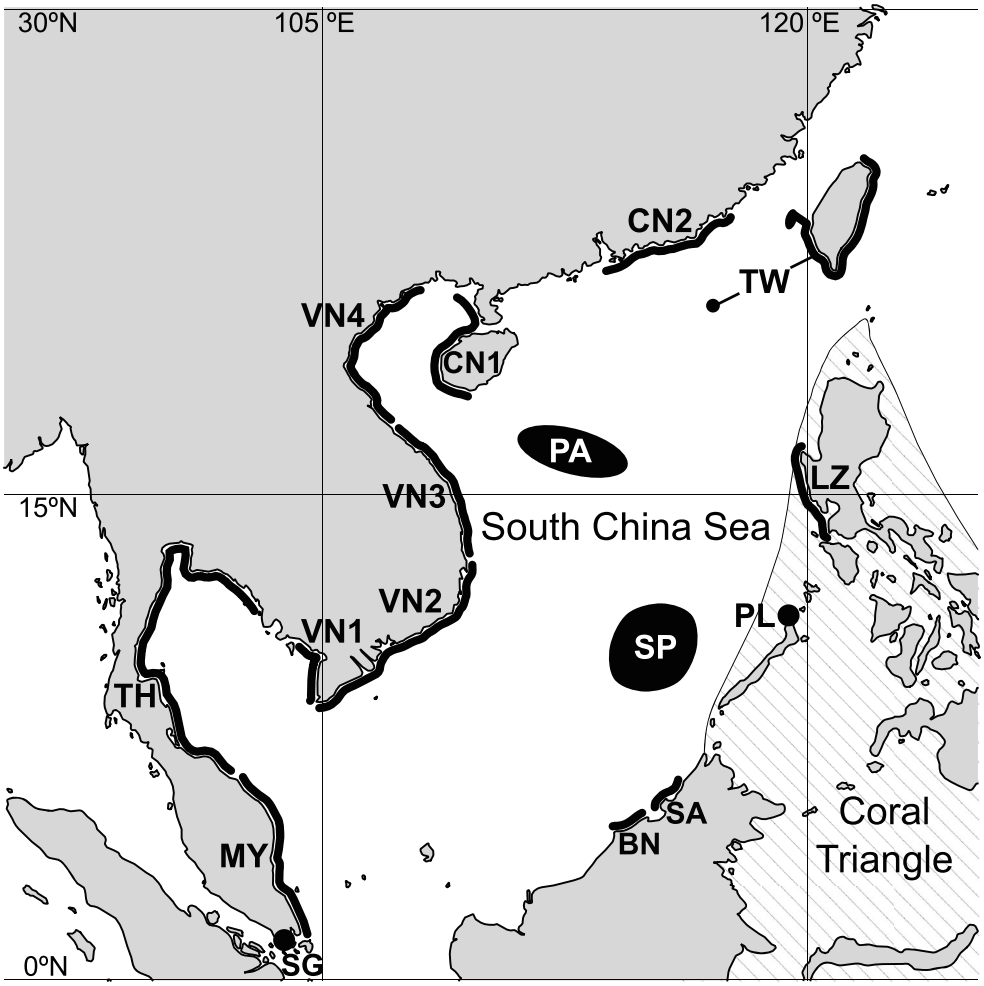

Fig. 1 Map of the South China Sea and part of the Coral Triangle, showing reef areas examined in this study as defined in Table 1

most of the western continental coast, but data are more patchy on the east side, comprising the northwest coast of Borneo and western shores of the Philippine islands. Notable gaps in species-level information include the coasts of Cambodia with a short coastline (~70 species according to Spalding et al. 2001), Sarawak with many large river outlets, southern Palawan, and northwestern Luzon.

The total number of reef coral species recorded in all of the areas is 571. Richness ranges from 95 at southeastern China, one of the northernmost areas, to 433 species in western Luzon (Table 1). Areas on the southeast Asian continent typically harbour moderate to high species counts (251–398 species) up to 17°N latitude (central Vietnam). From there, richness attenuates sharply northwards; pooling of all the Chinese mainland sites only results in 151 species. To the east, diversity remains moderate to high (≥ 248 species) in Brunei, western Sabah, Philippines, and even Taiwan (including Pratas Islands to its southwest). Note that data from Taiwan encompass records from the northeastern part of the main island, which is more often considered as part of the East China Sea. Nevertheless, they are included in this study, as its species composition closely resembles that of Penghu Islands in the Taiwan Strait (Chen 1999).

Because the richness gradient is inevitably influenced by the varying spatial scales of the examined areas, we focus on the similarity profile and ordination analyses to provide a more unbiased interpretation of the distributional patterns.

The SIMPROF analysis reveals 11 significantly distinct groups ($p<0.05$) from the 16 reef areas analysed (Fig. 2a). Only four groups form significant clusters ($p=1$); the Chinese pair of areas (CN1 and CN2) are spatially adjacent to each other, but not the southwest-central Vietnam (VN1 and VN3) and southern Vietnam-Spratlys (VN2 and SP) clusters. The Philippine pair of areas (PL and LZ) are grouped with Brunei (BN). Despite the distinctiveness among most reef areas, two general clusters at similarity index of ~40 have been recovered—the two Chinese areas, and all other areas. The species-poor, non-reef-building communities fringing the coastline of southern and southeastern China (Morton and Blackmore 2001) are characterised by a large proportion of generally massive species in the families Lobophylliidae, Merulinidae and Poritidae (46.4 % vs. 36.3 % for the entire SCS) with far fewer *Acropora* spp. (11.9 % vs. 17.2 % for the entire SCS)—

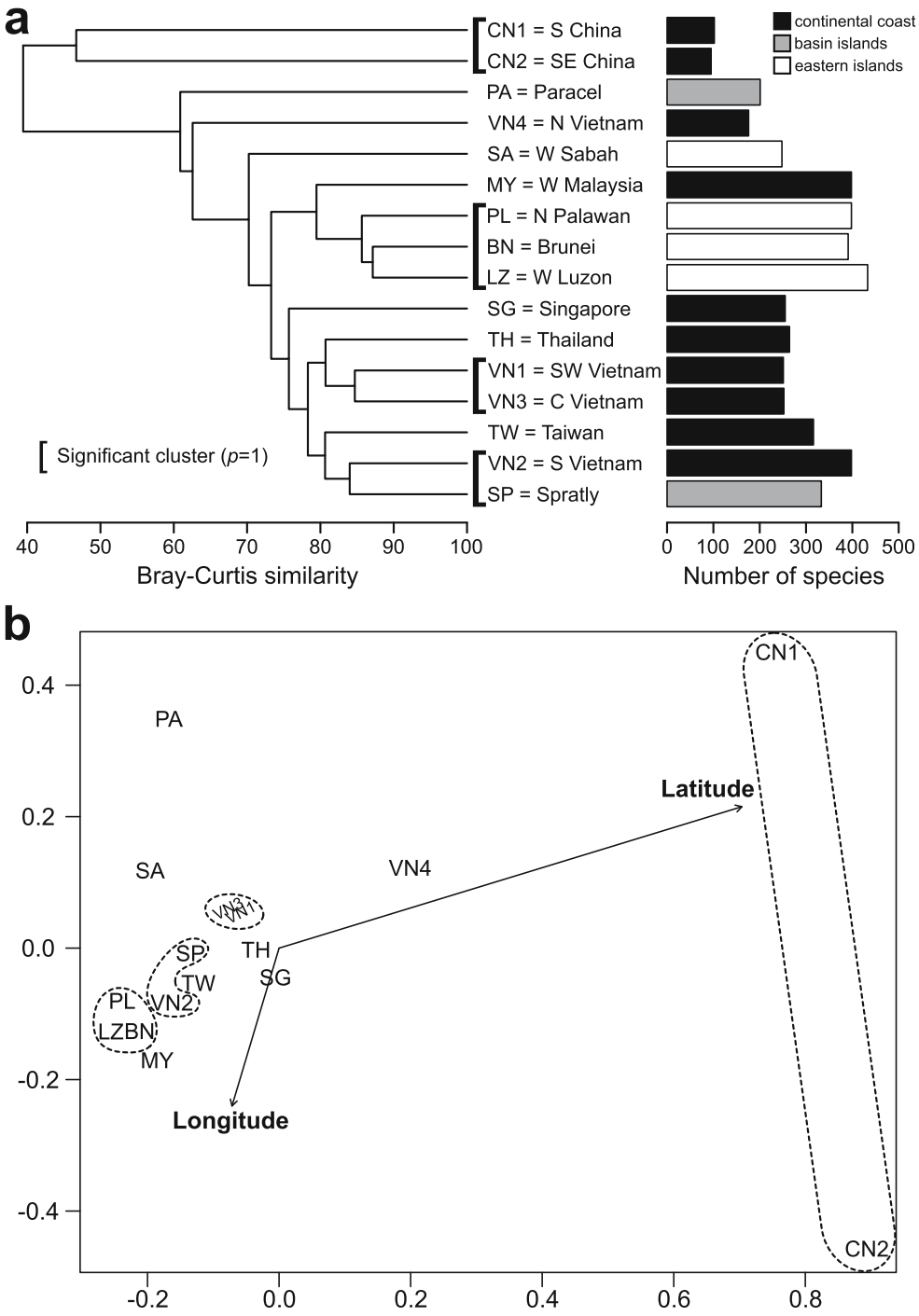

Fig. 2 **a** Similarity profile (SIMPROF) computed from coral presence/absence data for 16 reef areas along with their corresponding species richness, and **b** non-metric multidimensional scaling (NMDS) of reef areas showing effects of latitude (p=0.058) and longitude (p=0.82) in structuring the coral distribution

only 15 and five species in southern and southeastern China, respectively. The low number of species here and moderately high level of chaining confined to all other areas suggest that richness is an important determinant in the clustering pattern.

NMDS shows a broadly consistent picture with the SIMPROF results (Fig. 2b). The two-cluster pattern is clearly discernible on the two-dimensional and three-dimensional plots, which are qualitatively similar to one another even among various pairs of axes. The two-dimensional analysis found two convergent solutions with a good fit of stress 0.046 (Kruskal 1964a) after six attempts and without transforming the data. The three-dimensional scaling achieved an excellent fit of stress 0.024 (Kruskal 1964a) after 12 tries. The two-dimensional analysis found latitude to be a marginally significant vector in structuring the diversity among areas (p= 0.058; three-dimensional scaling p=0.053). Longitude is not significant for both scalings ($p \geq 0.82$), consistent with the richness similarity between the extreme eastern and western

reef areas. It should be noted that most of the low latitude sites have low longitudes due to the shape of the region, although tests for a linear relationship between the two variables—with and without high-latitude areas CN1 and CN2—show non-significance ($p>0.14$). Furthermore, omission of the distinct areas CN1 and CN2 (Fig. 2a) does not recover longitude as a significant factor ($p=0.46$).

Geographically, the SCS has a total surface area of 3.4 million km^2, falling within the range of earlier estimates (Clark and Li 1993; Randall and Lim 2000; Morton and Blackmore 2001). This includes ~12,000 km^2 of reefs, or 4.7 % of the world's total reef surface area. We corroborate the computation by Burke et al. (2012) of the Coral Triangle reef area—nearly 73,000 km^2 (29 % of global)—contained within 5.5 million km^2 of sea surface.

Discussion

The present study assembles the most comprehensive coral data set of the SCS to illustrate its extraordinary richness. At 571 species, total diversity here rivals that of the Coral Triangle, which has been reported by the spatial database Coral Geographic to contain 605 species (Veron et al. 2009, 2011). In fact, subjecting the Coral Geographic to our taxonomic scheme reveals 566 species in the Coral Triangle (see detailed lists of Coral Triangle species and synonyms in the supplementary Online Resource). Herein lies the 'extraordinary' statistic, that the SCS, despite being six times smaller in reef area, is more coral-diverse than the Coral Triangle, the supposed centre of maximum marine biodiversity.

We note that the data used in our analysis are derived from various sources, being accumulated over time by various observers using different species concepts that could result in inflated species numbers. Some records are also not supported by museum collections that enable verification and minimise misidentifications. In contrast, during a survey of eastern Indonesia in the Coral Triangle, approximately 350 coral species were recorded and sampled from nine reef areas (Best et al. 1989). These numbers appear low in comparison to the SCS, but they were obtained after specimens were studied and compared by the same observers, effectively guaranteeing uniformity in species concepts among areas. It is therefore possible that actual species numbers in the SCS are lower than presently reported, as specimens identified as distinct species from different localities and environments become reconciled as ecotypes of the same species.

Total diversity aside, our analyses also uncover a high level of compositional variability within the SCS. At a maximum of 433 species in one area (western Luzon), and with most areas harbouring less than 300 species, including southeastern and southern China ($n=95$ and $n=102$ respectively), variation among areas is expected to be high. Indeed, the SIMPROF analysis recognises 11 distinct groups, with most areas being significantly dissimilar from one another. This variability is also high when comparing the seven ecoregions defined by Veron et al. (2009, 2011) that are fully contained within the SCS—coral faunas range from 94 species in Hong Kong to 435 species in their South China Sea ecoregion. In contrast, each of the 16 Coral Triangle ecoregions is reported to contain over 500 species (Veron et al. 2009, 2011), approaching the total richness. Thus the Coral Triangle has smaller margins for variation among ecoregions as compared to the SCS.

Our analyses demonstrate that latitude is a marginally significant factor in structuring the distribution of corals in the region. Previous analyses have shown that coral richness (Connolly et al. 2003; Obura 2012b) and composition (Bellwood and Hughes 2001) are well predicted by the latitudinal gradient across the Indo-Pacific domain (see Hughes et al. 2013). Results here provide support at a smaller scale within the SCS. Interestingly, species distribution exhibits no significant structure with respect to longitude, and richness is comparable between the extreme eastern and western reef areas. These findings strongly suggest that the general pattern of decreasing diversity with increasing distance from the Coral Triangle (e.g., Briggs 1974; Hughes et al. 2002; Bellwood and Meyer 2009) is modulated by local dynamics specific to the SCS.

Habitat area and diversity are known to play crucial roles in the spatial structuring of coral species (Done 1982; Karlson and Cornell 1998; Cornell and Karlson 2000; Bellwood and Hughes 2001). The coasts of the eastern islands Luzon and Palawan have some of the highest concentration of reefs, while parts of the Asian continental coastline are influenced by high freshwater and terrigenous inputs, and therefore have limited reef development (Morton and Blackmore 2001). The clustering of assemblages reflect this distinction in part, with the Philippine island areas and Brunei grouping together, though not with western Sabah (Fig. 2). However, this pattern belies the marked complexity of the diversity gradient within the SCS basin, as the Paracel and Spratly islands are significantly distinct in richness and composition, neither clustered with each other nor with adjacent reef areas.

Many hypotheses have been proposed to explain the high biodiversity in the Central Indo-Pacific realm, particularly the Coral Triangle region (Rosen 1988; Hoeksema 2007). The most compelling arguments generally involve planktonic larval dispersal via large-scale oceanic circulation. The North and South Equatorial Currents flow westward across the entire tropical Pacific Ocean, transporting larvae into the Central Indo-Pacific (Scheltema and Williams 1983; Scheltema 1986, 1988; Jokiel and Martinelli 1992). Upon arrival at the western Pacific, currents channel oceanic water mainly through the Coral Triangle region, generating complex local circulation patterns associated with the Indonesian Throughflow (Wyrtki 1961; Gordon and Fine 1996; Lukas

et al. 1996; Gordon et al. 2003). Possibly coupled with eustatic fluctuations since the Pleistocene (Voris 2000; Siddall et al. 2003), these lead to changes in population subdivisions that ultimately drive the diversity gradient (Potts 1983; Rosen 1984; McManus 1985; Pandolfi 1992; Veron 1995; Wilson and Rosen 1998; Santini and Winterbottom 2002; Hoeksema 2007).

However, part of the full circulation that connects the western Pacific with the Indian Ocean also goes through the SCS between Vietnam and Borneo (Qu et al. 2005; Humphries and Webb 2008; Xu and Malanotte-Rizzoli 2013). Larvae carried into the SCS via this route are entrained within water masses in complex gyres that form over the Gulf of Thailand and eastern SCS (Qu 2000; Morton and Blackmore 2001; Fang et al. 2002; Xu and Malanotte-Rizzoli 2013), facilitating their settlement and supporting reef diversity (McManus 1994; McManus and Meñez 1997). Circulatory patterns used to explain the Coral Triangle diversity maximum can be invoked for our focal region. Indeed, with greater internal compositional variability and aggregate richness of corals within a considerably smaller reef area, there is reason to suggest that this physical forcing is more pertinent to coral distribution in the SCS than previously thought. This diversity is even more striking considering the relatively recent establishment of the present fauna. During the Late Pleistocene, sea levels were ≥ 40 m below current levels for more than 50 % of the time (Voris 2000; Hoeksema 2007). The Sunda Shelf was thereby exposed, cutting off the marine connection between the SCS and Java Sea, and drastically reducing habitable area in the region (Umbgrove 1947; Veron 1995; Hoeksema 2007). Following the Last Glacial Maximum, corals recolonised the SCS, eventually resulting in the modern distribution (Potts 1983; McManus 1985; Hanebuth et al. 2000; Renema et al. 2008; see also Wood et al. 2014).

Overall, our results do not diminish the biogeographical significance of the Coral Triangle. They certainly should not weaken the scientific justification for its conservation. After all, each of the Coral Triangle ecoregions does contain an exceptionally large number of coral species (> 500), with more records added when specific scleractinian families are targeted (Waheed and Hoeksema 2013). Rather, our goal is to highlight the remarkable diversity of reef corals in the adjacent SCS. Future research may find the western boundary of the Coral Triangle further west inside the SCS than presently established (Veron et al. 2009, 2011), which would be concordant with the delineation by Spalding et al. (2007). Previous richness estimates of the SCS have proven to be exceedingly low (e.g., UNEP 2004), yet we continue to underestimate its diversity because of spatial gaps in our data, such as the less-explored regions of the Spratly Archipelago and northwestern Luzon. Poorly known ecosystems, such as mesophotic reefs (> 40 m depth; see Kahng et al. 2010; Bridge et al. 2012) and caves, have been sources of new species discoveries in recent years (Kahng and Maragos 2006; Hoeksema 2012; Luck et al. 2013), but these have not been studied in the SCS. We thus hope that findings here will motivate scientific explorations that can provide further information relevant to the conservation of this large marine region.

Acknowledgments We thank Emre Turak and Lyndon DeVantier for providing unpublished data. Kari Ellingsen and an anonymous reviewer provided comments that helped improve the manuscript. DH is supported by US National Science Foundation grant DEB-1145043-1145408, POA by Hong Kong RGC GRF 460013, and STV by the Vietnam National Foundation for Science and Technology Development project 106.14-2010.67.

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