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Conservation of reef corals in the South China Sea based on species and evolutionary diversity

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Abstract The South China Sea in the Central Indo-Pacific is a large semi-enclosed marine region that supports an extraordinary diversity of coral reef organisms (including stony corals), which varies spatially across the region. While one-third of the world's reef corals are known to face heightened extinction risk from global climate and local impacts, prospects for the coral fauna in the South China Sea region amidst these threats remain poorly understood. In this study, we analyse coral species richness, rarity, and phylogenetic

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diversity among 16 reef areas in the region to estimate changes in species and evolutionary diversity during projected anthropogenic extinctions. Our results show that richness, rarity, and phylogenetic diversity differ considerably among reef areas in the region, and that their outcomes following projected extinctions cannot be predicted by species diversity alone. Although relative rarity and threat levels are high in species-rich areas such as West Malaysia and the Philippines, areas with fewer species such as northern Vietnam and Paracel Islands stand to lose disproportionately large amounts of phylogenetic diversity. Our study quantifies various biodiversity components of each reef area to inform conservation planners and better direct sparse resources to areas where they are needed most. It also provides a critical biological foundation for targeting reefs that should be included in a regional network of marine protected areas in the South China Sea.

Keywords IUCN Red List · Marine biodiversity · Phylogenetic diversity · Rarity · Scleractinia · Species richness

Introduction

The South China Sea (SCS) is a large and species-rich marine region in the Central Indo-Pacific (Fig. 1). Despite being situated adjacent to the Coral Triangle and hosting comparable levels of biodiversity, including 571 species of scleractinian reef corals (Huang et al. 2015) and over 3000 species of fish (Randall and Lim 2000), this region has received much less research attention. The shortfall in biodiversity research on the SCS needs to be addressed as coral reefs are being destroyed at an alarming rate (Madin 2015).

Besides exhibiting high species diversity, scleractinian corals in the SCS display a remarkable degree of spatial variability in species composition (Huang et al. 2015). The most coral-rich areas of the SCS include western Luzon and southern Vietnam, which contain more than 400 species ($n = 433$ and $n = 406$ respectively; Vo et al. 2014; Huang et al. 2015), but most other areas have less than 300 species. More specious areas stand to lose more species (Roberts et al. 2002), ultimately putting the entire ecosystem at risk by reducing functional redundancy and jeopardising key ecological functions (Jones et al. 2011; Hooper et al. 2012).

However, species richness is not the sole determining factor of ecosystem functioning; other components of biodiversity such as relative abundance and functional diversity are also key determinants that should be considered for conservation (Hooper et al. 2005; Bellwood et al. 2006; D'agata et al. 2014). For complex ecosystems, despite a wealth of literature linking greater diversity to increased resilience to disturbance, work is emerging that demonstrates the contrary (Bellwood et al. 2006; Cadotte et al. 2011; Mouillot et al. 2014). Indeed, reefs with more coral species have lower resistance to crown-of-thorns seastar (*Acanthaster planci*) outbreaks, coral bleaching and storm impacts, and furthermore

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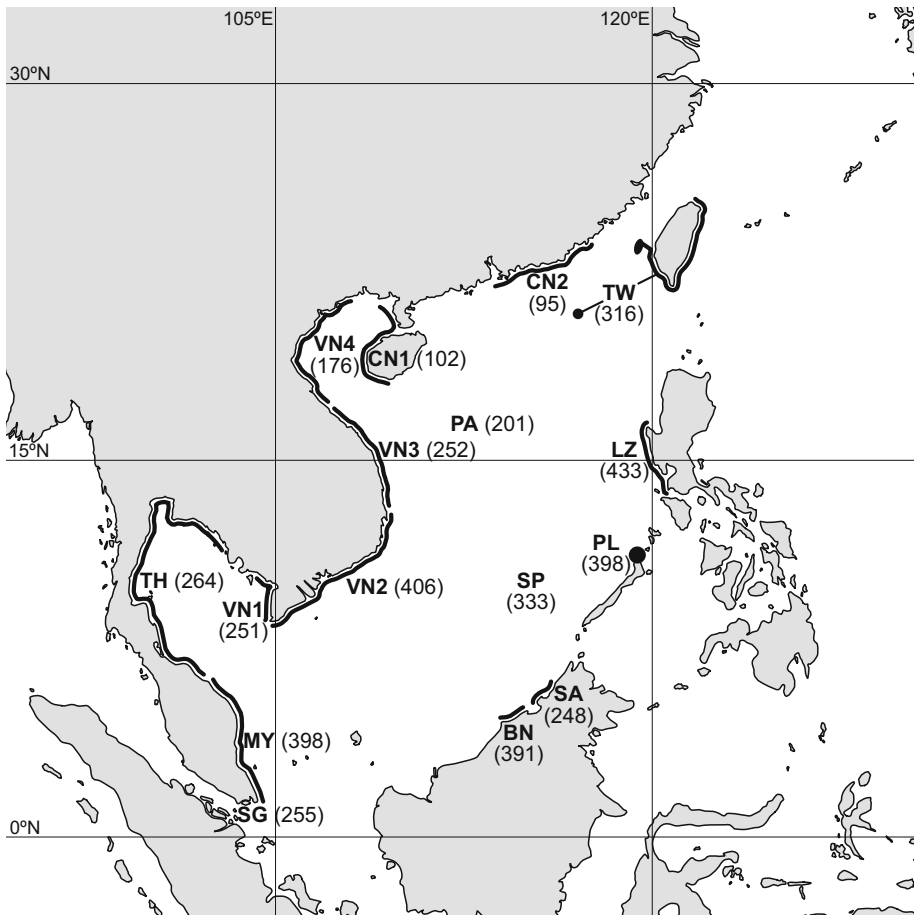
Fig. 1 South China Sea reef areas examined in this study, indicating the respective species richness of stony corals

do not recover faster (Zhang et al. 2014). Better understanding of the links between diversity, functional redundancy and resilience is therefore critical for predicting the future of reefs.

For instance, important ecosystem contributions are made by species that are rare, both in terms of local abundance (Lyons et al. 2005) and geographic range (Mouillot et al. 2013; Jain et al. 2014), yet these species tend to have the highest extinction risk (Harnik et al. 2012). While over 10 % of coral species are considered to have restricted or highly fragmented ranges (Carpenter et al. 2008), aspects like their distribution in diverse areas, the overall extinction risk they face, and how their contributions to reef diversity will change in the future remain poorly known. Our study aims to fill this gap by characterising the degree of rarity contained within each SCS area.

For more than two decades, evolutionary diversity has become a major component of conservation research (Vane-Wright et al. 1991; Nee and May 1997; Faith et al. 2010; Curnick et al. 2015). Preservation of the tree of life is now often set as a goal in itself (Posadas et al. 2001; Rodrigues and Gaston 2002; Forest et al. 2007), or as a proxy for the

protection of ecosystem functioning (Maherali and Klironomos 2007; Cadotte et al. 2008; Flynn et al. 2011). Although biodiversity has been interpreted primarily in terms of species richness, it can also be quantified as evolutionary lineages (Altschul and Lipman 1990; May 1990; Faith 1992), which in turn can be used to examine phyloecological trends in distribution patterns (Hoeksema 2012) and other features relevant to species communities, such as coloniality and associated fauna in scleractinian corals (Barbeitos et al. 2010; Gittenberger et al. 2011; Hoeksema et al. 2012). In conserving biodiversity, a broader and more representative goal could be approached by prioritising species or areas that most likely protects the diversity of the tree of life (Witting and Loeschcke 1995; Isaac et al. 2007; Rosauer and Mooers 2013). Recent studies have shown that anthropogenic extinction threats against corals are not distributed randomly on a species phylogeny (Huang 2012). Rather, many risk factors such as mass bleaching, disease and crown-of-thorns seastar outbreaks have the potential to devastate evolutionary diversity of coral reefs on a global scale (Huang and Roy 2013). The future of evolutionary diversity at local and regional levels remains uncertain, but given the availability of species distributional data in the region (Huang et al. 2015), this now becomes possible to predict for the SCS.

The primary objective of this study is to quantify and project changes in species and evolutionary diversity of 16 reef areas in the SCS region to better understand and prioritise conservation resources. We update coral distribution records compiled recently by Huang et al. (2015) and compare species richness, rarity and phylogenetic diversity among 16 reef areas in the SCS (Fig. 1; Table 1). Rarity is defined based on geographic range limitation (Gaston 1994), and the level of rarity in each area is determined by averaging species weights assigned based on their range restrictedness. We then integrate conservation status data from the IUCN Red List of Threatened Species (IUCN 2001; Carpenter et al. 2008) and perform extinction simulations to predict changes in phylogenetic diversity (Faith 1992) of reef areas caused by species loss. Our findings underscore the conservation value of particular SCS areas whose immense biodiversity is threatened by impending extinction.

Materials and methods

The SCS is a large marine region with a surface area of 3.4 million km^2 (Fig. 1; Morton and Blackmore 2001), including about 12,000 km^2 or 4.7 % of the world's total coral reef area (Huang et al. 2015), and is surrounded by the coastlines of ten Asian nation states.

Species distributional data of scleractinian reef corals in the SCS were previously consolidated by Huang et al. (2015). The dataset comprised occurrences for a total of 571 species (see Online Resource 1) recorded among 16 reef areas in the region (Table 1). Records for southern Vietnam (VN2) were updated (Vo et al. 2014).

To determine the relationship between regional and global patterns of coral diversity, we supplemented the SCS distributional data with geographic range information from the Coral Geographic database (Veron et al. 2009, 2011, 2015). This database of 798 species divided the seas containing reef corals into 141 ecoregions. Data for SCS species not available in the Coral Geographic were obtained from the IUCN Red List of Threatened Species (IUCN 2001; Carpenter et al. 2008) and the Global Biodiversity Information Facility (GBIF; http://data.gbif.org). A total of 547 (out of 571) species were covered by these global databases. For each species, we computed ecoregion (global) and area (SCS) occupancies for each species by summing the number of the respective geographic units that contain it. The predictive capacity of the SCS data on global ecoregion occupancy was

Table 1 South China Sea reef areas (according to Huang et al. 2015) examined in this study, showing species richness, the Index of Relative Rarity (I_{RR}) (Leroy et al. 2012, 2013), number (and percentage) of species in each IUCN Red List Category (*EN* endangered, *VU* vulnerable, *NT* near threatened, *LC* least concern, *DD* data deficient) (Carpenter et al. 2008), and mean percent (and 95 % confidence interval) excess loss of phylogenetic diversity (PD) (Parhar and Mooers 2011)

Area	Richness	I_{RR}	EN	VU	NT	LC	DD	Excess PD loss (%)
Singapore (SG)	255	0.0063	1 (0.4)	39 (15.3)	83 (32.5)	130 (51.0)	2 (0.8)	−1.05 (−1.10, −1.01)
West Malaysia (MY)	398	0.0500	5 (1.3)	100 (25.1)	115 (28.9)	162 (40.7)	16 (4.0)	1.31 (1.24, 1.37)
Thailand (TH)	264	0.0025	0 (0.0)	40 (15.2)	79 (29.9)	144 (54.5)	1 (0.4)	−0.88 (−0.93, −0.84)
Southwestern Vietnam (VN1)	251	0.0073	0 (0.0)	34 (13.5)	74 (29.5)	138 (55.0)	5 (2.0)	0.53 (0.48, 0.57)
Southern Vietnam (VN2)	406	0.0228	3 (0.7)	93 (22.9)	117 (28.8)	179 (44.1)	14 (3.4)	−1.38 (−1.42, −1.33)
Central Vietnam (VN3)	252	0.0058	0 (0.0)	40 (15.9)	74 (29.4)	137 (54.4)	1 (0.4)	−1.67 (−1.71, −1.62)
Northern Vietnam (VN4)	176	0.0034	0 (0.0)	25 (14.2)	60 (34.1)	90 (51.1)	1 (0.6)	1.20 (1.15, 1.25)
Paracel Islands (PA)	201	0.0249	2 (1.0)	34 (16.9)	57 (28.4)	101 (50.2)	7 (3.5)	1.31 (1.26, 1.37)
Southern China (CN1)	102	0.0271	0 (0.0)	11 (10.8)	32 (31.4)	51 (50.0)	8 (7.8)	−0.88 (−0.91, −0.85)
Southeastern China (CN2)	95	0.0210	0 (0.0)	12 (12.6)	37 (38.9)	45 (47.4)	1 (1.1)	0.62 (0.58, 0.66)
Brunei (BN)	391	0.0275	4 (1.0)	92 (23.5)	116 (29.7)	175 (44.8)	4 (1.0)	−1.21 (−1.27, −1.16)
Western Sabah (SA)	248	0.0212	1 (0.4)	42 (16.9)	69 (27.8)	131 (52.8)	5 (2.0)	−0.87 (−0.92, −0.82)
Spratly Islands (SP)	333	0.0108	0 (0.0)	59 (17.7)	97 (29.1)	168 (50.5)	9 (2.7)	−1.24 (−1.29, −1.20)
Northern Palawan (PL)	398	0.0333	4 (1.0)	95 (23.9)	110 (27.6)	180 (45.2)	9 (2.3)	−0.50 (−0.55, −0.45)
Western Luzon (LZ)	433	0.0296	3 (0.7)	112 (25.9)	122 (28.2)	188 (43.4)	8 (1.8)	−1.01 (−1.06, −0.96)
Taiwan (TW)	316	0.0253	1 (0.3)	54 (17.1)	97 (30.7)	157 (49.7)	7 (2.2)	−0.82 (−0.86, −0.78)
All areas	571	0.0848	11 (1.9)	160 (28.0)	145 (25.4)	210 (36.8)	45 (7.9)	0.17 (0.12, 0.23)

estimated by fitting a linear model through the origin. We then used the global distributional data to assign species rarity weights for the characterisation of relative rarity among the 16 SCS assemblages. Gaston's (1994) quartile definition was set as the rarity threshold, being the number of ecoregions at which 25 % of all species with the lowest global occurrence were considered rare (Leroy et al. 2012). These rare species were assigned weights that increased exponentially with the difference between their occurrences and the rarity cutoff. Finally, using the R (R Core Team 2013) package Rarity (Leroy et al. 2013), we computed the Index of Relative Rarity (I_{RR}), given by the average weight of rarity for all species in each assemblage. The index was also calculated for the SCS as a whole.

We derived coral conservation status data from the IUCN Red List of Threatened Species that included 827 reef-building scleractinian species assessed by many of the world's leading coral experts in 2006 and 2007 (IUCN 2001; Carpenter et al. 2008). The assessment concluded that one-third of the 688 species not deemed data deficient (DD) faced heightened extinction risk (i.e., *CR* critically endangered, *EN* endangered, *VU*
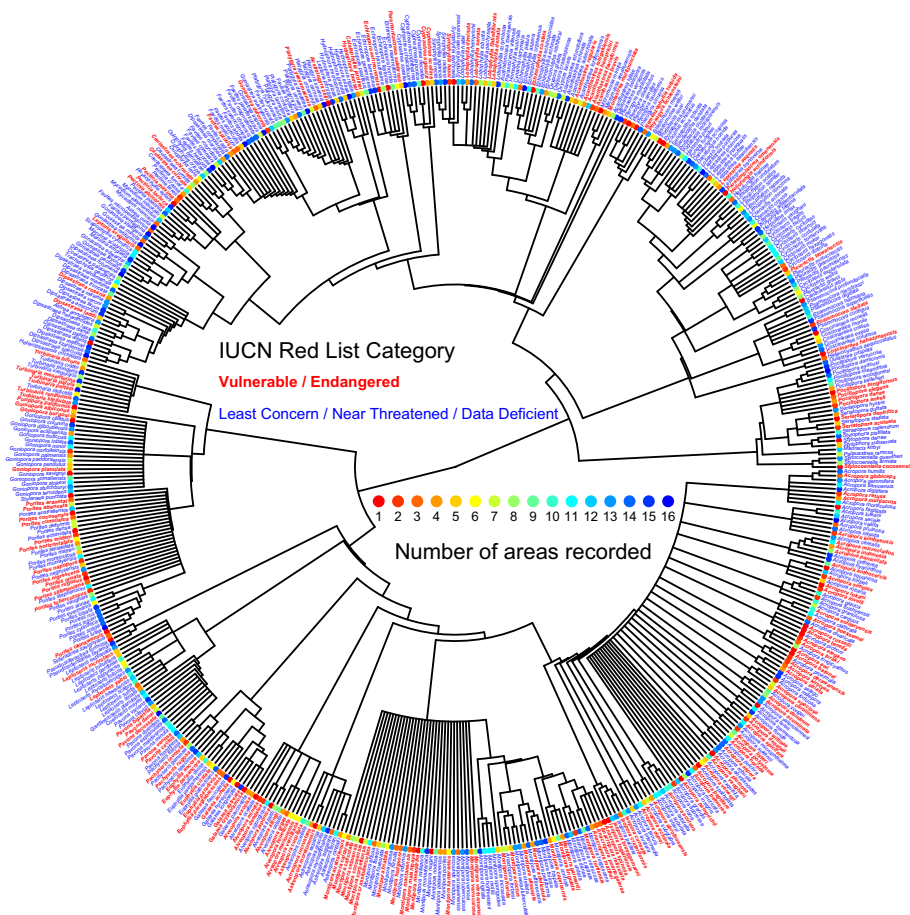

Fig. 2 Strict consensus phylogenetic tree of reef corals in the South China Sea. The number of reef areas recorded for each species is shown using a *coloured circle*, with IUCN Red List threat status denoted as *red* (threatened) or *blue* (non-threatened) tip label

vulnerable). Of the 571 coral species recorded in the SCS, 543 were characterised based on the IUCN Red List categories. The remaining 28 species not assessed previously were categorised as DD. We note that the lack of information for DD species may be related to inadequate taxonomic study, or to their possible rarity and restricted distribution range, in which case the number of threatened species may be underestimated (see below).

Based on the threat levels for species, we carried out a simulation study to predict regional changes in evolutionary diversity arising from projected extinctions. To quantify the pre- and post-extinction diversity of each SCS area and the region as a whole, we employed the phylogenetic diversity (PD) measure (Faith 1992), computed in R (R Core Team 2013) packages caper (Orme et al. 2013) and Picante (Kembel et al. 2010) as the total branch length in the phylogeny of species present in an area (Davies et al. 2008; Fritz and Purvis 2010). For this computation, we pruned the 1000 time-calibrated posterior supertrees of reef scleractinian corals reconstructed recently (Huang 2012; Huang and Roy 2013) to a taxon subset corresponding to the species complement of each area (Fig. 2). Species loss was simulated by assuming that all threatened (CR, EN or VU) corals in an area would go extinct, with the results compared to a null model of random extinction repeated 1000 times with the same extinction rate (Purvis et al. 2000; Sechrest et al. 2002; Fritz and Purvis 2010). We then calculated the excess loss of PD as the extra loss of actual PD over the null result, expressed as a proportion of the latter (Parhar and Mooers 2011), and assessed for statistical significance using the Student's *t* test. The analysis was carried out for each of the 1000 posterior trees, with results summarised as means and 95 % confidence intervals.

Results and discussion

Our study brings together species and phylogenetic diversity data at the regional scale with global distribution and extinction risk information of the 571 reef coral species in the SCS (see Online Resource 1). Species occurring in the SCS include geographically-restricted species such as *Physophyllia ayleni* in the Macclesfield Bank (Paracel Islands reef area) and *Pseudosiderastrea formosa* in Taiwan, as well as widespread species such as *Pocillopora damicornis* that inhabits every SCS area and are present in nearly all (118) of the reef ecoregions in the Indo-Pacific marine realm (Veron et al. 2009).

There is a statistically significant positive linear relationship between SCS area occupancy and global ecoregional distribution (slope = 6.39, $p < 10^{-15}$, $R^2 = 0.942$; Online Resource 2). As expected, species that are rare in the SCS region tend to be less widespread at the global level. Therefore, focusing on reef conservation efforts at the regional level, like an implementation of a regional network of marine protected areas, or MPAs (Clifton 2009; Walton et al. 2014; White et al. 2014), will help preserve a good representation of global species diversity.

Despite the strong positive relationship between global and regional occupancies, there are considerable variations in the global distribution of species (Online Resource 2). For example, *Cycloseris distorta* is recorded in 89 reef ecoregions according to the Coral Geographic (Veron et al. 2009, 2011), yet it is only present in two SCS areas (Fig. 2)—Thailand and southern Vietnam—which could also be related to differences in species identifications among studies as seen in the Great Barrier Reef (Hoeksema 2015). There are also regionally widespread species such as *Montipora florida*, *Pleuractis gravis* and *Turbinaria bifrons* that are present in as many as half of the SCS reef areas (Hoeksema

1993; Veron et al. 2009), but are in fewer of the world's ecoregions (15–20) than expected ($\sim$50). These variations in global occupancy are useful in helping to determine the relative rarity of species hosted by each SCS area. The globally widespread *Cycloseris distorta* (for locality records, see Hoeksema 1989), for instance, receives a weight of zero and is not in the quartile of species with the lowest global occurrence to be considered rare (Leroy et al. 2012). By contrast, *Montipora florida*, *Pleuractis gravis* and *Turbinaria bifrons* meet the threshold of rarity and have weights of 0.163, 0.285 and 0.205, respectively.

The index of relative rarity (I_{RR}), calculated by averaging these weights for all species in an area, gives an indication of the relative proportion of globally geographically-restricted corals present in the area (Leroy et al. 2013). The SCS reef areas with the highest I_{RR} are the east coast of West Malaysia and northern Palawan (Table 1), which contain globally and regionally rare species such as *Euphyllia paradivisa* and *E. paraglabrescens*. In particular, West Malaysia's east coast harbours 70 species, or 17.6 % of its total species richness, that meet the rarity threshold of ≤29 ecoregion occupancy. Northern Palawan has far fewer rare species (50), but these include extremely rare corals such as *Plerogyra cauliformis* and *P. multilobata*. Each of these species is present in only one ecoregion, although both of them have been recorded in nearby eastern Sabah (Waheed and Hoeksema 2013). Other noteworthy areas in terms of relative rarity are western Luzon and Brunei, which have slightly lower I_{RR} but contain more rare species overall (66 and 51 respectively) than northern Palawan. While the richness component cannot be completely isolated from our rarity statistics, this set of reef areas does not include southern Vietnam, the second most species-rich area in the SCS, with greater richness than even West Malaysia. Consequently, the choice to focus on either component of biodiversity—richness or rarity—can affect regional priorities of conservation considerably (Prendergast et al. 2002; Lennon et al. 2004; Orme et al. 2005). Note that this set of results is robust to variations in rarity thresholds; the use of 15 and 35 % rather than Gaston's (1994) quartile definition gives rank contrasts of only 1.75 and 1.00 respectively, with I_{RR} values that are ranked identically among many reef areas.

Almost one-third of the SCS species (29.9 %) are threatened according to the IUCN Red List of Threatened Species (Carpenter et al. 2008), including 11 and 160 in EN and VU categories respectively (Table 1). While there are no CR species in the SCS, the proportion of non-DD species facing elevated extinction risk is nearly identical regionally and globally ($\sim$33 %). Interestingly, areas with the largest proportions of threatened species—West Malaysia (26.4 %), northern Palawan (24.9 %) and western Luzon (26.6 %)—are also those with the highest relative rarity. This should hardly be surprising given that at the global scale, a greater proportion of range-restricted species (44.7 %) are threatened as compared to those that are more widespread (31.0 %) (Carpenter et al. 2008). That is, the greater the number of threatened species in an area, the more likely it will contain geographically-restricted species.

Although the east coast of West Malaysia has the highest number of DD species (16), there is no clear pattern of how IUCN Red List data deficiency relates to the rarity of species within an area. Southern Vietnam, for instance, contains numerous DD species (14) as well, but it ranks eighth in terms of relative rarity. However, when species in the SCS are pooled, DD species occupy only an average of 21 reef ecoregions globally, compared to 36 ecoregions for threatened and 66 for non-threatened species. Indeed, our results suggest that species deemed DD during the IUCN assessment are lacking in data mainly because their global range restriction hinders understanding which is necessary for conservation evaluation (see Robbirt et al. 2006).

Five reef areas stand to lose significantly more PD than expected by the extinction risk of their coral assemblages, including the most species-poor area of southeastern China (Table 1). Excess losses in the latter area and southwestern Vietnam are projected to be 0.62 and 0.53 % respectively, whereas Paracel Islands, West Malaysia's east coast and northern Vietnam could lose at least an extra 1.20 % of phylogenetic diversity compared to a random extinction event. Threatened species in these areas are thus likely to be clustered on the area phylogeny and/or consist of highly distinctive species (Purvis et al. 2000; Vamosi and Wilson 2008; Huang and Roy 2013). In the Paracel Islands, for example, the excess PD loss is caused mainly by the projected extinction of evolutionarily distinct Vulnerable species *Acropora echinata* (sister to 42 other *Acropora* spp. in the area), *Isopora brueggemanni* (sister to the rest of *Isopora*), *Alveopora excelsa* and *Heliofungia actiniformis* (the only representatives of their genera in the area). The loss of the Vulnerable, monotypic *Physogyra* also leads to the depletion of a long phylogenetic branch. By contrast, because West Malaysia's east coast contains a much larger tree with nearly twice the species richness, it is more likely to have taxa that are closely related to these distinct species. Unfortunately, the clustering of threatened species in particular parts of the tree, such as *Isopora*, *Alveopora* and *Turbinaria* results in imperilment of entire clades.

Southeastern China and southwestern Vietnam could also lose significantly more PD than random species extinction, but are less likely than the Paracel Islands, east coast of West Malaysia and northern Vietnam to lose deep lineages. Across the entire SCS, excess PD loss is positive, indicating that the threatened unique lineages in these five reef areas are not buffered from extinction by the rest of the region's coral fauna. The remaining 11 reef areas stand to lose less PD than if extinction were by chance, suggesting that these areas either contain proportionally fewer threatened long-branch species, or have more instances of persistent species that are closely related to threatened species.

Species in an assemblage contribute differently to ecological functioning, but the actual variation is difficult to establish (Cadotte 2013). Nevertheless, phylogenetic diversity has been shown to correlate strongly with ecosystem productivity and stability (Maherali and Klironomos 2007; Cadotte et al. 2008; Flynn et al. 2011). This relationship generally results from the increase in trait diversity as more phylogenetically-diverse species are included in an assemblage. The projected excess decline of PD in the five SCS reef areas mentioned above could therefore spell the inordinate loss of coral traits that are important for local ecosystem functioning. While the link between phylogenetic and functional diversity needs to be tested, trait information for a majority of corals remains scant (Díaz and Madin 2011; Darling et al. 2012, 2013). Moreover, high diversity systems like coral reefs have historically been expected to possess a certain level of functional redundancy (McCann 2000; Bellwood et al. 2004; Nyström 2006), but more recent research on reef fishes shows that only a limited number of functional groups are actually buffered against species loss (Bellwood et al. 2003, 2006; Mouillot et al. 2014). This dire pattern and lack of coral data suggest that conservation of PD specifically by minimising excess loss over random extinction is a prudent strategy for preserving ecosystem functioning. Furthermore, an enhanced conservation focus on the tree of life is ultimately key to protecting evolutionary heritage, a critical biodiversity component (Purvis and Hector 2000; Mace et al. 2003; Rosauer and Mooers 2013).

Overall, our results highlight the need to go beyond the conventional emphasis on species richness when planning for conservation in the SCS (see Devictor et al. 2010). Coral richness, rarity, and phylogenetic diversity differ considerably among reef areas in the region, and their outcomes from projected extinctions due to anthropogenic disturbances are not predicted simply by species numbers. On the one hand, rare species in terms

of global ecoregion occupancy are more likely to be threatened with extinction and should be prioritised for conservation (Arponen 2012). West Malaysia's east coast and the Philippine reef areas harbour the greatest levels of rarity and threat, so clearly, they are of potential conservation interest, yet species-poor areas such as southern China and the Paracel Islands also contain many rare species. On the other hand, areas that stand to lose more-than-expected levels of PD, such as the Paracel Islands, east coast of West Malaysia and southeastern China, are also critical for biodiversity conservation. Taken together, while a few areas with moderate to high species richness (e.g., West Malaysia and the Paracel Islands) feature prominently on the basis of various measures used here, areas containing the fewest species (e.g., China and northern Vietnam) also need to be protected for their contributions to rarity and evolutionary diversity. Given that rare species are known to contribute disproportionately more to the functioning of coral reef ecosystems (Mouillot et al. 2013), it may be more cost effective to target these areas. Ultimately, priorities to be developed must take into account conservation financing and potential returns on investment (Murdoch et al. 2007), as well as diverging socioeconomic costs associated with the protection of large marine regions (Klein et al. 2010). This may require a multilateral framework that prioritises investment at the national level based on complementary sets of objectives for achieving regional conservation goals (Beger et al. 2015).

Anthropogenic threats to the coral reefs of the SCS include overfishing, destructive fishing, coral mining, the aquarium trade, coastal development, sedimentation and pollution (McManus 1997; Kimura et al. 2008; Tun et al. 2008), all of which have led to an estimated 16 % regional loss of live coral cover between 1994 and 2004 (UNEP 2007). Many reef areas bordering the SCS are under some form of management but conservation effectiveness remains weak for much of the region (UNEP 2007; Vo et al. 2013). Apart from the need to improve management effectiveness, recommendations have been proposed for the development of a network of MPAs as a regional strategy to conserve coral reefs globally (MOE Japan 2010; see also McManus 1994; McManus and Meñez 1997; McManus et al. 2010). Our results show that such a network can help preserve a considerable portion and representation of global coral diversity, as well as enhance spatial links for maintaining ecosystem connectivity and resilience (Walton et al. 2014; White et al. 2014). The findings here will also aid conservation planners in efficiently directing different resources to the most suitable reef areas, depending on the goal of individual MPAs (see Bennett et al. 2014), and will provide a foundation for identifying reefs that should be included in an MPA network. For example, an MPA designed to give equal consideration to species richness, rare species and evolutionary diversity ought to include the east coast of West Malaysia as it has the highest I_{RR} (0.0500) and is one of the top two reef areas in projected rate of extinction (26.4 %) and excess PD loss (1.31 %) from a diverse assemblage (398 species). More broadly, the practical tools used here can be applied to areas and taxa in the SCS not covered by our study to attain a more comprehensive understanding of various reef diversity components and extinction risk.

Corals are hosts to a large array of associated fauna and the loss of any particular coral could lead to the demise of other species, especially if these are host-specific (Hoeksema et al. 2012). In the SCS, extinctions of large proportions of threatened corals (Table 1) could compromise the complex three-dimensional architecture of coral reefs, putting at risk the existence of reef inhabitants such as fish (Graham et al. 2006; Wilson et al. 2006; Chong-Seng et al. 2012) and invertebrates (Idjadi and Edmunds 2006; Pratchett et al. 2009; Fabricius et al. 2014). Therefore, comprehensive protection of coral species and evolutionary diversity via the formation of an MPA network in the SCS will go a long way towards securing the future of reef faunal assemblages in the region.

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