

The Coral Triangle

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Abstract Spatial analyses of coral distributions at species level delineate the Coral Triangle and provide new insights into patterns of diversity and endemism around the globe. This study shows that the Coral Triangle, an area extending from the Philippines to the Solomon Islands, has 605 zooxanthellate corals including 15 regional endemics. This amounts to 76% of the world's total species complement, giving this province the world's highest conservation priority. Within the Coral Triangle, highest richness resides in the Bird's Head Peninsula of Indonesian Papua, which hosts 574 species, with individual reefs supporting up to 280 species ha⁻¹. The Red Sea/Arabian region, with 364 species and 27 regional endemics, has the second highest conservation priority. Reasons for the exceptional richness of the Coral Triangle include the geological setting, physical environment, and an array of ecological and evolutionary processes. These findings, supported by parallel distributions of reef fishes and other taxa, provide a clear scientific justification for the Coral Triangle Initiative, arguably one of the world's most significant reef conservation undertakings.

Keywords Coral triangle • coral reefs • biogeography • conservation

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1 Introduction

Over the past several decades, biogeographers have proposed centers of marine biodiversity of varying shapes, all centered on the Indonesian/Philippines Archipelago. Some stem from biogeographic theory or geological history, others from coral and reef fish distributions. These centers have been given a variety of names: Wallacea, East Indies Triangle, Indo-Malayan Triangle, Western Pacific Diversity Triangle, Indo-Australian Archipelago, Southeast Asian center of diversity, Central Indo-Pacific biodiversity hotspot, Marine East Indies, among others (reviewed by Hoeksema 2007).

It was not until the postwar era that coral biogeography came to the forefront of marine biogeography, a position initiated by the American paleontologist John Wells (1954) when he published a table of coral genera plotted against locations. Many reiterations of this table formed the basis of sequence of published maps (Stehli and Wells 1971; Rosen 1971; Coudray and Montaggioni 1982; Veron 1993). These publications, all at generic level, highlighted the Indonesian/Philippines Archipelago as the center of coral diversity. Significantly, they also included the Great Barrier Reef of Australia as part of that center.

This view was fundamentally altered when global distributions were first compiled at species level, an undertaking that needed a computer-based spatial database. This compilation clearly indicated that the Indonesian/Philippines Archipelago, but not the Great Barrier Reef, was the real center of coral diversity (Veron 1995), a pattern now well established (see below).

The significance of this seemingly innocuous finding was not lost on conservationists. It meant that the international focus for coral and, by extrapolation, reef conservation shifted from the highly regulated World Heritage province of the Great Barrier Reef to the relatively understudied region to the north, where reefs were largely unprotected, and where human population densities and consequent environmental impacts were high by most world standards.

Political response to the delineation of the Coral Triangle (CT) was prompt. In August 2007, President Yudhoyono of

Indonesia proposed a new, six-nation Coral Triangle Initiative (CTI), as a mechanism to conserve key components of the global center of coral reef biodiversity. In September 2007, 21 world leaders attending the Asia Pacific Economic Cooperation (APEC) summit in Sydney formally endorsed CTI. At the CTI Summit in May 2009, involving leaders from all six CT countries, extraordinary political commitments to coral reef and marine conservation were made. The CTI has become one of the biggest conservation initiatives ever undertaken in the marine world.

2 Delineating the Coral Triangle

Delineation of the CT (Veron et al. 2009b) was established by the spatial database *Coral Geographic*, a major update of the original species maps of Veron (2000). This database contains comprehensive global species maps of zooxanthellate coral distributions in GIS format, allowing them to be

interrogated to compare geographic regions or to elucidate patterns of diversity and endemism.

The 798 species maps in the *Coral Geographic* database are each divided into 141 ecoregions (Fig. 1), an approach increasingly used in biogeography (Spalding et al. 2007). These maps, which include verified published occurrences of each species in each ecoregion together with original data are from two sources: (1) revisions of the database used to generate the species distribution maps of Veron (2000) and (2) species complements derived from original fieldwork by the first three authors in 83 of the 141 ecoregions. Continually updated details of this dataset, currently including >2,500 georeferenced sites linked to habitat data, will be available online in 2010.

In summary, coral ecoregions provide a blueprint for establishing a globally representative network of coral reef MPAs. The world's highest diversity occurs in the CT, an area where more than 500 coral species are found in each ecoregion (Fig. 2). Species attenuate latitudinally according to ocean temperature (a) northward to mainland Japan, dispersed by the Kuroshio, (b) southward along the west

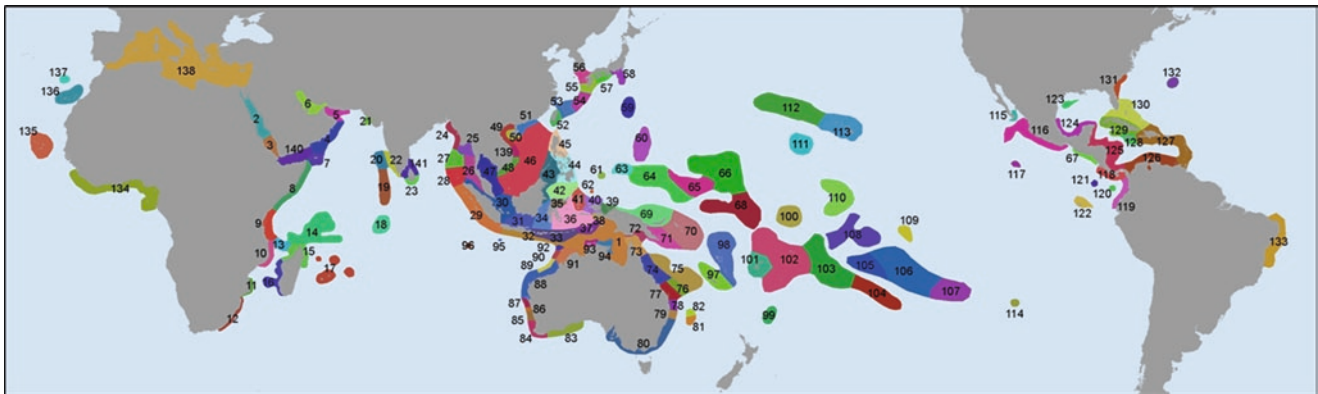


Fig. 1 Coral ecoregions of the world, delineated on the basis of known internal faunal and/or environmental uniformity and external distinctiveness from neighboring regions. The identity of the numbered

ecoregions and the number of species in them is in Veron et al. (2009a) (From the spatial database *Coral Geographic*, see text)

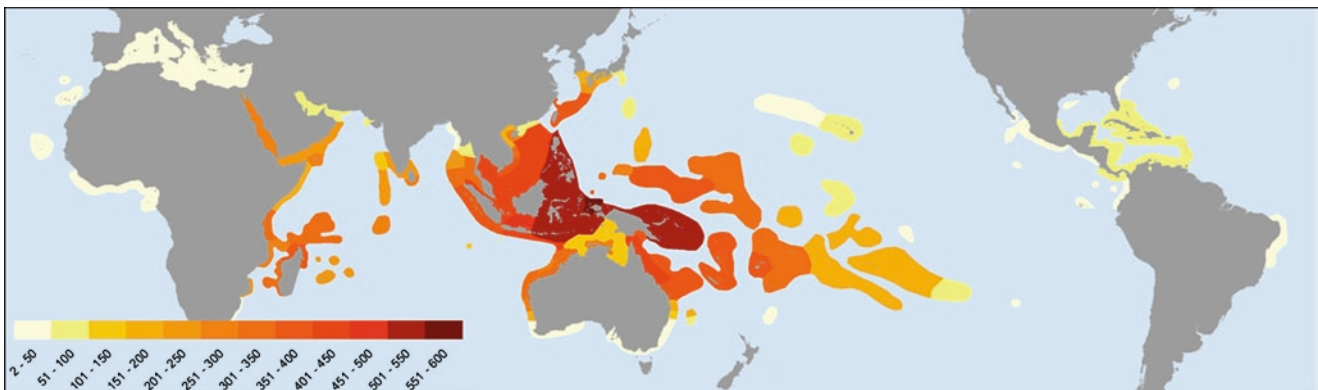


Fig. 2 Global biodiversity of zooxanthellate corals. Colors indicate total species richness of the world's 141 coral biogeographic "ecoregions" (From the spatial database *Coral Geographic*, see text)

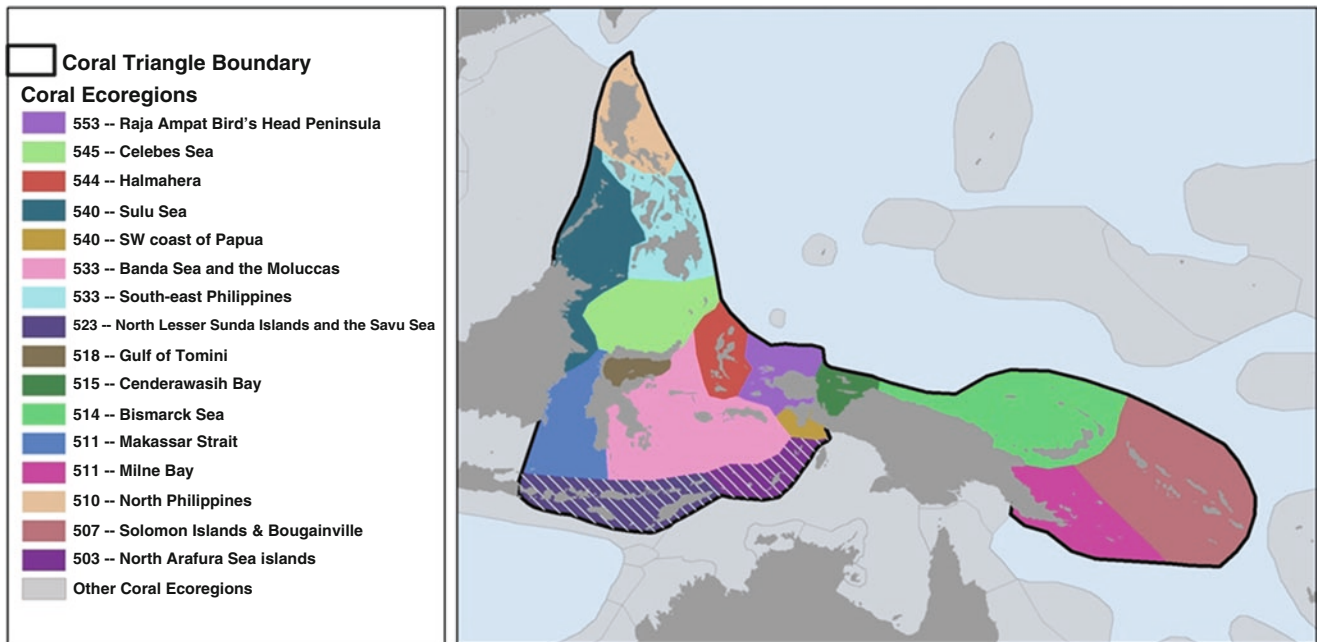


Fig. 3 Ecoregions and species richness of zooxanthellate corals of the CT (determined by the spatial database Coral Geographic, see text). A total of 1,118 sites were studied within the 16 ecoregions of this province (*left panel*, showing number of species per ecoregion); however,

some islands of southern Indonesia (the two hatched ecoregions), especially their southern coastlines, remain data-deficient. Each ecoregion has >500 species (From the spatial database *Coral Geographic*, see text)

Australian coast, dispersed by the Indonesian Through-flow and the Leeuwin Current and (c) southward along the east Australian coast, dispersed by the East Australian Current. Species attenuate longitudinally eastward across the Pacific according to geographic distance and the concentration of reefs. The Indian Ocean has a more uniform longitudinal (east–west) distribution of diversity, although the eastern and western edges of this region are separated by a paucity of reefs in the equatorial center around Chagos (Sheppard 1999). All localities of the Atlantic are relatively depauperate and there are no obligate hermatypic species in common between the Atlantic and Pacific.

Sixteen ecoregions of the world have >500 species; these define the CT and reveal its internal components to the level or resolution of this study (Fig. 3).

3 Hotspots of Biodiversity and Endemism

“Hotspot” is a term frequently used by conservation biologists to denote a relatively restricted geographic area containing exceptionally high levels of biodiversity and/or endemism, a concept that has been effective in prioritizing conservation activities where resources are limited (Mittermeier et al. 1998). The term was introduced to the marine realm by Roberts et al. (2002) in a study based on fish, corals, molluscs, and lobsters, where 18 hotspots were

identified in areas ranging in size from tiny Easter Island to the whole of the Great Barrier Reef. Methodologies and conclusions of that study were criticized as having questionable relevance to conservation (Hughes et al. 2002; Baird 2002). However, several conclusions of Hughes et al. (2002) with respect to levels of endemism and the lack of concordance with richness are in turn not supported by the present study. Here, we demonstrate that certain reef areas do in fact rate highly in richness and endemism, meeting both hotspot criteria.

Diversity may be the result of (1) a high level of endemism or (2) the overlap in the ranges of species with wide ranges (Veron 1995). The former category contributes 2.5% and 7.4% of the diversity of the CT and the Red/Arabian Sea region, respectively, and is a smaller component of all other diverse ecoregions. With 605 species, amounting to 83% of all the species of the Indo-Pacific or 76% of the species of the world, the coral diversity of the CT creates an overwhelming case for top conservation priority (see below). Within the Red Sea (with a total of 333 species), the Sinai Peninsula (205 species), northern Saudi Arabia (260 species), and Eritrea (219 species) have conservation merit based on diversity and endemism combined.

Patterns of endemism are created by isolation: either geographic distance (locations remote from centers of diversity) or geographic enclosure. It is a complex issue to address in corals and other taxa that are widely dispersed because it requires knowledge of where a species does not occur as well

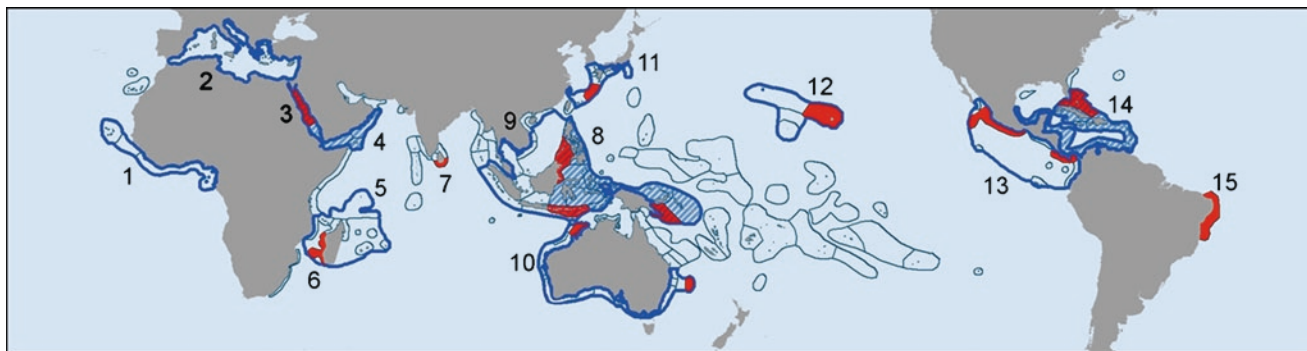


Fig. 4 Global endemism of zooxanthellate corals excluding species described after year 2000 (see text). (1) Eastern Atlantic: two regional species. (2) Mediterranean: three of the four species are regional species. (3) Red Sea: the north has six local endemics (*in red*); 15 regional species for the whole Red Sea. (4) Red Sea/Arabia combined: (hatched) 27 regional species. (5) SW Indian Ocean: four regional species including Madagascar endemics. (6) Madagascar: two local endemics (*in red*). (7) Sri Lanka: three local endemics (*in red*). (8) The CT: 15 regional species (hatched) with

three centers of endemism (*in red*). (9) The CT and adjacent Asia: 41 regional species. (10) Australia: six regional species including two local endemics (*in red*). (11) Japan: six regional species including three local endemics. (12) Hawaii and Johnston Atoll: four regional species, of which three are endemic to Hawaii (*in red*). (13) Far Eastern Pacific: seven regional species including two local endemics (*in red*). (14) Caribbean: 24 regional species (hatched) including one endemic (*in red*). (15) Brazil: four local endemics (*in red*) (From the spatial database *Coral Geographic*, see text)

as where it does. Analyses thus require comprehensive data covering entire oceans. Levels of endemism also vary according to the size of selected areas and their geographic position relative to adjacent areas. Furthermore, new species are commonly thought to be endemic to their place of discovery, but are usually found elsewhere in subsequent studies. For these reasons, previous assessments of endemism are not adequately supported by relevant data. *Coral Geographic* reveals the best documented patterns of endemism to date, located in a complex of overlapping regions (Fig. 4).

4 Characteristics of the Coral Triangle

Indonesia and surrounding countries have attracted more attention from reef biogeographers than all other regions of the world combined (e.g. Briggs 2005). As noted above, the proposed centers of diversity derived from coral and reef fish distributions, biogeographic theory, and geological history have led to diverse opinions about where the global center of reef diversity actually is and what it should be called (reviewed by Hoeksema 2007). The present authors argue that the name “Coral Triangle” should be delineated by scleractinian coral diversity and that of coral-associated organisms, especially reef fishes for which comprehensive data are also available (Allen 2006, 2007). This name was first used in this context by Werner and Allen (1998) and has since gained wide acceptance in biogeographic, conservation, and faunistic studies.

The first comprehensive species-level diversity map (Veron 1995) showed that northern New Guinea was part of the center as earlier indicated by the distribution of mushroom corals (Hoeksema 1993). However, the Solomon

Islands remained conspicuously data-deficient until a survey in 2004 (Green et al. 2006) revealed a high diversity of both corals (Veron and Turak 2006) and reef fish (Allen 2006), studies which formed the basis of a demarcation of the CT close to that which we now have (Green and Mous 2008).

The CT was delineated on the basis that it is an area that contains a high proportion of the species diversity of the Indo-Pacific and that this diversity occurs in an area small enough to permit meaningful conservation. With this delineation, the 16 ecoregions of the CT each host >500 reef coral species. If the CT were extended to include the northern Great Barrier Reef, Vanuatu, New Caledonia, and Fiji (an additional nine ecoregions), the total area would be approximately doubled for an addition of only 12 species including only three endemics. Conversely, if all conservation effort were centered in the Papuan Birds Head Peninsula of Western Papua diversity center (hosting 92% of the species of the CT), there would be little redundancy and extensive areas where human impact is low would be excluded (notably most of Papua New Guinea and the Solomon Islands).

The CT defined by *Coral Geographic* – that adopted by the CTI – is an area of 5.5×10^6 km² of ocean territory of Indonesia, the Philippines, Malaysia (Sabah), Timor Leste, Papua New Guinea, and the Solomon Islands – less than 1.6% of the world’s total ocean area. Although the CT boundary was determined on the basis of coral diversity, this delineation does not provide any new biogeographic insights. The CT is not a distinct biogeographic unit, but comprises portions of two biogeographic regions (Indonesian-Philippines Region, and Far Southwestern Pacific Region, Veron 1995). Within the CT, highest richness resides in the Bird’s Head Peninsula of Indonesian Papua, which hosts 574 species. Individual reefs there have up to 280 species ha⁻¹, over four times the total zooxanthellate scleractinian species richness

of the entire Atlantic Ocean (Turak and DeVantier *in press*). Within the Bird's Head, The Raja Ampat Islands ecoregion has the world's coral biodiversity bullseye, with 553 species (Veron 2000; Turak and Souhoka 2003).

Importantly, boundaries of the Raja Ampat "bullseye" and the Birds Head diversity center are not highly distinctive. Indeed, more than 80% of all CT species are found in at least 12 of the 16 CT ecoregions. Nor is this region markedly distinct from neighboring ecoregions to the south and southeast. Ninety-five percent of CT species are found in one or more adjacent ecoregions (notably other parts of SE Asia including Malaysia, Thailand and Vietnam, Micronesia, the northern Great Barrier Reef, Vanuatu, New Caledonia, and Fiji), although all exhibit marked declines in species richness and ubiquitousness. It may therefore be asked: are the corals of the CT representative of larger areas; is their pattern of diversity seen in other taxa; and are the environmental and/or biological properties of the region unique? Many authors have commented on these questions in the context of evolutionary processes or conservation issues. They clearly have interlinked answers, involving the region's geological setting, its present physical environment, and an array of ecological issues that are not just relevant to corals.

Although the present chapter is about corals, the distribution of coral reef fishes, the only other major taxon for which comprehensive data are available (Allen 2007, who analyzed distribution patterns of 3,919 Indo-Pacific species) strongly supports the present delineation of the CT. In total, this area contains 52% of the reef fishes of the Indo-Pacific (37% of reef fishes of the world). Regional endemism is also significant in reef fish (100, 28, and 22 species for Indonesia, Philippines, and Papua New Guinea, respectively); however, the highest percentage of endemism, as for corals, is exhibited by remote island locations. Other major faunal groups, notably molluscs (Wells 2002) and crustaceans (De Grave 2001), have very high numbers of undescribed or cryptic species and thus are relatively little known at species level (e.g. Meyer et al. 2005). However, many biogeographic publications indicate that a wide variety of taxa reach maximum diversity in areas within the CT (reviewed by Hoeksema 2007). Although most of these taxa occupy shallow marine habitats, coral reefs are sometimes of secondary importance, as seen in the distributions of mangroves (Ricklefs and Latham 1993; Hogarth 1999; Groombridge and Jenkins 2002) and seagrass (Spalding et al. 2003), which also have the highest diversity within the CT. Even azooxanthellate corals, which have none of the physiological restrictions of zooxanthellate species, have a center of global diversity within the CT (Cairns 2007). These diversity maxima of fauna and flora, especially those not associated with reefs, are only seen in provinces the size of several ecoregions; areas large enough to contain an extreme diversity of habitats created by the complex coastlines of island archipelagos.

5 Reasons for Existence of the Coral Triangle

So much interest from so many points of view begs the question: why does the CT exist? There is no one simple answer, rather there are several interacting factors operating over different temporal and spatial scales.

5.1 Geological History

Two aspects of the geological history of the CT are relevant:

1. The southern half of the CT has been tectonically unstable as far back as the Eocene (38 million years ago), creating a constantly changing geography leading to repeated environmental perturbations, habitat complexity, and (it can only be presumed) evolutionary changes. The Philippines archipelago has had a different, perhaps a less dramatic, geological past, although the Miocene Ryukyu limestones, extending from Japan to Indonesia, show that reef distributions have changed beyond recognition over that time. The fossil record suggests that the corals of the CT are the world's youngest – less than half the mean age of their Caribbean counterparts. These relatively young genera either evolved in the region of the CT or have survived there since going extinct elsewhere (Stehli and Wells 1971; Veron 1995).
2. However important plate tectonic movements were to ocean circulation patterns of the distant past, they are small when compared with the impacts of sea-level changes during the Pleistocene. At least eight times during the last two million years, the shorelines of the CT region have alternated between present sea level and minus 130 m (approximately) (Siddall et al. (2003) (Fig. 5). All reefs were repeatedly aurally exposed, yet deep water remained in close proximity. The CT is thus characterized by complex island shorelines creating diverse shallow habitats adjacent to deep (>150 m) ocean. This created conditions for minimal broad-scale dislocation during times of rapid sea-level change, while also causing more localized changes in oceanographic patterns and isolation of populations to greater or lesser degree within marginal seas and large embayments, thus driving reticulation (see below).

5.2 Dispersion

1. The CT acts as a "catch-all" for larvae moving towards the region, entrained in both the South Equatorial Current and the North Equatorial Current (Jokiel and Martinelli 1992; Veron 1995)

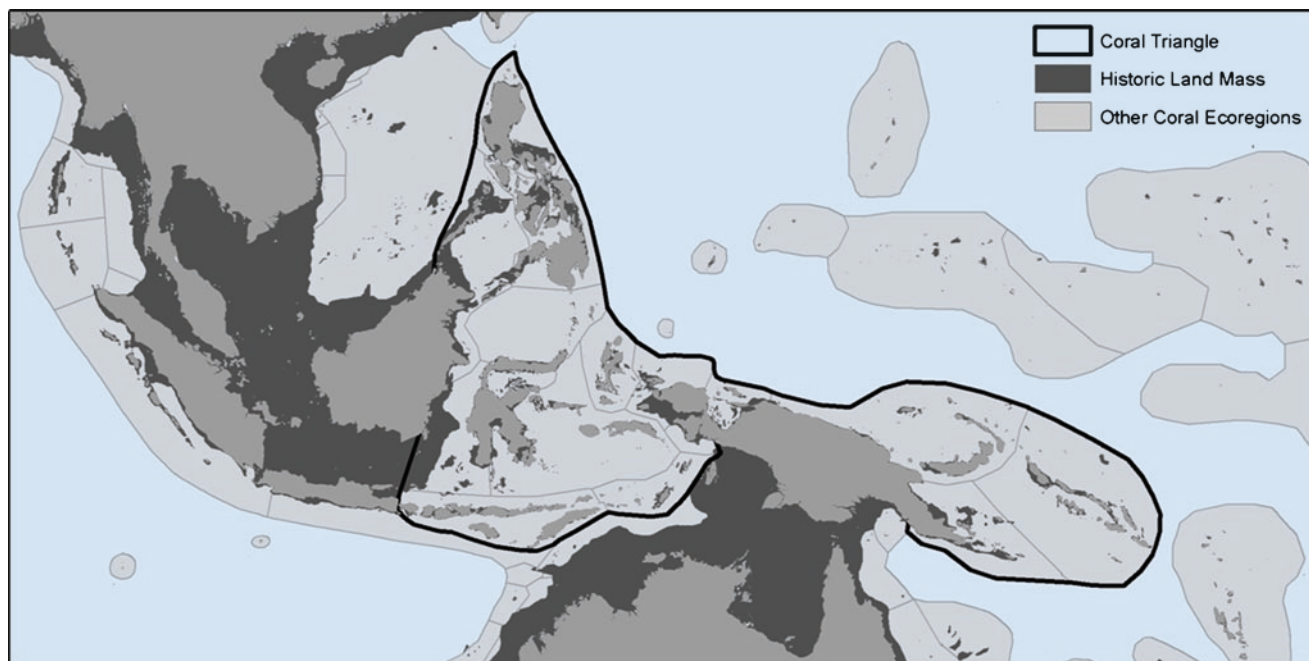


Fig. 5 At least eight times during the last 2 million years, the shorelines of the CT region alternated between those shown here. All reefs (which cannot be viewed at this scale) were repeatedly aerially exposed, yet deep water

remained in close proximity. The CT is seen to be characterized by complex island shorelines creating diverse habitats and adjacent deep (>150 m) ocean providing minimal dislocation during times of sea-level change

2. Dispersion occurs away from the CT so that, at progressively increasing distance, species attenuate according to ocean temperature (a) northward to mainland Japan, dispersed by the Kuroshio, (b) southward along the west Australian coast, dispersed by the Indonesian Through-flow and the Leeuwin Current, and (c) southward along the east Australian coast, dispersed by the East Australian Current (Veron 1995). This suggests that the CT is the most diverse part of the whole central Indo-Pacific simply because all other regions have attenuated species richness
3. Complex eddies created by the Indonesian Through-flow (Gordon and Fine 1996) drive genetic mixing, which constantly changes with wind, season, and (over geological time) sea level. Genetic mixing of this nature creates genetic heterogeneity through vicariance (see below); it also drives reticulate evolution (see below)

5.3 Biogeographic Patterns

Biodiversity is reflected in biogeographic patterns and the environments that created those patterns:

1. Diversity may be the result of (a) a high level of endemism or (b) the overlap in the ranges of species with wide ranges. Importantly, the first category contributes only

2.5% of the coral diversity of the CT. The biodiversity of corals is therefore due to the overlap of species ranges, ranges which extend eastwards into the Pacific and westwards into the Indian Ocean. Endemism becomes relatively more important with fish (Allen 2006) and other taxa in which species longevity is less than that of corals or which have a lesser capacity for long-distance dispersal or which are specialized for narrow niches.

2. Ocean temperatures of the CT are commonly near the thermal cap of 31°C (Kleypas et al. 2008). This temperature, or maxima close to it, is commonly maintained for months during the summer of much of the CT. It is a well-established maxim of biogeography (“Rapoport’s Rule”) that the mean latitudinal range of major taxa increases with increasing latitude (Stevens 1989). This is another way of saying that increasing latitude is correlated with increasing environmental tolerance. Perhaps, this is less well established for marine life (Clarke 1992), but it does suggest that temperature tolerance is least limiting at equatorial latitudes.

5.4 Evolution

Because it links many scientific disciplines including taxonomy, biogeography, and genetics, the subject of evolution

has led to several general theories, three of which (Darwin's Centres of Origin, Vicariance, and Reticulate Evolution) have special relevance to marine biodiversity, biogeography, and (therefore) the CT (see Veron, *Coral Taxonomy and Evolution*, this volume).

In summary, the diversity of the CT has no single explanation. Plate tectonics created the biogeographic template, one of the complex island coastlines and extreme habitat heterogeneity. Patterns of dispersion, mediated by ocean currents, formed sequences of attenuation away from the equator leaving the CT with the region's highest biodiversity. Many environmental parameters, especially ocean currents and temperature, underpin this pattern. Evolutionary patterns, the genetic outcomes of environmental drivers, show why the CT is a center of biodiversity.

6 Future Impacts in the Coral Triangle

Whatever the drivers of diversity once were, it is the future that matters as far as conservation is concerned. Anthropogenic increase in tropical ocean temperature has been less than 0.8°C to date but could be as much as 2–3°C this century (IPCC 2007a, b), further magnified 1–2°C above normal by El Niño events. The latter have already caused extensive mass bleaching of corals in most major regions of the world although not in the southern CT (in part due to upwelling), nor in the southern Red Sea (which has particularly temperature-tolerant corals). If temperature extremes of the western Pacific are capped at 31°C, the CT, particularly areas in the Pacific Warm Pool of eastern Indonesia to the Solomon Islands, will be relatively protected because corals there already tolerate that limit.

Ocean acidification is another matter. In a business-as-usual regime of anthropogenic carbon dioxide increase, calcification of equatorial corals will be marginal by the year 2030 (Guinotte et al. 2003; Veron et al. 2009a). Corals within the CT will be among the last to be affected (Hoegh-Guldberg et al. 2007, 2009) because carbon dioxide absorption will be slowest at the lowest (and therefore warmest) latitudes. From a conservation perspective, all corals are threatened by the dual process of mass bleaching and ocean acidification; however, those of the CT have a relatively good prognosis.

Human impacts are likely to be severe. Approximately 225 million people live within the CT, of which 95% live adjacent to the 131,254 km of coast. This population is largely dependent on the productivity of coral reefs and adjacent waters and a larger population is dependent on protein from these sources. There are no estimations of the value of the reefs of the CT; however, as Indonesia's reefs were valued at \$1.6 billion annually in 2002 (Burke et al. 2002), the current value of the CT is at least \$2.3 billion annually. Almost 90% of Southeast Asian fisheries are in shallow continental shelf waters including coral reefs, industries that

provide an estimated 65–70% of the animal protein consumed in these countries (Valencia 1990; Chua and Garces 1994). Just what economic downturns are likely to follow in the wake of impacts from climate change are unknown, but they will not be counted as an annual cost for their effect will be permanent as far as humans are concerned. By one estimate, Indo-Pacific reefs are declining at >2% per year (Bruno and Selig 2007), a conclusion supported by others (Burke et al. 2002; Allen and Werner 2002; Bellwood et al. 2004; Hoeksema 2004; Briggs 2005; Mous et al. 2005; Carpenter et al. 2008). Furthermore, although correlations between ecological and economic impacts on reefs stemming from environmental decline cannot be estimated with certainty, it is likely that both are becoming increasingly difficult to reverse (Hoegh-Guldberg et al. 2009).

This decline is now a major focus of the CTI, which aims to bring together relevant governments in multilateral partnerships to safeguard the marine resources of the region. Local communities, governments, and nongovernment organizations are currently working together to establish networks of MPAs that are specifically designed to address climate change (West and Salm 2003), reinforced by other conservation strategies, notably ecosystem approaches to fisheries and integrated coastal management. The Indonesian Government has now pledged to conserve 10% of its marine environment in MPAs by 2010 and 20% by 2020 and has called on other governments of CT countries to do likewise. Furthermore, one of the world's first MPA networks specifically designed to address climate change is now being established in Papua New Guinea (Green et al. 2007), an approach that will now be applied to MPA design throughout the CT.

Despite a substantial commitment to coral reef conservation on the ground, drastic international action on greenhouse gas emissions is still required to ensure the long-term survival of coral reefs in the CT and elsewhere around the world. The future of these mega-diverse reefs, and the livelihoods of the people who depend on them, will be determined by the success of these undertakings.

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