



Naturalis Repository

Understanding the murky history of the Coral Triangle: Miocene corals and reef habitats in East Kalimantan (Indonesia)

Nadiezhdha Santodomingo, Willem Renema & Kenneth G. Johnson

Downloaded from:

<https://doi.org/10.1007/s00338-016-1427-y>

Article 25fa Dutch Copyright Act (DCA) - End User Rights

This publication is distributed under the terms of Article 25fa of the Dutch Copyright Act (Auteurswet) with consent from the author. Dutch law entitles the maker of a short scientific work funded either wholly or partially by Dutch public funds to make that work publicly available following a reasonable period after the work was first published, provided that reference is made to the source of the first publication of the work.

This publication is distributed under the Naturalis Biodiversity Center 'Taverne implementation' programme. In this programme, research output of Naturalis researchers and collection managers that complies with the legal requirements of Article 25fa of the Dutch Copyright Act is distributed online and free of barriers in the Naturalis institutional repository. Research output is distributed six months after its first online publication in the original published version and with proper attribution to the source of the original publication.

You are permitted to download and use the publication for personal purposes. All rights remain with the author(s) and copyrights owner(s) of this work. Any use of the publication other than authorized under this license or copyright law is prohibited.

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the department of Collection Information know, stating your reasons. In case of a legitimate complaint, Collection Information will make the material inaccessible. Please contact us through email: collectie.informatie@naturalis.nl. We will contact you as soon as possible.

Understanding the murky history of the Coral Triangle: Miocene corals and reef habitats in East Kalimantan (Indonesia)

Nadiezha Santodomingo^{1,2} · Willem Renema² · Kenneth G. Johnson¹

Received: 3 August 2015 / Accepted: 16 February 2016 / Published online: 3 March 2016
© Springer-Verlag Berlin Heidelberg 2016

Abstract Studies on ancient coral communities living in marginal conditions, including low light, high turbidity, extreme temperatures, or high nutrients, are important to understand the current structure of reefs and how they could potentially respond to global changes. The main goal of this study was to document the rich and well-preserved fossil coral fauna preserved in Miocene exposures of the Kutai Basin in East Kalimantan, Indonesia. Our collections include almost forty thousand specimens collected from 47 outcrops. Seventy-nine genera and 234 species have been identified. Three different coral assemblages were found corresponding to small patch reefs that developed under the influence of high siliciclastic inputs from the Mahakam Delta. Coral assemblages vary in richness, structure, and composition. Platy coral assemblages were common until the Serravallian (Middle Miocene), while branching coral assemblages became dominant in the Tortonian (Late Miocene). By the late Tortonian massive coral assemblages dominated, similar to modern-style coral framework. Our results suggest that challenging habitats, such as the Miocene turbid habitats of East Kalimantan, might have played an important role during the early diversification of the Coral Triangle by hosting a

pool of resilient species more likely to survive the environmental changes that have affected this region since the Cenozoic. Further research that integrates fossil and recent turbid habitats may provide a glimpse into the dynamics and future of coral reefs as “typical” clear-water reefs continue to decline in most regions.

Keywords Mesophotic · Species turnover · Paleoenvironments · Diversity

Introduction

The exceptional biological diversity of the Indo-Australian Archipelago has captivated the interest of scientists for over a century (Wallace 1863). Marine diversity is mainly associated with coral reefs; hence, the region has been called the “Coral Triangle” (Hoeksema 2007). Despite the increasing documentation of species distributions (Bellwood et al. 2005; Carpenter et al. 2011), the mechanisms responsible for the origins and maintenance of the Coral Triangle biodiversity hotspot remain poorly understood (Halas and Winterbottom 2009; Bellwood et al. 2012).

The fossil record contains the only direct evidence of past biotic and environmental change, but to date most work on the fossil record of corals in the Coral Triangle has been based on taxonomic lists from relatively small collections (Wilson and Rosen 1998; Bromfield and Pandolfi 2012; Johnson et al. 2015b). These studies have revealed that regional richness has been high since at least the Late Oligocene, but in the absence of ecological information including species abundance, community assembly, and environmental context we cannot understand how coral ecosystems functioned in the past and which processes were responsible for diversification.

Communicated by Geology Editor Prof. Chris Perry

Electronic supplementary material The online version of this article (doi:10.1007/s00338-016-1427-y) contains supplementary material, which is available to authorized users.

✉ Nadiezha Santodomingo
nsantodomingo@gmail.com

¹ Department of Earth Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, UK

² Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands

In this study, we focus on the Miocene coral fauna of East Kalimantan using large new collections of well-preserved fossils. We benefit from a well-documented geological framework (Wilson 2005) and the results of a multidisciplinary effort to study the sedimentology, stratigraphy, paleoceanography, and other components of the biota such as foraminifera, coralline algae, mollusks and bryozoans in the same outcrops (Johnson et al. 2015a). We use these new data on diversity and habitats to reconstruct the Miocene history of the Coral Triangle. In particular, we document the changing distribution of diversity among habitats and compare ancient assemblages with present-day communities in similar habitats to better understand how the early history of the hotspot shaped the modern diversity of the Coral Triangle.

Geological setting

The studied exposures occur in the northeastern part of the Kutai Basin in East Kalimantan, Indonesia (Fig. 1). The

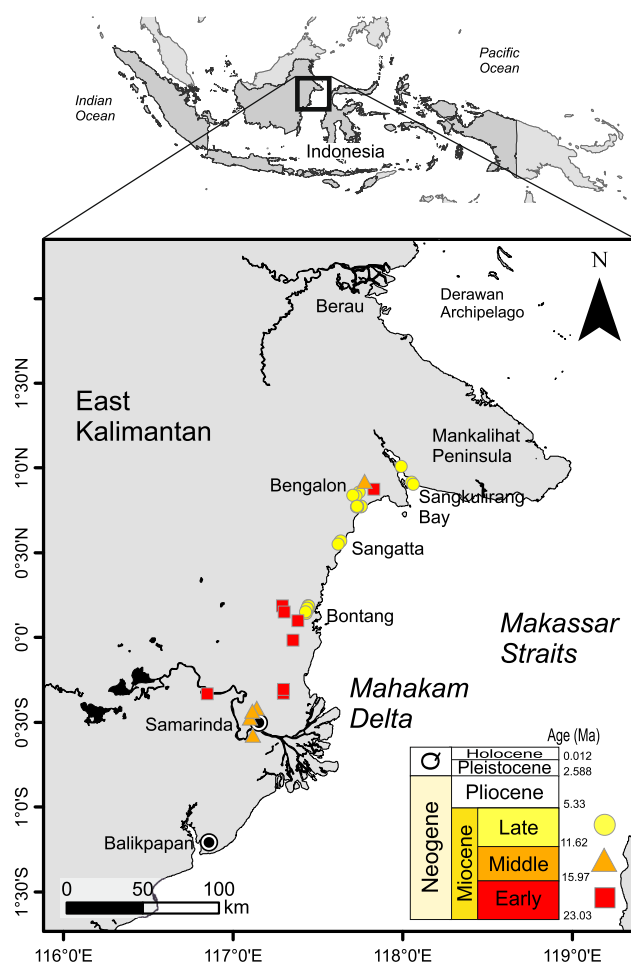


Fig. 1 Study area and location of the outcrops of the Throughflow Project (TF). Coordinates in Table 1

basin formed during the Middle Eocene via extensional tectonics that also resulted in the opening of the Makassar Straits and is characterized by intervals of subsidence, faulting, and uplift during the Late Eocene to Oligocene (Moss and Chambers 1999). Basin inversion during the late Early Miocene and progressive uplift of central Borneo during the Middle Miocene resulted in the deposition of thick clastic sedimentary units in rapidly prograding deltas (Wilson and Moss 1999; Marshall et al. 2015) including the delta of the ancestral Mahakam River. The modern delta is tidal-dominated due to its location on a coast characterized by relatively low wave energy. The regional oceanography is influenced by the southward-flowing Indonesian Throughflow Current that results in less turbid waters to the north favoring the recent concentration of carbonates around this area (Allen and Chambers 1998).

The sampled coral assemblages occur in small outcrops of mixed siliciclastic-carbonate facies that include series of clay shales, carbonaceous shales and siltstones to sandstones that have been dated using microfossils, magnetostratigraphy, and strontium isotope stratigraphy (Wilson 2005, 2012; Johnson et al. 2015a). Ages of the sampled units range from 5 to 20 Ma (Table 1; Electronic Supplementary Material, ESM, Fig. S1).

Materials and methods

Coral occurrences

Coral fossils were collected from 47 outcrops (Table 1) during two field campaigns (Johnson et al. 2015a). Sampling included removal of bulk sediment samples of 5–7 kg that were systematically collected within each unit containing coral fossils in each outcrop. Additional coral specimens were collected from the outcrop's surface during intervals of approximately 15 min within an area of approximately 1 m². In the laboratory, samples were soaked in water, washed, and wet sieved through a series of screens (5, 2 mm, 500 and 125 μm). Corals were picked from the larger than 2-mm sediment fractions. Finer fractions of 500 and 125 μm were partially used to complement sedimentary characterizations. All material included in this study is deposited in the collections of the Natural History Museum London (NHMUK).

Coral specimens were identified to the lowest taxonomic grade possible, according to their preservation and the taxonomic framework available for each group (see ESM, Taxonomic identifications). Because of the large number of specimens and ongoing rapid change in coral taxonomy (Budd et al. 2010), names for most morphotaxa were applied at a generic level with species left in open nomenclature pending detailed taxonomic study. An

Table 1 Location of outcrops and ages, including tallies of genera and species richness and respective occurrences

| Outcrop | Equivalent as | Group | Latitude | Longitude | Sector | Age min (Ma) | Age max (Ma) | Samples | Genera richness | Genera occurrences | Species richness | Species occurrences | Fragments | Weight (g) |
|---------|-----------------|-------|----------|-----------|------------|--------------|--------------|---------|-----------------|--------------------|------------------|---------------------|-----------|------------|
| TF10 | TF10 | - | -0.332 | 116.8497 | Samarinda | -20 | -18 | 1 | 4 | 4 | 4 | 5 | 5 | 2722.5 |
| TF11 | TF10 | - | -0.333 | 116.8488 | Samarinda | -20 | -18 | 1 | 6 | 6 | 6 | 11 | 11 | 1347.5 |
| TF18 | TF126 | P | 0.1847 | 117.293 | Bontang | -17.9 | -15.3 | 1 | 11 | 11 | 12 | 21 | 21 | 5403.5 |
| TF51 | TF51 | P | -0.5857 | 117.119 | Samarinda | -11.64 | -11.64 | 26 | 36 | 243 | 70 | 332 | 2616 | 49,546 |
| TF52 | TF12 | P | -0.4689 | 117.1213 | Samarinda | -15.3 | -14.8 | 3 | 16 | 21 | 20 | 49 | 61 | 10,677.5 |
| TF53 | TF6, TF7 | P | -0.3152 | 117.298 | Samarinda | -17.9 | -14.8 | 2 | 21 | 30 | 28 | 115 | 141 | 5507 |
| TF56 | TF8 | P | -0.322 | 117.2975 | Samarinda | -17.9 | -14.8 | 23 | 30 | 97 | 49 | 134 | 608 | 12,052 |
| TF57 | TF57 | P | -0.5847 | 117.1198 | Samarinda | -11.64 | -11.64 | 32 | 40 | 227 | 70 | 301 | 1839 | 58,422.1 |
| TF59 | TF13 | P | -0.0182 | 117.3535 | Bontang | -17.9 | -15.3 | 9 | 29 | 49 | 42 | 116 | 314 | 9239 |
| TF76 | TF3, TF9, TF165 | P | -0.4663 | 117.1218 | Samarinda | -15.3 | -14.8 | 5 | 17 | 20 | 20 | 40 | 87 | 6366.5 |
| TF79 | TF76 | P | -0.4323 | 117.1378 | Samarinda | -15.3 | -14.8 | 2 | 5 | 6 | 6 | 6 | 9 | 554 |
| TF102 | TF102 | B | 0.1673 | 117.4435 | Bontang | -9.8 | -9.4 | 9 | 23 | 84 | 32 | 108 | 3592 | 1669 |
| TF107 | TF102 | B | 0.189 | 117.4445 | Bontang | -9.8 | -9.4 | 1 | 2 | 2 | 2 | 2 | 38 | 368.5 |
| TF108 | TF102 | B | 0.1853 | 117.4464 | Bontang | -9.8 | -9.4 | 1 | 5 | 5 | 6 | 6 | 28 | 27 |
| TF110 | TF505 | B | 0.1405 | 117.4269 | Bontang | -9.8 | -9.4 | 8 | 17 | 57 | 29 | 74 | 2851 | 3332.1 |
| TF126 | TF21 | P | 0.1513 | 117.3044 | Bontang | -17.9 | -15.3 | 19 | 26 | 98 | 34 | 142 | 774 | 50,372 |
| TF130 | TF76 | P | -0.4812 | 117.1141 | Samarinda | -15.3 | -14.8 | 1 | 2 | 2 | 2 | 2 | 1405 | 2633 |
| TF151 | TF154 | B | 0.1672 | 117.4374 | Bontang | -9.8 | -9.4 | 2 | 7 | 8 | 7 | 8 | 21 | 36 |
| TF153 | TF153 | P | 0.0964 | 117.3804 | Bontang | -17.9 | -15.3 | 11 | 27 | 66 | 40 | 110 | 891 | 13,847.5 |
| TF154 | TF154 | B | 0.1673 | 117.4397 | Bontang | -9.8 | -9.4 | 9 | 19 | 93 | 33 | 156 | 14,629 | 4402.5 |
| TF168 | TF171 | B | 0.85696 | 117.7442 | Bengalon | -8 | -5 | 1 | 1 | 1 | 1 | 1 | 1 | 50 |
| TF171 | TF518 | B | 0.8361 | 117.7241 | Bengalon | -8 | -5 | 7 | 24 | 44 | 32 | 69 | 487 | 6878.5 |
| TF173 | TF174 | - | 0.7724 | 117.7551 | Bengalon | -7 | -6.4 | 1 | 4 | 4 | 4 | 11 | 14 | 435.5 |
| TF174 | TF271 | - | 0.7709 | 117.7531 | Bengalon | -7 | -6.4 | 1 | 4 | 4 | 4 | 6 | 6 | 711.5 |
| TF175 | TF175 | - | 0.7696 | 117.729 | Bengalon | -7 | -6.4 | 1 | 2 | 2 | 2 | 2 | 2 | 505 |
| TF271 | TF272 | - | 0.7723 | 117.755 | Bengalon | -7 | -6.4 | 1 | 2 | 2 | 2 | 2 | 2 | 154.5 |
| TF272 | TF272 | - | 0.8385 | 117.708 | Bengalon | -7 | -6.4 | 1 | 1 | 1 | 1 | 1 | 1 | 5131 |
| TF273 | TF522 | P | 0.9123 | 117.7766 | Kari Orang | -13 | -11.64 | 1 | 1 | 1 | 1 | 1 | 1 | 38 |
| TF274 | TF527 | - | 0.841 | 117.8679 | Bengalon | NA | NA | 1 | 1 | 1 | 1 | 1 | 2 | 1 |
| TF275 | TF525 | NG | 0.8749 | 117.8265 | Kari Orang | -20 | -18 | 1 | 14 | 14 | 19 | 23 | 858 | 1132 |
| TF500 | TF508 | B | 0.1674 | 117.4375 | Bontang | -9.8 | -9.4 | 4 | 4 | 8 | 7 | 9 | 69 | 2874 |
| TF501 | TF508 | B | 0.1615 | 117.4345 | Bontang | -9.8 | -9.4 | 2 | 2 | 3 | 2 | 3 | 3 | 2001 |
| TF502 | TF502 | M | 0.1413 | 117.4315 | Bontang | -9.8 | -9.4 | 5 | 29 | 47 | 43 | 65 | 628 | 30,206.5 |

Table 1 continued

| Outcrop | Equivalent | Analyzed as | Group | Latitude | Longitude | Sector | Age min (Ma) | Age max (Ma) | Samples | Genera richness | Genera occurrences | Species richness | Species occurrences | Fragments | Weight (g) |
|----------------------------------|------------|-------------|-------|----------|-----------|--------------|--------------|--------------|---------|-----------------|--------------------|------------------|---------------------|-----------|------------|
| TF504 | | TF508 | B | 0.1722 | 117.4377 | Bontang | -9.8 | -9.4 | 4 | 4 | 6 | 6 | 8 | 33 | 254.5 |
| TF508 | | TF508 | B | 0.1489 | 117.4282 | Bontang | -9.8 | -9.4 | 4 | 17 | 29 | 28 | 40 | 556 | 969 |
| TF510 | | TF510 | M | 0.7708 | 117.7356 | Bengalon | -7 | -6.4 | 7 | 19 | 29 | 28 | 43 | 71 | 31,382 |
| TF511 | | TF511 | M | 0.7718 | 117.7356 | Bengalon | -7 | -6.4 | 25 | 36 | 123 | 64 | 199 | 459 | 70,858.8 |
| TF512 | | TF512 | M | 0.7732 | 117.7316 | Bengalon | -7 | -6.4 | 5 | 19 | 34 | 32 | 61 | 152 | 9547 |
| TF516 | | TF516 | M | 0.5657 | 117.6325 | Sangatta | -9.3 | -8.9 | 22 | 30 | 112 | 61 | 162 | 455 | 31,179.5 |
| TF517 | | TF517 | M | 0.5678 | 117.6342 | Sangatta | -9.3 | -8.9 | 6 | 18 | 31 | 28 | 36 | 1411 | 8821.1 |
| TF522 | | TF522 | P | 0.9117 | 117.7739 | Kari Orang | -13 | -11.64 | 4 | 24 | 35 | 28 | 40 | 736 | 13,301 |
| TF526 | | TF526 | - | 0.8715 | 117.8263 | Kari Orang | -18 | -13 | 1 | 3 | 3 | 4 | 5 | 6 | 56 |
| TF529 | | TF530 | - | 0.9155 | 118.0526 | Sangkulirang | -7.3 | -5.4 | 1 | 1 | 1 | 1 | 1 | 1 | 5630 |
| TF530 | | TF530 | - | 0.9041 | 118.0635 | Sangkulirang | -7.3 | -5.4 | 1 | 2 | 2 | 2 | 2 | 2 | 2 |
| TF531 | | TF530 | - | 1.0064 | 117.9931 | Sangkulirang | -7.3 | -5.4 | 1 | 1 | 1 | 1 | 1 | 2 | 1 |
| TF533 | | TF533 | M | 0.7737 | 117.7303 | Bengalon | -7 | -6.4 | 3 | 19 | 33 | 29 | 58 | 163 | 9727.5 |
| TF534 | | TF517 | M | 0.5488 | 117.6198 | Sangatta | -9.3 | -8.9 | 2 | 7 | 7 | 7 | 7 | 46 | 1659.5 |
| Summary of datasets for analyses | | | | | | | | | | | | | | | |
| Full dataset | | | | 47 | | 279 | 83 | | 243 | | 2595 | | 36,108 | | 472,032.6 |
| Turnover analysis | | | | 46 | | 269 | 79 | | 234 | | 1940 | | 34,933 | | 467,340.5 |
| Ordination analysis (faunules) | | | | 23 | | 258 | 81 | | 235 | | 1957 | | 35,541 | | 451,772.8 |

Different collection events on the same outcrops are indicated as "equivalent". Outcrops of the same faunule are indicated as "analyzed as". Groups found in the ordination analyses are (B) Branching, (P) Platy and (M) Massive. (NG) no group and "-" were excluded from the analyses

occurrence is defined as the record of a taxon from a particular sample. Abundances of corals per sample were obtained both as the number of fragments and weight given by dry weight in grams. Coral growth forms include four principal categories: massive (massive and columnar), branching (ramose and phaceloid), solitary (free-living and flabello-meandroid), and platy (thin platy and tabular).

Diversity patterns

The raw coral occurrence dataset was first filtered to merge samples gathered from the same outcrop during different collection events. The full database includes 2595 occurrences from 279 samples in 47 outcrops (Table 1). Different subsets of the full data were prepared for the turnover and ordination analyses (ESM, Taxonomic identifications). For the turnover analyses, we discarded taxa with poor taxonomic resolution and outcrops outside the Miocene of East Kalimantan. This resulted in a dataset with 1940 occurrences from 46 outcrops. For the ordination analyses, data from outcrops from the same geographic sector within the same time interval were combined into faunules. This resulted in a dataset of 23 faunules and 1957 occurrences.

Statistical analyses were performed with the R statistical software environment (R-Core Team 2014). Ordinations were based on non-metric multidimensional scaling analysis (NMDS), using the meta-MDS function in the vegan package (Oksanen et al. 2013) that searches for a stable solution using several random starts and standardizes the resulting scaling. Bray–Curtis dissimilarities were used and analyses were tried for untransformed data and data transformed using the Wisconsin double standardization. Tests of groups were performed using the adonis function from the vegan package for the analysis and partitioning sums of squares using semi-metric and metric distance matrices. Insofar as this approach partitions sums of squares of a multivariate data set, it is directly analogous to the multivariate analysis of variance (MANOVA) and considered as a robust “permutational MANOVA” (McArdle and Anderson 2001) analogous to redundancy analysis. Ordinations are shown in two dimensions and were based on presence/absence data and untransformed fragments and weights. Outcrop TF275 was not included in the permutation multivariate analysis tests, as it could not be unambiguously assigned to groups observed in the ordination. However, including this outcrop within an additional group did not have a significant impact on the results of the analysis. Cumulative diversity curves were plotted for outcrops included in the ordination to assess sampling completeness for each faunule (ESM Fig. S2).

Taxonomic turnover was studied following methods in Johnson and McCormick (1999). For estimates of the range

of genera beyond the temporal scope of the studied material, pre-Miocene occurrences of genera were compiled from the taxonomic list of McMonagle (2012) and records from the Paleobiology database (<http://fossilworks.org>). Recent occurrences of genera were taken from the World Registry of Marine Species (WoRMS, Hoeksema and Cairns 2014). Turnover analysis at species level is limited to the Miocene coral assemblages of East Kalimantan. Rates of taxonomic turnover were estimated by counting taxa richness and the number of first and last occurrences of taxa within each stage of the Miocene. A taxon was recorded as present within a stage if the median age of the sample in which the taxon occurred fell within that stage. Range-through taxa were also counted to assess sample completeness among bins and are defined as taxa that were not recorded in samples within a bin but occurred in both older and younger bins.

Results

Coral assemblages

The Miocene fossil coral assemblages have 234 species from 79 genera, including 213 species from 67 genera of zooxanthellate scleractinians. A few azooxanthellate scleractinian corals were recovered, including the genera *Caryophyllia*, and *Flabellum*. Hydrozoans include three species of *Millepora* and one species of *Distichopora*. Octocorals were represented by *Heliopora* sp., *Isis* sp. and some unidentified octocoral sclerites. Overall, the most abundant genus is *Porites*, both in terms of number of fragments and weight, with branching *Porites* sp. 2 as the most abundant species in number of fragments. Platy *Porites* sp. 1 and massive *Porites* sp. 3 are within the top species with highest weight. Other abundant genera in number of fragments were branching *Seriatopora*, *Dictyariaea*, *Acropora* and *Stylophora*. In terms of weight, platy or massive forms of the genera *Dipsastraea*, *Cyphastrea*, and *Progyrosmilia* are among the most abundant genera.

Ordination analyses clearly differentiate three assemblages of fossil corals (Fig. 2). Differences among the three assemblages were consistently significant regardless of whether occurrence, number of fragments or weight were used in the analyses. Coral fauna from outcrop TF275 is a mixed community from shallow and deep waters that did not group within any of the three assemblages. The complete list of species found in each assemblage is shown in ESM Table S1, together with the top quartile of genera and species per assemblage (ESM Tables S2–S7). The first assemblage was characterized by platy corals (Figs. 3, 4) and contained the highest coral richness with 145 species,

from which 56% are known exclusively from this assemblage, for example *Cyphastrea* sp. B (Fig. 4d), ‘*Echinopora*’ *pelarangensis* (Fig. 4h), and *Cyphastrea* sp. C (Fig. 4i). Platy corals were dominant in outcrops TF51,

TF52, TF57, and TF76 in Samarinda, TF53 and TF56 in Badak, TF59, TF126, and TF153 in Bontang, and TF522 in Bengalon. The most common genera in the platy coral assemblage were *Porites*, *Leptoseris*, *Cyphastrea*, *Astrospora*, and *Pachyseris*, and among the most common species were *Porites* sp. 1 (Fig. 4c), *Cycloseris sinensis* (Fig. 4e), *Pachyseris* sp. 4 (Fig. 4i) and *Leptoseris* cf. *explanata* (Fig. 4g). The data on number of fragments (Fig. 3a) are very variable as platy corals were more abundant in outcrops TF51, TF52, TF53, TF57, and TF126 (Fig. 3; 50–90% of fragments), while branching corals were dominant in TF56, TF76, TF153, and TF522 (60–95% of fragments). Platy corals represented 50–90% of the total mass in each outcrop (Fig. 3b). Important species were the platy corals *Porites* sp. 1 concentrating about 25% of the total coral weight in this assemblage, followed by *Progyrosmilium* sp. 2, *Cyphastrea* sp. 3, *Progyrosmilium* sp. 1 and *Leptoseris* cf. *explanata*.

The second assemblage was dominated by branching corals (Figs. 3, 5). Ninety percent of the fragments from the Bontang outcrops TF102, TF110, TF154, TF171, and TF508 were branches. Species richness of the branching coral assemblage was the lowest of the three assemblages, with 71 species, of which only 23% are known exclusively from this assemblage, including seven species of *Acropora* (ESM Table S1). The most common genera were

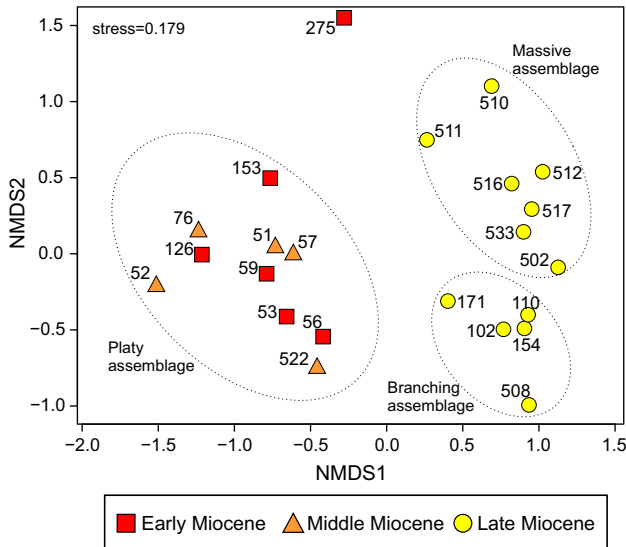


Fig. 2 Ordination (NMDS) of coral abundance data (weight) of the 23 faunules studied in the Miocene of East Kalimantan

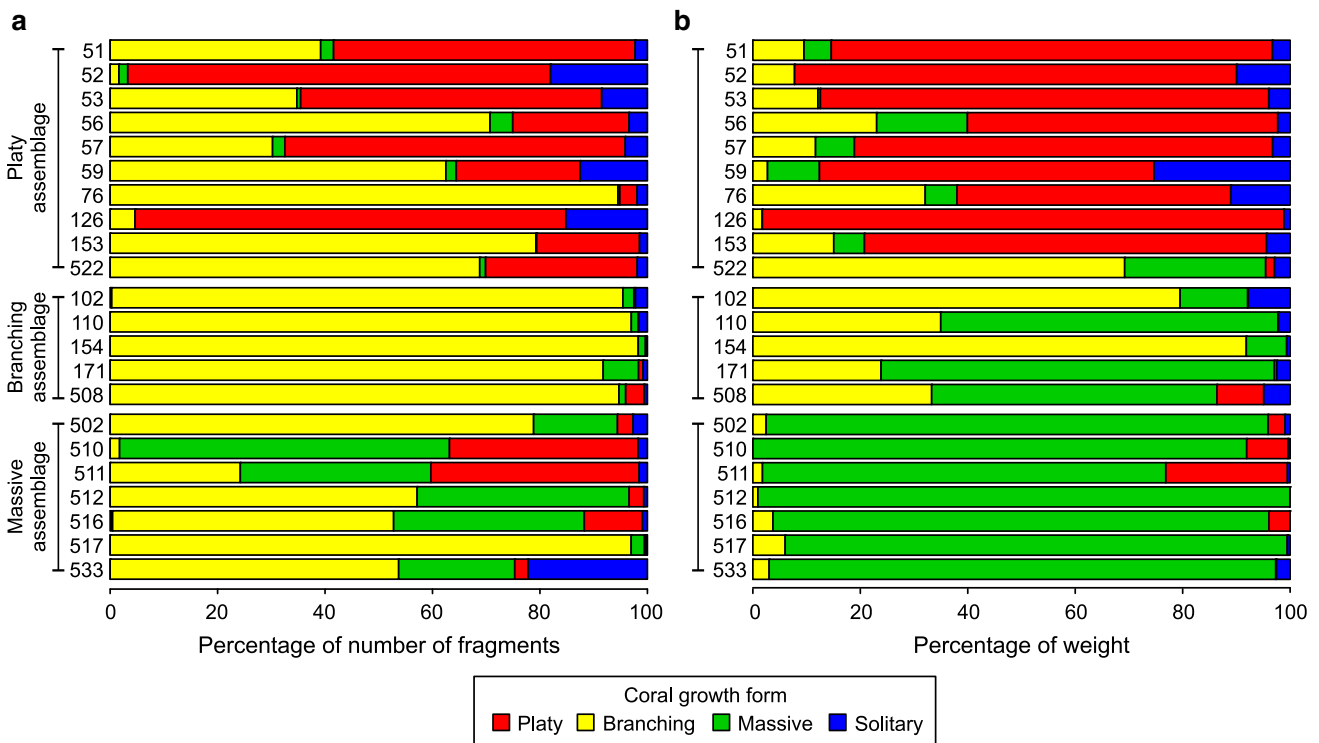


Fig. 3 Composition of the three coral assemblages of Miocene faunules studied in East Kalimantan. Abundances of colony growth forms are indicated in terms of (a) percentage by number of fragments and (b) percentage by weight

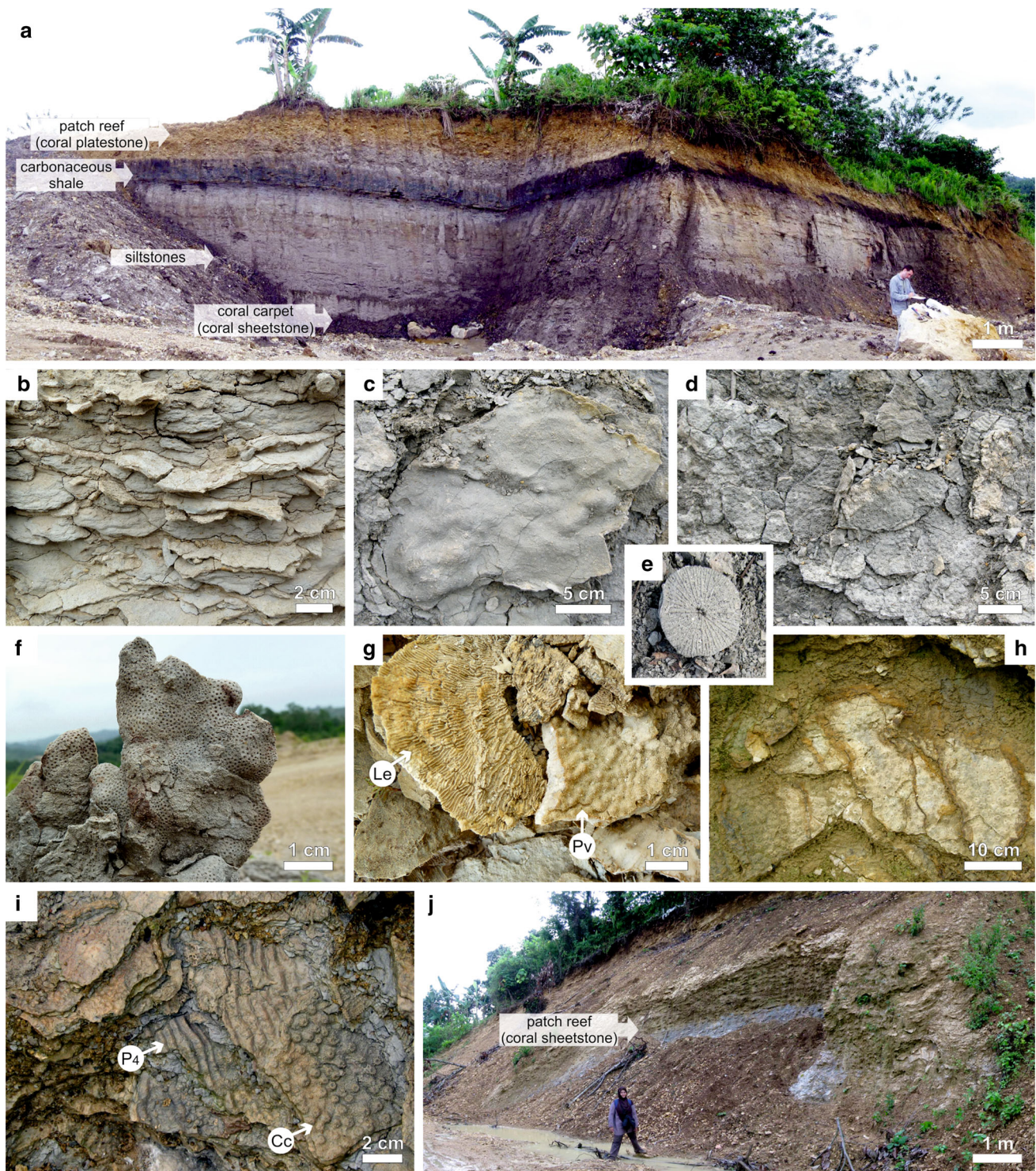


Fig. 4 Platy coral assemblages: **a** general view of outcrop TF56 in Badak, Samarinda; **b** stacks of platy corals in TF56, *Astreopora* and *Porites*; **c** *Porites* sp. 1 in TF76, Samarinda; **d** *Cyphastrea* sp. B. in TF52, Samarinda; **e** mushroom coral *Cycloseris* sp. in TF126, Bontang; **f** *Stylophora* sp. W, TF56, Badak; **g** *Leptoseris* cf. *explanata*

(Le) and *Pavona* cf. *varians* (Pv), TF59, Bontang; **h** large platy coral '*Echinopora*' *pelarangensis*, TF153, Bontang; **i** stacks of platy corals of *Pachyseris* sp. 4 (P4) and *Cyphastrea* sp. C (Cc) in TF153, Bontang; **j** general view of outcrop TF153 in Bontang

Seriatopora, *Acropora*, *Dictyaraea*, *Porites*, and *Montipora*, from which the most common species were the branching *Porites* sp. 2 (Fig. 5b), *Dictyaraea micrantha*

large (Fig. 5c), *D. micrantha* small (Fig. 5g), and *Seriatopora* cf. *irregularis* (Fig. 5g). *Porites* sp. 2 was also the most abundant coral in terms of number of fragments.



Fig. 5 Branching coral assemblages: **a** general view of outcrop TF110 (= TF505) in Bontang and some representative species (**b–f**); **b**, *Porites* sp. 2; **c** *Dictyaraea micrantha* with large corallites; **d** *Dictyaraea anomala*; **e** *Alveopora* sp. 1 (A1) and *Montipora dubiosa* (Md); **f** *Oulophyllia* sp. D; **g–h** some representative species in

TF154, Bontang; **g** *Seriatopora irregularis* (Si), *Porites* sp. 2 (P2), *D. micrantha* small corallites; **h** *Trachyphyllia* sp. A (TA), *M. dubiosa* (Md), *S. hystrix* (Sh), *Acropora duncani* (Ad); **i** *A. borneoensis* in TF110, Bontang; **j** general view of outcrop TF154

Scattered massive colonies of *Oulophyllia* sp. D (Fig. 5f), *Acanthastrea* sp. A and *Favites* sp. B, together made up about 30% of the coral weight in this assemblage.

The third assemblage was dominated by massive coral species (Figs. 3, 6). This dominance is best observed in the weight of corals in the assemblage (Fig. 3b). The massive

coral assemblage was found in outcrop TF502 in Bontang, TF510, TF511, TF512, and TF533 in Bengalon, and TF516 and TF517 in Sangatta. Coral richness was high with 123

species, from which 46% were found exclusively in this assemblage (ESM Table S1), for example *Platygyra* sp. N (Fig. 6h) and seven species of *Dipsastraea*. The most

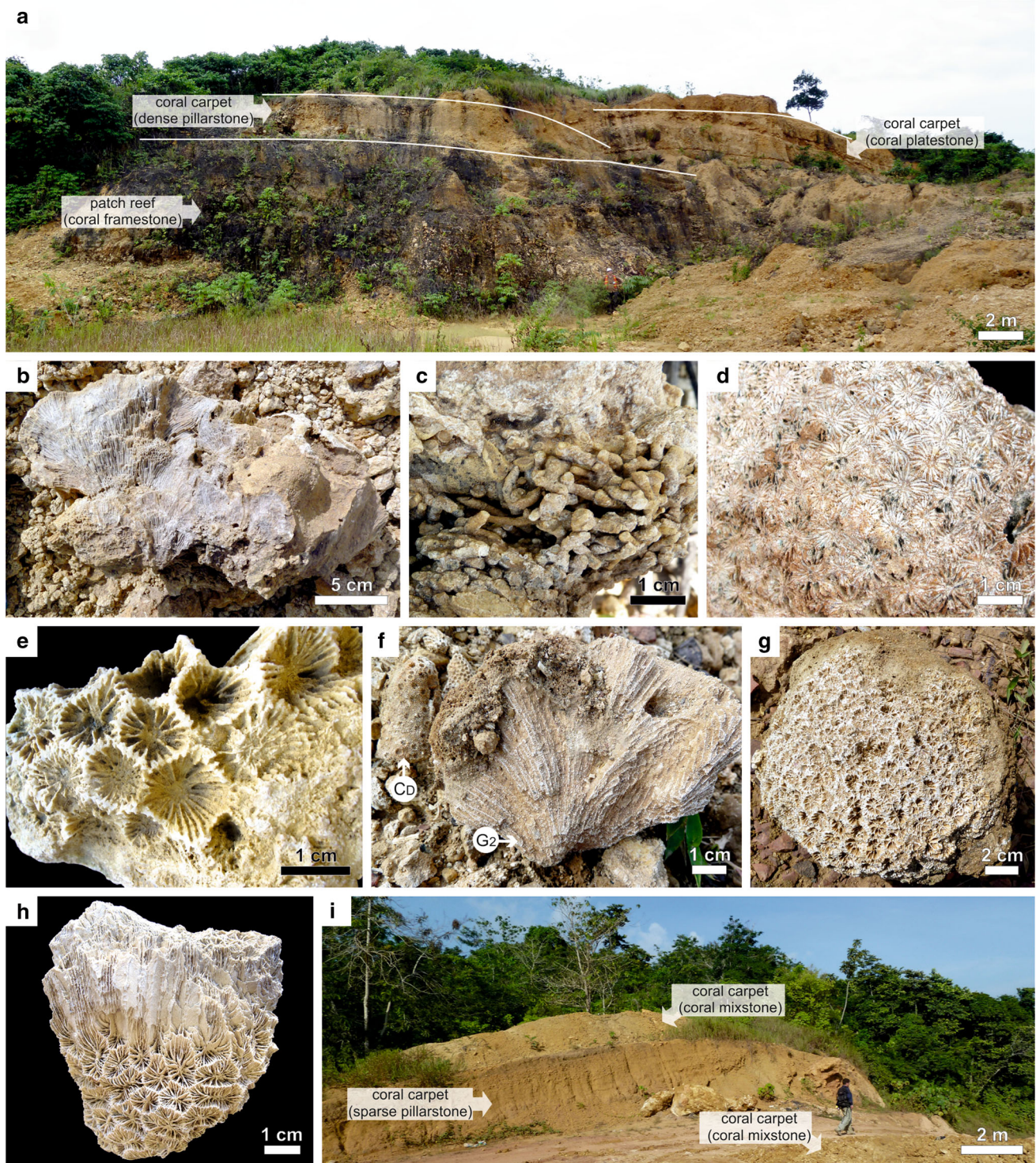


Fig. 6 Massive coral assemblages: **a** general view of coral framework in outcrop TF511, Bengalon and some representative colonies (**b–e**), mostly highly recrystallized; **b** large massive *Porites* sp. 3; **c** branching *Porites* sp. 2; **d** *Diploastrea* sp. B; **e** *Favites* sp. B; **f**, **g**, **i**,

some aragonitic colonies in outcrop TF516, Sangatta; **f** *Goniopora* sp. 2 (G2) and *Cyphastrea* sp. D (CD); **g** *Dipsastraea* sp. A; **h** *Platygyra* sp. N in TF517, Sangatta; **j** general view of outcrop TF516

common genera were *Porites*, *Dipsastraea*, *Platygyra*, *Cyphastrea* and *Favites*, and the most common species were the branching *Porites* sp. 2 (Fig. 6c), *Goniopora* sp. 2 (Fig. 6f), *Porites* sp. 3 (Fig. 6b), *Alveopora* sp. 1, *Dipsastraea* sp. A (Fig. 6g) and *Favites* sp. B (Fig. 6e). As measured by number of fragments, the most abundant species was the branching coral *Acropora hasibuani*, with 1120 fragments counted from a single collapsed colony recovered in outcrop TF517; this was followed by *S. hystrix*, *Porites* sp. 2, *Caulastraea* sp. A and *S. irregularis*. However, these branching corals did not contribute much to this assemblage in terms of weight, as they do not appear among the 30 most abundant species by weight. Massive *Dipsastraea*, *Favites* and *Platygyra* species, *Porites* sp. 3 and *Diploastrea* sp. B (Fig. 6d) are the most abundant by this measure.

Of the 22 species from 15 genera that were found in all three assemblages, *Porites* sp. 2 and *Goniopora* sp. 2 were also among the abundant species in all outcrops. Branch fragments of *S. hystrix*, *Dictyariaea* spp., and *Alveopora* sp. 1 were usually recovered from the smaller fractions of most samples (2–5 mm).

Reef habitats

Combined evidence including larger benthic foraminifera, coralline calcareous algae and sedimentology indicates that the three coral assemblages occurred in transient reef environments in a region dominated by clastic sedimentation (Wilson 2005; Renema et al. 2015). As part of the dynamics of the Kutai Basin, in particular the development of the Mahakam delta, these ephemeral reef habitats comprise 1–3 cycles of coral development (Figs. 4, 5, 6). Most of the habitats have been interpreted as low-relief patch reefs or coral carpets that developed in low-light environments, mainly controlled by siliciclastic input (sedimentation rate, frequency and grain size) and position on the continental platform with respect to river influence (Wilson 2005; Novak and Renema 2015).

Platy coral assemblages were deposited as coral sheetstones or platestones in a range of habitats characterized as varying from the delta front to shelf edge (Novak and Renema 2015). Platy coral assemblages on top of carbonaceous shales in outcrops TF51 and TF57 near Samarinda have been interpreted as developing in a pro-delta setting (shallow water) under low-light conditions within the highest range of terrigenous input that is not lethal for coral growth (Santodomingo et al. 2015b). This interpretation could be extended to outcrops TF53 and TF56 in Badak, as cycles of coral growth were observed both on top and below the carbonaceous shale (Fig. 4a). Platy coral assemblages in TF126 near Bontang developed in pro-delta

settings under low-light conditions in deeper habitats with little differentiation in subhabitats (Novak et al. 2013). Platy coral assemblages in the Batu Putih outcrops TF52 and TF76 of Samarinda are similar to those in TF126. The presence of shelf slope deposits below coral units and clays with planktonic foraminifera between the coral units indicates a position close to the shelf edge. The larger benthic foraminifera assemblages are more differentiated and include shallower (TF130) and deeper (TF52, TF76) facies (Novak and Renema 2015).

Branching coral assemblages are deposited as sparse or dense pillarstones within clay-rich siliciclastic sediments, interpreted as shallow coral carpet environments. In some outcrops, branching coral carpets intercalate with facies interpreted as seagrass environments with sparse branching corals (Reich et al. 2015a, b), for example in outcrop TF110 in Bontang (Fig. 5a). By definition, coral carpets develop as veneers along level seabeds that do not acquire significant relief (Riegl and Piller 2002). The benthic foraminiferal assemblage in these outcrops is characterized by species of the genus *Cellanthus* that are the most tolerant to high terrestrial influence (Renema 2006). The mollusk fauna is typical of seagrass beds (Reich et al. 2015a). These observations suggest that branching coral assemblages occurred in shallow lagoonal paleoenvironments with high terrestrial influence (Kusworo et al. 2015).

Massive coral assemblages occur in two habitats. First, they appear in mixed facies with branching corals in outcrops TF516 (Fig. 6i), TF517, and TF534 near Sangatta. The larger benthic foraminifera assemblage in these settings is typical for areas further away from deltaic settings, with locally abundant occurrences of *Operculina*, as well as *Heterostegina* cf. *depressa*, *Amphistegina radiata*, and *Calcarina* sp. (Renema and Troelstra 2001; Renema et al. 2015). The massive coral assemblages developed in lagoonal environments similar to those interpreted for branching coral communities, but with lower terrigenous input. In the second type of habitat, massive coral assemblages in outcrops TF510 and TF511 near Bengalon developed in consolidated framestones in reef structures of up to 40 m high (Fig. 6a). The outcrops TF512 and TF533 are located about 400 m west of TF510 and TF511 and include a mixed branching and massive coral assemblage that is interpreted as occupying back reef environment (Renema et al. 2015). On top of coral framestones in TF511, larger benthic foraminifera packstones to grainstones were deposited. These are dominated by *Operculina*, with rare *Palaeonummulites*, and *Amphisorus*, typical for midshelf conditions at >10 m depth (Renema and Troelstra 2001). Although these reef structures formed considerable relief on the sea floor, the shallowest parts did not develop into waters <10 m deep.

Coral assemblages in time and space

The coral assemblages of East Kalimantan are not distributed evenly in time ($p = 0.002$) nor space. Platy coral assemblages are dominant in the Burdigalian to Serravallian, branching coral assemblages are dominant in the Tortonian, and massive coral assemblages become dominant in the Messinian. The coral assemblages are also geographically unevenly distributed ($p = 0.001$), with platy coral assemblages concentrated toward the south of the study area, and branching and massive coral assemblages to the north. Exceptions to this general pattern are the platy coral assemblages in outcrops around Kari Orang (Bengalon) such as TF522, located in the northernmost part of the study area (Fig. 1). Single units with facies of platy corals were also observed in outcrop TF504 in Bontang and in outcrop TF511 in Bengalon. Nevertheless, the fauna of these latter outcrops grouped together with the branching coral and massive coral assemblages, respectively.

Stratigraphic ranges for the 79 genera found in this study are presented in Fig. 7 and for the 234 species in Fig. 8. We found that there was no significant taxonomic turnover at generic level in the Miocene of East Kalimantan (Fig. 9a, c). From the 69 genera in the Burdigalian, only 12% had their first occurrence in this period and none became extinct. During the Langhian and Serravallian, only the genus *Placosmiliopsis* was added to the assemblages while this genus and three others, namely *Pironastrea*, *Actinastrea*, and *Cyathoseris* became globally extinct. Slightly greater changes were observed during the Tortonian and Messinian, with the first occurrence of four genera in the Tortonian and five genera in the Messinian, and only two genera became extinct, *Scalariogyra* and *Fungophyllia* (Fig. 10c). *Anisocoenia* (Fig. 10a), *Progyrosmilia* (Fig. 10b), *Dictyaraea* (Fig. 10c) and *Amphelia* occurred up to the early Pliocene ~5 Ma, when they subsequently became extinct.

Faunal turnover in East Kalimantan assemblages is more dynamic at species level (Fig. 8). About half of the identified species were already present in the Burdigalian, with only 13% of the species first occurring in the Langhian and 20% in the Serravallian (Fig. 9b, d). Significant turnover is associated with the Serravallian to Tortonian boundary, as 39% of the species became locally extinct in the Serravallian and 48.5% of the species first appeared in the Tortonian. During the Tortonian a further 36% of the species disappeared, whereas 22% of the species were first observed during the Messinian. Current taxonomic resolution does

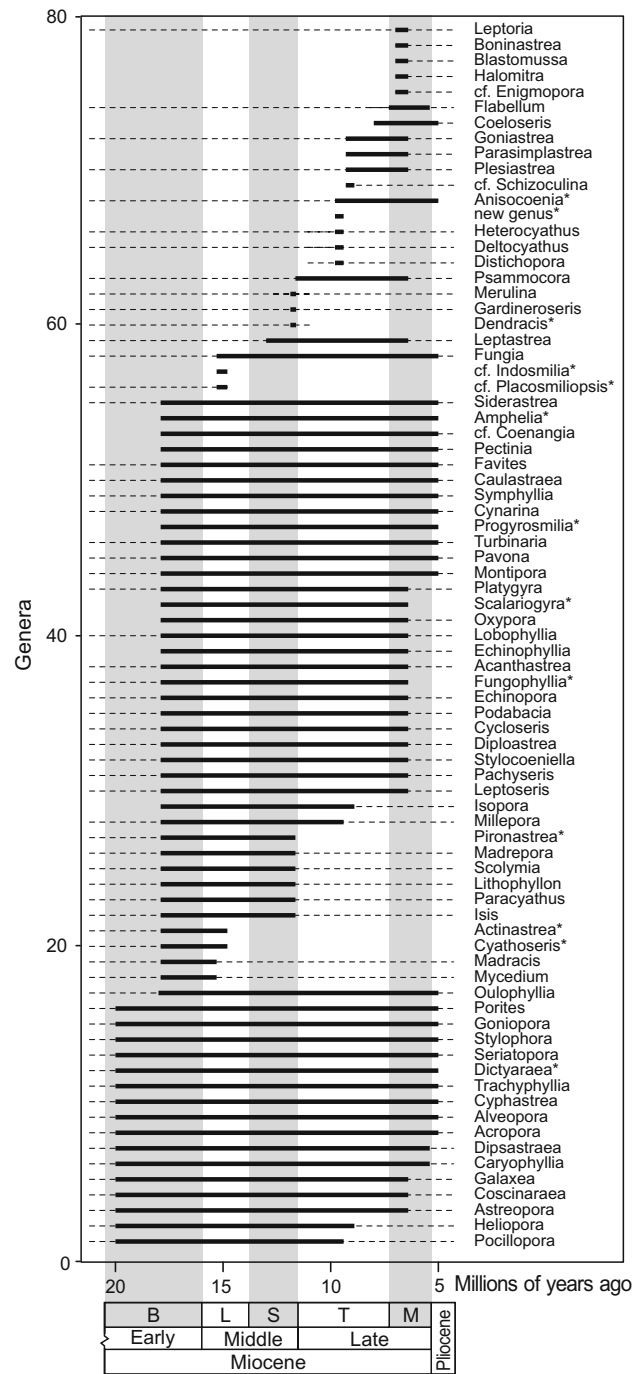


Fig. 7 Ranges of 79 genera of corals that occurred during the Miocene of East Kalimantan, Indonesia. Dotted lines to the left indicate pre-Miocene occurrences, dotted lines to the right indicate extension of ranges to the Recent, and asterisks are globally extinct genera. Stages of the Miocene are Burdigalian (B), Langhian (L), Serravallian (S), Tortonian (T), and Messinian (M)

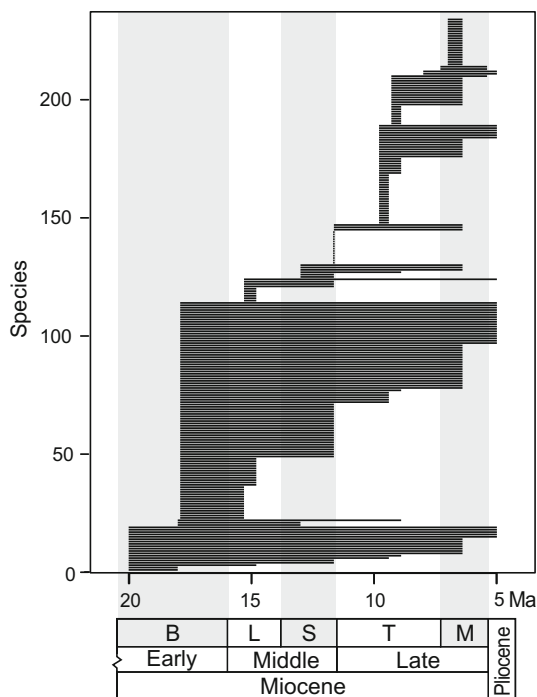


Fig. 8 Ranges of the 234 morphospecies identified in Miocene outcrops of East Kalimantan. Stages of the Miocene as in Fig. 7

not permit rigorous comparison with the extant fauna or with fossil assemblages from elsewhere in the region at a species level.

Discussion

Estimating abundance in highly diverse assemblages

In this study, the high richness and composition of coral fossils in Miocene environments of East Kalimantan were evaluated by collecting large volumes of sediments using ecological sampling methods, and estimating abundances using occurrences, number of fragments and weights. All methods revealed that corals were distributed in three distinct assemblages, but each method showed different aspects of the composition and structure of the assemblages. Occurrences indicated how frequent the taxa were among outcrops, but the contribution of common species with low abundances, such as *S. hystrix*, tended to be overestimated. Number of fragments was also biased, as branching corals and thin platy corals are more easily fragmented than massive corals so that numbers of

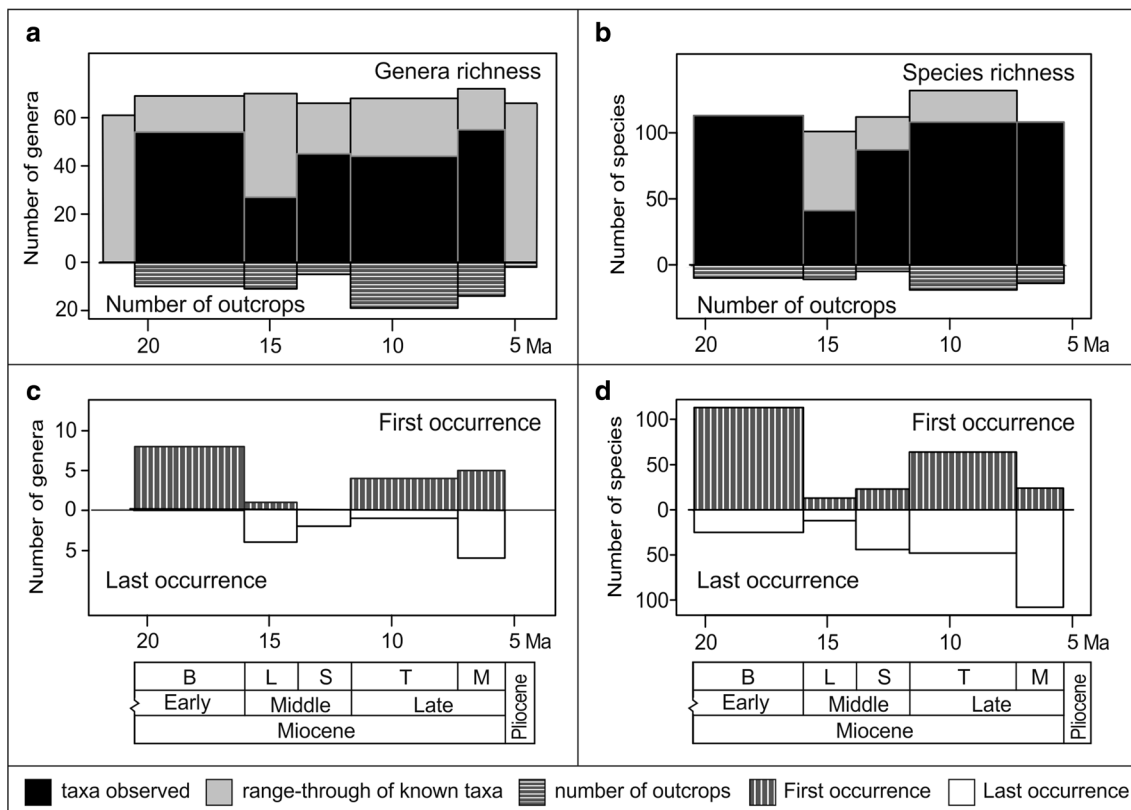


Fig. 9 Number of genera (a), species (b) and taxonomic turnover of genera (c) and species (d) during the Miocene in East Kalimantan. Stages of the Miocene as in Fig. 7

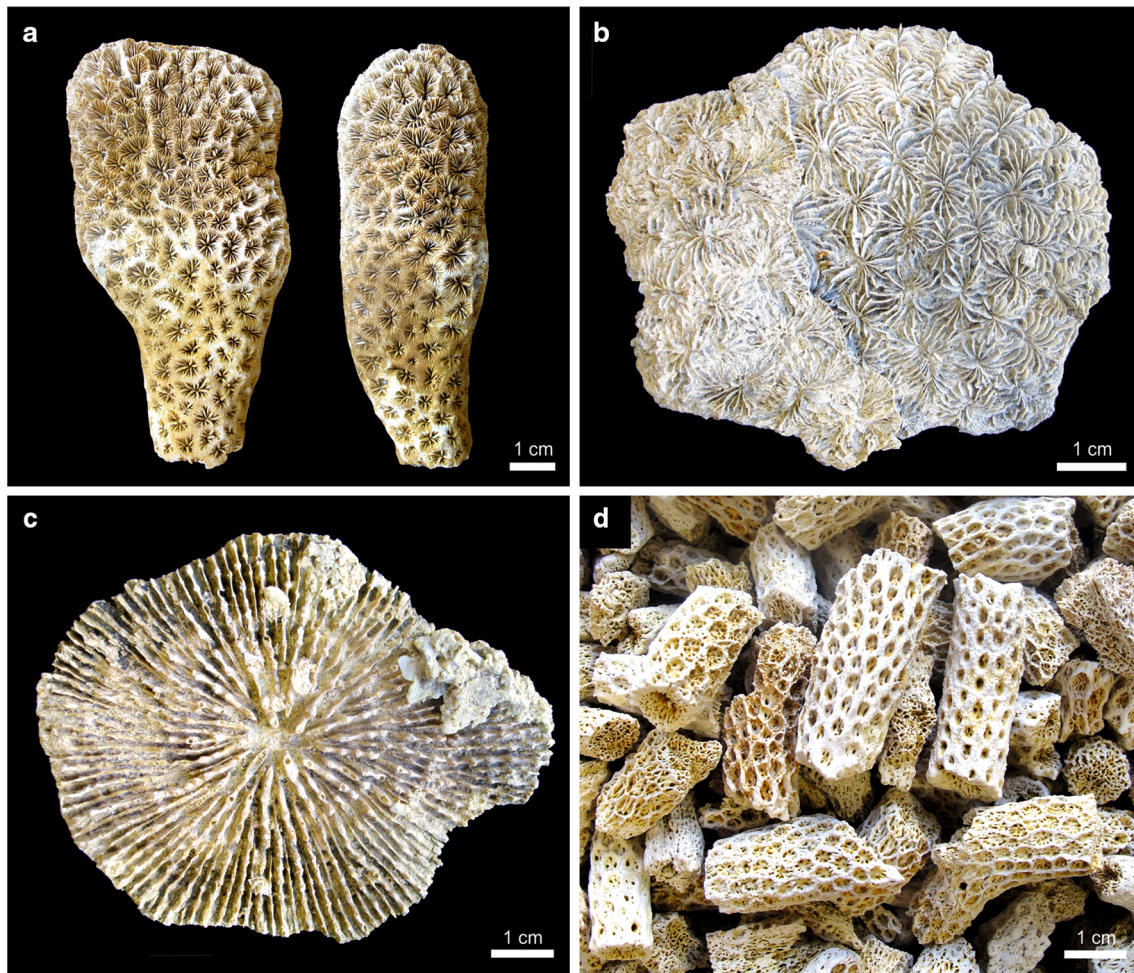


Fig. 10 Examples of globally extinct coral genera from the Miocene fauna of East Kalimantan. **a** *Anisocoenia variabilis*, NHMUK PI AZ8809 TF517, Sangatta. **b** *Progyrosmilia* sp. 1., NHMUK PI AZ

6669,TF56, Badak. **c** *Fungophyllia aspera*, NHMUK PI AZ9445, TF153, Bontang. **d** *Dictyaraea anomala* NHMUK PI AZ 5950, TF102, Bontang

fragments were much higher in units from the branching assemblage than in the massive assemblage. Weight of the coral fossils was expected to offer a better estimation of abundance, as weight encompasses the contribution of each taxon to the total amount of carbonate produced in the outcrop regardless of how fragmented the coral colonies are. Indeed, the composition of the three coral assemblages was better illustrated by the weight percentages of the colony forms (Fig. 3b) in comparison with the percentage of the number of fragments that showed higher abundances of branching corals regardless of the assemblage (Fig. 3a). Preservation could potentially bias weight estimations, as pore space in coral skeletons is filled either with fine-grained sediment or diagenetically produced carbonate. However, we observed that preservation was uniform within facies in each outcrop and it did not affect the results of the ordination (Fig. 2), as faunules of light aragonitic corals (TF 516–517, Fig. 6f–h) grouped together with faunules of highly recrystallized corals (TF510–

TF511, Fig. 6b–e). In conclusion, extensive systematic collections that include abundance data of taxa in terms of weight should be preferred over number of fragments as weights give a better estimation of the composition of coral assemblages.

Coral assemblages and reef habitats

Corals in East Kalimantan during the Miocene occurred in three different assemblages that varied in time and space. Independent information from larger benthic foraminifera, coralline algae and sedimentology (Novak and Renema 2015; Rösler et al. 2015) indicates that low light levels and high siliciclastic inputs characterized the habitats in which corals developed during their early history. Corals coped with the regime of turbid conditions that dominated the habitats of the Kutai Basin during the Miocene by adopting different strategies that in turn allow further interpretations of the environments in which they occurred. Platy coral

assemblages are common in the fossil record (Rosen et al. 2002). Flattening of the colonies has been interpreted as an eco-physiological strategy that zooxanthellate corals adopt to optimize the capture of light in poorly lit environments without compromising carbonate deposition (Fricke and Schuhmacher 1983). Reduced light levels in the Kutai Basin have been related to siliciclastic inputs and probably high sediment resuspension in low-energy environments (Wilson 2005; Santodomingo et al. 2015b). The largest platy colonies observed in these habitats covered up to 1 m² (Fig. 4h), but only reached a few millimeters thickness. Platy assemblages usually form dense accumulations (Fig. 4b) of stacked colonies of different species (Fig. 4i), suggesting that competition was a dominant mechanism that favored the highest coral richness observed in these assemblages. Branching coral assemblages may have developed under higher turbidity and sedimentation regimes, as fast-growing ramose forms seem to cope better with siliciclastic inputs by minimizing the horizontal surface exposed to sediment suffocation (Sanders and Baron-Szabo 2005). Branching assemblages have about half the number of species compared to the platy assemblage, suggesting that fewer taxa could cope with more challenging environmental conditions in these settings. Massive coral assemblages are interpreted to have developed under higher light levels, probably related to lower siliciclastic inputs and higher hydrodynamic levels, allowing the development of large framework structures. However, massive colonies with large corallites can also be efficient at sediment rejection (Stafford-Smith and Ormond 1992) and are dominant in environments with episodic terrigenous inputs (Loya 1976). Coral richness in these assemblages is high due to mixing with branching assemblages most likely due to local habitat partitioning. In a few outcrops, the corals developed a framework similar to modern reefs with differentiated front and back reef zones.

Did coral assemblages of the Kutai Basin respond to regional or global drivers?

One possible explanation for the observed variation in fossil coral assemblages is that the fauna responded to the local evolution of the Kutai Basin. Platy coral assemblages from the Burdigalian to Serravallian are distributed in the south (Samarinda), middle (Bontang), and north (Bengalon) of the study area. These habitats are interpreted as located in the delta front or pro-delta of rivers, suggesting that during this time terrestrial drainage was distributed homogeneously along the coast, resulting in the episodic appearance of low-relief patch reefs that waxed and waned as minimum thresholds of light and sediment input allowed coral development. Continuous faulting during the middle to late Miocene transition changed the drainage dynamics

(Moss and Chambers 1999) and probably had an effect on the local distribution of habitats, promoting the appearance of lagoonal environments to the north, where branching and massive coral assemblages could develop. However, more data from independent biotic and abiotic indicators are required to test this hypothesis and better understand the distribution of habitats throughout the Miocene in the study area.

A second alternative is that coral assemblages responded to global environmental changes. According to detailed descriptions of coral carbonates in Mediterranean areas, small patch reefs that did not build structures to sea level but thrived in meso-oligophotic conditions were common in the early Miocene and pre- to late Tortonian assemblages (Pomar and Hallock 2007). Although there are some reports of euphotic reefs in the middle Miocene of Egypt (Perrin 2000) and Turkey (Vescogni et al. 2014), extensive barrier reefs that reached sea level and exhibit zonation similar to that of modern reefs became common in the Mediterranean during the late Tortonian to early Messinian (Pomar et al. 2012). These authors suggest that the change in dominance of corals in high-light environments at shallower depths during the late Miocene was the result of acquisition of more diverse *Symbiodinium* lineages (Lajeunesse 2005). The increased ability of corals to tolerate higher light levels was coeval to changes in the geochemistry of seawater (rising of Mg:Ca ratios) that may also have increased the potential of corals to build skeletons at higher calcification rates (Pomar and Hallock 2008). Coral assemblages of East Kalimantan show a similar temporal distribution to that of the Miocene Mediterranean analogs: common low-relief patch reefs of platy corals dominated the environments up to the Serravallian, coral carpets were common pre- to late Tortonian, and the first appearance of a large framework (TF510, TF511) dates from the Messinian, although the latter did not grow to sea level. Nevertheless, more data are needed from other regions to establish the extent of this temporal change in coral assemblages of the Indo-Pacific.

Faunal turnover and modern coral fauna

Our data show that there was no significant turnover of coral genera in the fauna of East Kalimantan during the Miocene (Fig. 9a, c). Faunal turnover occurred at species level in the study area (Fig. 9b, d), but we currently lack a consistent taxonomic framework for most groups that would allow comparison with modern or other fossil assemblages. The only sufficiently documented taxon so far is the staghorn coral *Acropora*, which had differential turnover among species groups. Most of the species in the *horrida*, *humilis* and *elegans* groups that occurred in the Miocene of East Kalimantan are still living on modern

reefs, while most of the species in the *florida* and *aspera* group became extinct and/or were replaced by new species that occupy similar habitats (Santodomingo et al. 2015a).

We observed a change in dominance of genera of the Miocene assemblages relative to modern reefs in the region. Platy coral assemblages of the Burdigalian to Serravallian had abundant *Progyrosmilia*, *Cyphastrea* and agariciids (*Leptoseris* and *Pachyseris*). *Progyrosmilia* became extinct sometime in the early Pliocene, but *Cyphastrea*, *Leptoseris* and *Pachyseris* are still abundant and dominant in mesophotic environments. In contrast to the shallow turbid habitats that *Leptoseris* and *Pachyseris* occupied in the Miocene, on modern reefs these genera are typical dwellers of the deeper zones of clear-water reefs (Kahng et al. 2010; Bridge et al. 2011) or shallow low-light environments such as caves and overhangs (Dinesen 1983). In contrast, platy corals with low abundance in shallow turbid reefs during Miocene, such as *Turbinaria* and *Montipora*, became dominant on modern reefs (van Woesik et al. 1999; Browne et al. 2012). *Porites* shows a relatively stable response to regional changes as it is common and dominant since the Miocene.

Another important change in taxa occurred in the branching assemblage. *Dictyariaea* species were dominant in Miocene assemblages but became extinct in the early Pliocene. *Acropora* was diverse in the Miocene but it did not become abundant until the Plio-Pleistocene and has since become a dominant genus in modern reefs. Other abundant corals during the Miocene were the pocilloporids *Seriatopora* and *Stylophora* that continue to thrive on modern reefs together with *Pocillopora* (Veron 2000), but *Pocillopora* was rare in Miocene assemblages. Massive coral assemblages appear to have similar composition since their first occurrence in the late Miocene, as *Dipsastraea* and *Favites* are also dominant in modern coral frameworks (Best et al. 1984).

The murky history of the early Coral Triangle

Our results show that although patch reefs from the Kutai Basin developed in turbid habitats, they contained high richness of coral species and genera similar to the Recent fauna of clear-water reefs in Indonesia (Moll 1983) and the Great Barrier Reef (DeVantier et al. 2006).

Our results also suggest that habitats currently regarded as suboptimal, such as the turbid Miocene habitats of East Kalimantan, might have played an important role during the early diversification of the Coral Triangle by hosting a pool of species tolerant to high sediment inputs and low-light conditions that could potentially occupy a wider number of habitats as they became available. The potential role of turbid environments as past cradles of diversification and current refugia demands further study as modern

turbid settings located in the near-shore are increasingly damaged by present-day anthropogenic stressors (Edinger et al. 1998; Done 1999; Rogers 2013; Cleary et al. 2014).

In the search for candidate refugia habitats, investigations have been focused on resilient marginal ecosystems, such as deep mesophotic habitats in clear waters (Bongaerts et al. 2010; Smith et al. 2014). Mesophotic habitats located in clear, deep waters could potentially escape from current impacts such as pollution, storms and bleaching, yet they only host about 25% of shallow-water species and could only serve as a refugium for species with broad depth tolerances (Bongaerts et al. 2010; Muir et al. 2015). On the other hand, shallow turbid habitats might be more promising candidates to replenish populations diminished by mass mortality events in localities with low coastal development hence limited impacts due to pollution, destructive fisheries, tourism, etc. For example, corals growing in turbid waters in Palau bleached less during the 2010 event than those in clearer, offshore waters, even though they experienced the highest temperatures (van Woesik et al. 2012). Turbidity may act as a buffer of thermal stress for the coral-zooxanthellae symbiosis by reducing the effect of irradiance and preventing corals from bleaching (Iglesias-Prieto and Trench 1994). A recent modeling exercise predicted that major coral builders of the genus *Porites*, *Dipsastraea*, *Acropora* and *Montipora* from near-shore turbid habitats could potentially survive ocean warming thanks to shading by turbidity and proposed that turbid areas could be coral refuges under the current scenario of ocean warming (Cacciapaglia and van Woesik 2015). Furthermore, increasing evidence suggests that during the Holocene well-developed reefs with high accretion rates do exist in some shallow turbid habitats characterized by continuous high sedimentation and terrigenous inputs (Perry et al. 2009, 2012; Ryan et al. 2016).

In this context, our results provide more evidence to support the importance of turbid habitats for the survival of corals in the long term, as we found that during the Miocene these habitats hosted a high coral diversity that could cope with ancient environmental changes. We also suggest that turbid habitats have played a critical role during the origins and early history of the Coral Triangle. Further understanding of the dynamics of fossil reefs that developed in turbid habitats may provide a glimpse into the future of reef systems as “typical” clear-water reefs continue to decline in most regions.

Acknowledgments We are grateful for the support of colleagues from the Throughflow Project funded by the Marie Curie Actions Plan, Seventh Framework Programme of the European Union (Grant No. 237922). Thanks to Brian Rosen, Bert Hoeksema, Zarinah Waheed and Danwei Huang for interesting discussions. Jill Darrell, Lyndsey Douglas, and Lil Stevens assisted with the collections curation, and we gratefully acknowledge the enthusiastic support of

Ali Thomas and the NHM “V-Factor” volunteers for sample processing. This study was conducted under research license 0266/SIP/FRP/XI/2010 issued by RISTEK with special thanks to Professor Fauzie Hasibuan of the Indonesian Geological Agency.

References

- Allen GP, Chambers JLC (1998) Sedimentation in the Modern and Miocene Mahakam Delta. Indonesian Petroleum Association, Jakarta, Indonesia
- Bellwood DR, Renema W, Rosen BR (2012) Biodiversity hotspots, evolution and coral reef biogeography: a review. In: Gower DJ, Johnson KG, Richardson JE, Rosen BR, Rüber L, Williams ST (eds) Biotic evolution and environmental change in Southeast Asia. The Systematics Association Special Volume Series, 82. Cambridge University Press, New York, USA, pp 216–245
- Bellwood DR, Hughes TP, Connolly SR, Tanner J (2005) Environmental and geometric constraints on Indo-Pacific coral reef biodiversity. *Ecol Lett* 8:643–651
- Best MB, Boekschoten GJ, Oosterbaan A (1984) Species concept and ecomorph variation in living and fossil Scleractinia. *Palaeontographica Americana* 54:70–79
- Bongaerts P, Ridgway T, Sampayo EM, Hoegh-Guldberg O (2010) Assessing the “deep reef refugia” hypothesis: focus on Caribbean reefs. *Coral Reefs* 29:309–327
- Bridge TCL, Fabricius KE, Bongaerts P, Wallace CC, Muir PR, Done TJ, Webster JM (2011) Diversity of Scleractinia and Octocorallia in the mesophotic zone of the Great Barrier Reef, Australia. *Coral Reefs* 31:179–189
- Bromfield K, Pandolfi JM (2012) Regional patterns of evolutionary turnover in Neogene coral reefs from the central Indo-West Pacific Ocean. *Evol Ecol* 26:375–391
- Browne NK, Smithers SG, Perry CT (2012) Coral reefs of the turbid inner-shelf of the Great Barrier Reef, Australia: an environmental and geomorphic perspective on their occurrence, composition and growth. *Earth Sci Rev* 115:1–20
- Budd AF, Romano SL, Smith ND, Barbeitos MS (2010) Rethinking the phylogeny of scleractinian corals: a review of morphological and molecular data. *Integr Comp Biol* 50:411–427
- Cacciapaglia C, van Woessik R (2015) Climate-change refugia: shading reef corals by turbidity. *Glob Chang Biol*. doi:10.1111/gcb.13166
- Carpenter KE, Barber PH, Crandall ED, Ablan-Lagman MCA, Mahardika GN, Manjaji-Matsumoto BM, Juinio-Meñez MA, Santos MD, Starger CJ, Toha AH (2011) Comparative phylogeography of the Coral Triangle and implications for marine management. *J Mar Biol* 2011 [doi:10.1155/2011/396982]
- Cleary D, Polónia A, Renema W, Hoeksema B, Wolstenholme J, Tuti Y, de Voogd N (2014) Coral reefs next to a major conurbation: a study of temporal change (1985–2011) in coral cover and composition in the reefs of Jakarta, Indonesia. *Mar Ecol Prog Ser* 501:89–98
- DeVantier LM, De’ath G, Turak E, Done TJ, Fabricius KE (2006) Species richness and community structure of reef-building corals on the nearshore Great Barrier Reef. *Coral Reefs* 25:329–340
- Dinesen ZD (1983) Shade-dwelling corals of the Great Barrier Reef. *Mar Ecol Prog Ser* 10:173–185
- Done TJ (1999) Coral community adaptability to environmental change at the scales of regions, reefs and reef zones. *Am Zool* 39:66–79
- Edinger EN, Jompa J, Limmon GV, Widjatmoko W, Risk MJ (1998) Reef degradation and coral biodiversity in Indonesia: effects of land-based pollution, destructive fishing practices and changes over time. *Mar Pollut Bull* 36:617–630
- Fricke HW, Schuhmacher CF (1983) The depth limits of Red Sea stony corals: an ecophysiological problem (a deep diving survey by submersible). *Mar Ecol* 4:163–194
- Halas D, Winterbottom R (2009) A phylogenetic test of multiple proposals for the origins of the East Indies coral reef biota. *J Biogeogr* 36:1847–1860
- Hoeksema BW (2007) Delineation of the Indo-Malayan centre of maximum marine biodiversity: the Coral Triangle. In: Renema W (ed) Biogeography, time, and place: distributions, barriers, and islands. Springer, The Netherlands, pp 117–178
- Hoeksema BW, Cairns SD (2014) Scleractinia. World Register of Marine Species. <http://www.marinespecies.org/aphia.php?p=taxdetails&id=1363>
- Iglesias-Prieto R, Trench RK (1994) Acclimation and adaptation to irradiance in symbiotic dinoflagellates. 1. Responses of the photosynthetic unit to changes in photon flux density. *Mar Ecol Prog Ser* 113:163–176
- Johnson KG, McCormick T (1999) The quantitative description of biotic change using palaeontological databases. In: Harper D (ed) Numerical palaeobiology. Wiley, Chichester, pp 227–247
- Johnson KG, Hasibuan F, Todd JA, Müller W (2015a) Biotic and environmental origins of the Southeast Asian biodiversity hotspot. *Palaios* 30:1–6
- Johnson KG, Renema W, Rosen BR, Santodomingo N (2015b) Old data for old questions: what can the historical collections really tell us about the Neogene origins of reef-coral diversity in the Coral Triangle? *Palaios* 30:94–108
- Kahng SE, Spalding HL, Brokovich E, Wagner D, Weil E, Hinderstein L, Toonen RJ (2010) Community ecology of mesophotic coral reef ecosystems. *Coral Reefs* 29:255–275
- Kusworo A, Reich S, Wesselingh FP, Santodomingo N, Renema W (2015) Diversity and palaeoecology of Miocene coral-associated molluscs from East Kalimantan. *Palaios* 30:116–127
- Lajeunesse TC (2005) “Species” radiations of symbiotic dinoflagellates in the Atlantic and Indo-Pacific since the Miocene-Pliocene transition. *Mol Biol Evol* 22:570–581
- Loya Y (1976) Effects of water turbidity and sedimentation on the community structure of Puerto Rican corals. *Bull Mar Sci* 26:450–466
- Marshall N, Novak V, Cibaj I, Krijgsman W, Renema W, Young J, Fraser N, Limbong A, Morley R (2015) Dating Borneo’s Deltaic Deluge: Middle Miocene progradation of the Mahakam Delta. *Palaios* 30:7–25
- McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82:290–297
- McMonagle LB (2012) A diverse assemblage of corals from the Late Oligocene of eastern Sabah, Borneo: pre-Miocene origins of the Indo-West Pacific marine biodiversity hotspot. M.Phil. thesis, Department of Earth Sciences, Durham University, UK
- Moll H (1983) Zonation and diversity of Scleractinia on reefs off SW Sulawesi, Indonesia. Ph.D. thesis, Leiden University, Netherlands
- Moss SJ, Chambers JLC (1999) Tertiary facies architecture in the Kutai Basin, Kalimantan, Indonesia. *J Asian Earth Sci* 17:157–181
- Muir P, Wallace C, Bridge TCL, Bongaerts P (2015) Diverse staghorn coral fauna on the mesophotic reefs of north-east Australia. *PLoS One* 10:e0117933
- Novak V, Renema W (2015) Larger foraminifera as environmental discriminators in Miocene mixed carbonate-siliciclastic systems. *Palaios* 30:40–52

- Novak V, Santodomingo N, Rösler A, Di Martino E, Braga JC, Taylor PD, Johnson KG, Renema W (2013) Environmental reconstruction of a late Burdigalian (Miocene) patch reef in deltaic deposits (East Kalimantan, Indonesia). *Palaeogeogr Palaeoclimatol Palaeoecol* 374:110–122
- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Wagner H (2013) Vegan: community ecology package. Ordination methods, diversity analysis and other functions for community and vegetation ecologists. R-package version 2.0. <https://CRAN.R-project.org/package=vegan>
- Perrin C (2000) Changes of palaeozonation patterns within Miocene coral reefs, Gebel Abu Shaar, Gulf of Suez, Egypt. *Lethaia* 33:253–268
- Perry CT, Smithers SG, Johnson KG (2009) Long-term coral community records from Lugger Shoal on the terrigenous inner-shelf of the central Great Barrier Reef, Australia. *Coral Reefs* 28:941–948
- Perry CT, Smithers SG, Gulliver P, Browne NK (2012) Evidence of very rapid reef accretion and reef growth under high turbidity and terrigenous sedimentation. *Geology* 40:719–722
- Pomar L, Hallock P (2007) Changes in coral-reef structure through the Miocene in the Mediterranean province: adaptive versus environmental influence. *Geology* 35:899–902
- Pomar L, Hallock P (2008) Carbonate factories: a conundrum in sedimentary geology. *Earth Sci Rev* 87:134–169
- Pomar L, Bassant P, Brandano M, Ruchonnet C, Janson X (2012) Impact of carbonate producing biota on platform architecture: Insights from Miocene examples of the Mediterranean region. *Earth Sci Rev* 113:186–211
- R-Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Reich S, Di Martino E, Todd JA, Wesselingh FP, Renema W (2015a) Indirect paleo-seagrass indicators (IPSIs): A review. *Earth Sci Rev* 143:161–186
- Reich S, Warter V, Wesselingh FP, Zwaan JC, Lourens L, Renema W (2015b) Paleocological significance of stable isotope ratios in Miocene tropical shallow marine habitats (Indonesia). *Palaios* 30:53–65
- Renema W (2006) Large benthic foraminifera from the deep photic zone of a mixed siliciclastic-carbonate shelf off East Kalimantan, Indonesia. *Mar Micropaleontol* 58:73–82
- Renema W, Troelstra SR (2001) Larger foraminifera distribution on a mesotrophic carbonate shelf in SW Sulawesi (Indonesia). *Palaeogeogr Palaeoclimatol Palaeoecol* 175:125–146
- Renema W, Warter V, Novak V, Young JR, Marshall N, Hasibuan F (2015) Ages of Miocene fossil localities in the northern Kutai Basin (East Kalimantan, Indonesia). *Palaios* 30:26–39
- Riegl BM, Piller WE (2002) Reefs and coral carpets in the Miocene paratethys (Badenian, Leitha Limestone, Austria). *Proc 9th Int Coral Reef Symp* 1:211–216
- Rogers CS (2013) Coral reef resilience through biodiversity. *ISRN Oceanography*. doi:10.5402/2013/739034
- Rosen BR, Aillud GS, Bosellini FR, Clack NJ, Insalaco E (2002) Platy coral assemblages: 200 million years of functional stability in response to the limiting effects of light and turbidity. *Proc 9th Int Coral Reef Symp* 1:255–264
- Rösler A, Pretković V, Braga JC (2015) Coralline algae from the Miocene Mahakam Delta (East Kalimantan, SE Asia). *Palaios* 30:83–93
- Ryan EJ, Smithers SG, Lewis SE, Clark TR, Zhao JX (2016) Chronostratigraphy of Bramston Reef reveals a long-term record of fringing reef growth under muddy conditions in the central Great Barrier Reef. *Palaeogeogr Palaeoclimatol Palaeoecol* 441:734–747
- Sanders D, Baron-Szabo RC (2005) Scleractinian assemblages under sediment input: their characteristics and relation to the nutrient input concept. *Palaeogeogr Palaeoclimatol Palaeoecol* 216:139–181
- Santodomingo N, Wallace CC, Johnson KG (2015a) Fossils reveal a high diversity of the staghorn coral genera *Acropora* and *Isopora* (Scleractinia: Acroporidae) in the Neogene of Indonesia. *Zool J Linn Soc* 175:677–763
- Santodomingo N, Novak V, Pretković V, Marshall N, Di Martino E, Lo Giudice Capelli E, Rösler A, Reich S, Braga JC, Renema W, Johnson KG (2015b) A diverse patch reef from turbid habitats in the Middle Miocene (East Kalimantan, Indonesia). *Palaios* 30:128–149
- Smith TB, Glynn PW, Maté JL, Toth LT, Gyory J (2014) A depth refugium from catastrophic coral bleaching prevents regional extinction. *Ecology* 95:1663–1673
- Stafford-Smith MG, Ormond RFG (1992) Sediment-rejection mechanisms of 42 species of Australian scleractinian corals. *Mar Freshw Res* 43:683–705
- van Woesik R, Tomascik T, Blake S (1999) Coral assemblages and physico-chemical characteristics of the Whitsunday Islands: evidence of recent community changes. *Mar Freshw Res* 50:427–440
- van Woesik R, Houk P, Isechal AL, Idechong JW, Victor S, Golbuu Y (2012) Climate-change refugia in the sheltered bays of Palau: analogs of future reefs. *Ecol Evol* 2:2474–2484
- Veron JEN (2000) Corals of the world. Australian Institute of Marine Science, Townsville
- Vescogni A, Bosellini FR, Cipriani A, Gürlér G, Ilgar A, Paganelli E (2014) The Dağpazari carbonate platform (Mut Basin, Southern Turkey): facies and environmental reconstruction of a coral reef system during the Middle Miocene Climatic Optimum. *Palaeogeogr Palaeoclimatol Palaeoecol* 410:213–232
- Wallace AR (1863) On the physical geography of the Malay Archipelago. *The Journal of the Royal Geographical Society of London* 33:217–234
- Wilson MEJ (2005) Development of equatorial delta-front patch reefs during the Neogene, Borneo. *J Sediment Res* 75:114–133
- Wilson MEJ (2012) Equatorial carbonates: an Earth systems approach. *Sedimentology* 59:1–31
- Wilson MEJ, Rosen BR (1998) Implications of paucity of corals in the Paleogene of SE Asia: Plate tectonics or centre of origin? In: Hall R, Holloway JD (eds) *Biogeography and geological evolution of SE Asia*. Backburys Publisher, Leiden, The Netherlands, pp 165–195
- Wilson MEJ, Moss SJ (1999) Cenozoic palaeogeographic evolution of Sulawesi and Borneo. *Palaeogeogr Palaeoclimatol Palaeoecol* 145:303–337