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By Hita Pandita



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Neogene marine ostracod diversity and faunal composition in Java, Indonesia: Indo-Australian Archipelago biodiversity hotspot and the Pliocene diversity jump

Caren P. Shin¹, Moriaki Yasuhara^{1*}, Hokuto Iwatani¹, Tomoki Kase², Allan Gil S. Fernando³, Hiroki Hayashi⁴, Yukito Kurihara⁵ and Hita Pandita⁶

¹School of Biological Sciences and Swire Institute of Marine Science, University of Hong Kong, Kadoorie Biological Sciences Building, Pokfulam Road, Hong Kong;

²Department of Biological Sciences, Faculty of Science, Kanagawa University, 2946 Tsuchiya, Hiratsuka-shi, Kanagawa, 259–1293, Japan;

³National Institute of Geological Sciences, University of Philippines, Diliman, Quezon City, Philippines;

⁴Department of Geoscience, Interdisciplinary Graduate School of Science and Engineering, Shimane University, 1060 Nishikawatsu-cho, Matsue 690–8504, Japan;

⁵Department of Geology, Faculty of Education, Mie University, 1557 Kurimamachiya-cho, Tsu, Mie 514–8507, Japan; and

⁶Teknik Geologi, Sekolah Tinggi Teknologi Nasional Yogyakarta, Jl. Babarsari, Depok Sleman, Yogyakarta 55281, Indonesia

Correspondence: M. Yasuhara; e-mail: moriakiyasuhara@gmail.com, yasuhara@hku.hk

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ABSTRACT

Neogene diversity history in the world center of biodiversity known as the Indo-Australian Archipelago (IAA) or the Coral Triangle remains poorly understood. Of particular interest is the recently reported Pliocene diversity jump that is considered to have established present-day biodiversity level of the region needs rigorous inspections. We investigated Neogene fossil marine ostracods from Java, Indonesia and evaluate and test the Pliocene Diversity Jump hypothesis. We found a significant diversity increase from the late Miocene to the Pliocene, supporting the hypothesis. At the same time, there are considerable differences in depositional environments between the Miocene and Pliocene samples. Although it is unlikely that the main reason of the diversity increase is due to this paleoenvironmental difference, further samples and data from the IAA hotspot region are needed for more rigorous inspections. Our comparison between species-level and genus-level data indicated that species-level data are better to detect detailed macroevolutionary diversity histories, and genus level data are more useful for paleoenvironmental and paleoceanographic reconstructions.

Key Words: Cenozoic, Coral Triangle, Indo-West Pacific region, macroevolution, tropical western Pacific

EIGHTEENTH INTERNATIONAL SYMPOSIUM ON OSTRACODA

INTRODUCTION

The Indo-Australian Archipelago (IAA), also known as the Coral Triangle, a hotspot in the Indo-West Pacific region (IWP), is known as the area of highest marine biodiversity for various taxa (Paulay, 1997; Hoeksema, 2007; Tittensor *et al.*, 2010; Bellwood, 2012; Jablonski *et al.*, 2013). Fossil (larger benthic foraminifera, ostracods, corals) and molecular (gastropods) evidence consistently indicated the Early Miocene origin of the IAA hotspot (Wilson & Rosen, 1998; Crame & Rosen, 2002; Renema, 2007; Renema *et al.*, 2008; Williams & Duda, 2008; Yasuhara *et al.*, 2017), which

is probably related to the collision of Australia with Pacific arcs and the Southeast Asian margin at ~23–25 mya (Kuhnt *et al.*, 2004; Renema *et al.*, 2008; Hall, 2011; Yasuhara *et al.*, 2017). The Neogene diversity history after the origination of the hotspot is, however, poorly understood, because of the paucity of detailed fossil records (Renema *et al.*, 2008; Bellwood *et al.*, 2012; Johnson *et al.*, 2015; Leprieur *et al.*, 2016). Compared to the relatively well-investigated tropical western Atlantic region (Jackson *et al.*, 1993, 2010; Collins & Coates, 1999; Jackson & Johnson, 2000; Johnson *et al.*, 2008; O’Dea & Jackson, 2009; Smith & Jackson, 2009; Di Martino *et al.*, 2018), the IWP is seriously understudied regarding

fossil-based biodiversity research. Yasuhara *et al.* (2017) investigated IWP and northwestern Pacific fossil ostracods and showed a remarkable Pliocene diversity jump at ~3–5 mya that established the modern-level high species diversity. In regional perspective, this Pliocene diversity jump may be related to the initiation of the present-day tectonic regime involving regional changes of plate motions at the Eurasian continental margin in the West Pacific at ~5 mya (Hall, 2002; Renema *et al.*, 2008). A Pliocene diversification, however, is also known in the tropical western Atlantic in fossil reef corals and molluscs (Budd, 2000; Jackson & Johnson, 2000; Johnson *et al.*, 2008). If this Pliocene diversity jump is a pervasive event, it may be explained by the Pliocene glacioeustatic sea-level changes through a species pump model and/or habitat fragmentation and re-connection (Bellwood *et al.*, 2012; Yasuhara *et al.*, 2017). Generic diversity of larger benthic foraminifera in the IWP, however, does not show any diversity increase from the late Miocene to the Pliocene (Renema, 2007). Furthermore, the data of fossil ostracods of Yasuhara *et al.* (2017) are rather preliminary: All Pliocene data are from one island, Leyte, Philippines, and similarly all late Miocene samples are from Kalimantan Island, Indonesia. Faunal compositional data are not shown in Yasuhara *et al.* (2017), and Cenozoic fossil ostracod fauna remains poorly understood in the IWP (Kingma, 1948; Keij, 1964, 1966, 1974, 1979). Information on modern ostracod fauna is also limited in this region (Whatley & Zhao, 1987, 1988; Whatley & Watson, 1988; Dewi, 1997; Mostafawi *et al.*, 2005; Warne *et al.*, 2006; Tanaka *et al.*, 2009; Titterton & Whatley, 2009; Fauzielly *et al.*, 2013).

This under-sampling could have crucial impact on diversity estimations. For example, modern bivalve diversity was estimated in the 1960s to be similar between the IWP and the tropical western Atlantic (Stehli *et al.*, 1967), but it is now known that the IWP diversity is at least 1.5 times higher than that of the tropical western Atlantic (Jablonski *et al.*, 2013). It is, thus, very important to collect and accumulate more fossil samples and data from the

IWP, not only to better evaluate the validity of the Pliocene diversity jump specifically, but also to accurately reconstruct Cenozoic biodiversity of the region in general. We investigated Neogene marine ostracods in outcrop samples from Java, Indonesia. The aims were to evaluate and test if the Pliocene diversity jump is a pervasive event (the Pliocene Diversity Jump hypothesis) using our new dataset and to contribute a better understanding of the Cenozoic IWP ostracod fauna and diversity.

MATERIALS AND METHODS

Nine outcrop sediment samples were collected from Java, Indonesia (Fig. 1, Table 1) (see below for details on localities and age). We followed a standard sample processing protocol (Yasuhara *et al.*, 2017). Ostracods were picked from the >150 µm size fraction, a standard mesh size that retains adults and juveniles from late molt stages of most species (Yasuhara *et al.*, 2009; 2017). All specimens in a sample were picked up, sorted on a cardboard slide under a stereomicroscope, and identified to the species level where possible. We counted an isolated valve and an articulated trapace as a single specimen (see Yasuhara *et al.*, 2017). Ostracod diversity was calculated as rarefaction $E(S_{50})$, estimated number of species when the sample size was 50 (Hurlbert, 1971), to address sample size artifact. Non-metric multidimensional scaling (NMDS) was used to visualize and summarize differences and similarities of ostracod faunal compositions among samples. We used Bray-Curtis dissimilarity and biquadratic-root transformed relative species abundance data for NMDS. The diversity and multivariate analyses were conducted on both species- and genus-level datasets and were implemented in the R programming language (R Core Team, 2018) using the functions “rarefy” and “metaMDS” from the R package vegan (Oksanen *et al.*, 2018). We used the R package ggplot2 to plot most of the data and results (Wickham, 2009).

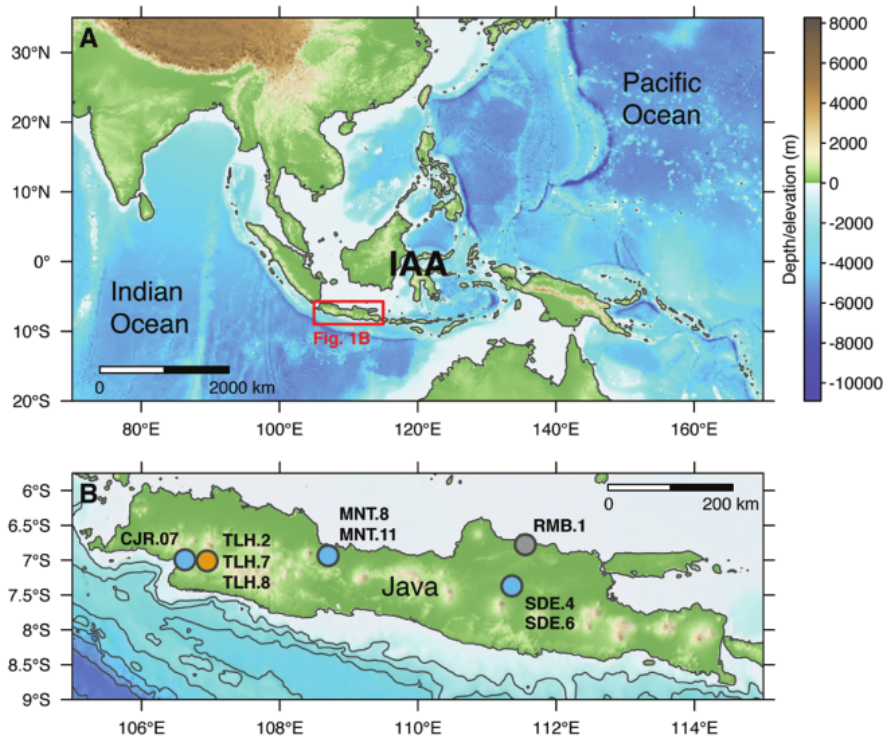


Figure 1. The Indo-West Pacific region showing Indo-Australian Archipelago (IAA) biodiversity hotspot (A). Detailed map of Java showing ostracod sample sites (B). The geologic ages of samples are indicated in various shades. This figure is available in color at *Journal of Crustacean Biology* online.

Table 1. List of the Neogene Java samples studied.

Sample	Latitude	Longitude	Region	Location	Sediment	Age
RMB.1	6°47.346'S	111°33.095'E	Central Java	Rembang	Concretional bed. Fine-grained sandstone with pebble. Sediment bearing solitary corals and larger foraminifers	Middle Miocene
TLH.2	7°01.271'S	106°56.580'E	West Java	Small stream, Tjitalahab	Calcareous sandy silt	Late Miocene
TLH.7	7°01.271'S	106°56.580'E	West Java	Small stream, Tjitalahab	Sandy silt	Late Miocene
TLH.8	7°01.271'S	106°56.580'E	West Java	Small stream, Tjitalahab	Sandy silt with many shells	Late Miocene
CJR.07	7°0.0583'S	106°37.760'E	West Java	River cliff and bed, Cijarian River, Pelabuhanratu	Shell-bearing sandy silt to silty sand	Early Pliocene
MNT.8	6°56.114'S	108°42.171'E	West Java	Menenteng Valley	Siltstone	Early Pliocene
MNT.11	6°56.114'S	108°42.158'E	West Java	River bed, Ci Sanggarung River, Menenteng Valley	Blue-green siltstone with shells and calcareous concretions	Early Pliocene
SDE.4	7°22.060'S	111°21.616'E	Central Java	River cliff of Solo River, Sonde area, Ngawi	Marly silt	Early Pliocene
SDE.6	No data	No data	Central Java	River cliff of Solo River, Sonde area, Ngawi	Marly silt	Early Pliocene

LOCALITIES AND GEOLOGICAL AGES

The localities and geological ages of the samples used are summarized as follows (also see Fig. 1, Table 1):

RMB.1. Kali Ngaglik creek bed, Sedan area of Rembang, Central Java. Planktonic foraminiferan and calcareous nannofossil biostratigraphies indicate the age of this locality as Middle Miocene in age (Kase *et al.*, unpublished).

TLH.2, TLH.7, and TLH.8. Continuous exposure of the Nyalindung Formation along a stream, Tjitalahab Valley, Nyalindung area of Pelabuhanratu, West Java. Larger benthic foraminiferan and calcareous nannofossil biostratigraphies consistently indicate a Late Miocene age of the formation (Batenburg *et al.*, 2011; Kase *et al.*, 2015).

CJR.07. River-bed outcrop, Cijarian River, Pelabuhanratu, West Java, which is the type locality of the Odengian Stage. Calcareous nannofossils indicate an Early Pliocene age (Kase *et al.*, unpublished).

MNT.8 and MNT.11. River-bed outcrop in the Menenteng Valley along Ci Sanggarung River, Kuningan, West Java. The stratum is known to have been deposited during the Cheribonian Stage, Early Pliocene (BouDagher-Fadel, 2002; Kase *et al.*, unpublished).

SDE.4 and SDE.6. Klitik Member of the Kalibeng Formation exposed on river beds at Solo River, Sonde area, Ngawi, Central Java. The Klitik Member is Early Pliocene based on planktonic foraminiferan biostratigraphy using samples collected from nearby localities (Kase *et al.*, 2008).

RESULTS

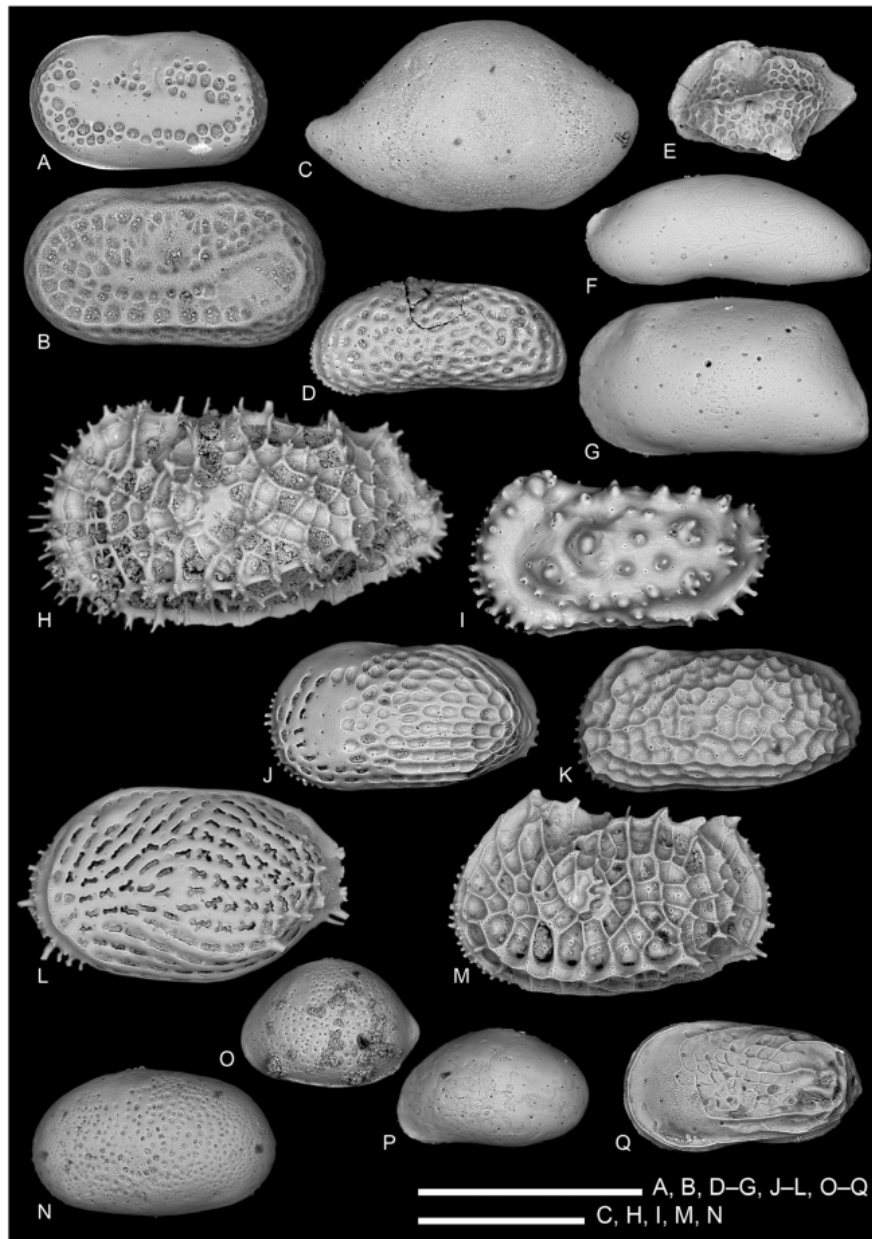
A total of 80 genera and 171 species were identified from 37 fine samples (Figs. 2, 3). The Middle Miocene sample RMB.1 is characterized by the dominance (40 % of the total assemblage) of *Pistocythereis* aff. *euplectella* (Brady, 1869) and high abundance (16–18%) of *Neonesidea* spp. and *Actinocythereis?* *scutigera* (Brady, 1868) (see Yasuhara *et al.*, 2015). Among the Late Miocene samples (TLH.2, TLH.7, and TLH.8), TLH.7 and TLH.8 are dominated by *Neocyprideis* spp. This species shows almost monospecific dominance (> 90%) in TLH.8. *Lankacythere* sp. 1 occurs abundantly (40%) in TLH.7 as the second dominant species next to *Neocyprideis* spp. (44%). Faunal composition of TLH.2 is distinct from the other Late Miocene samples and characterized by high abundance of

Ajehella aff. *mckenziei* Keij, 1979 (41%) and *Neomonoceratina macrofona* Kingma, 1948 (23%). Early Pliocene samples (CJR.07, MNT.8, MNT.11, SDE.4, and SDE.6) show high variation in their faunal compositions: CJR.07 is dominated by *Lankacythere* sp. 2 (62%) and *Neocyprideis* spp. (24%); MNT.8 is characterized by the high abundance (5–18%) of *Xestoleberis* spp., *Neonesidea* spp., *Pontocythere?* sp., *Bradleya* sp. 1, and *Uroleberis* cf. *ymchengi* Malz, 1980; MNT.11 is characterized by the dominance (42%) of *Keijella* sp. 2 and the high abundance (8–11%) of *Actinocythereis?* *scutigera*, *Keijella* sp. 1, and *Keijella* cf. *multisulcus* Whatley & Zhao, 1988; SDE.4 and SDE.6 show the high abundance of *Kirithe* spp. (22–25%), *Xestoleberis* spp. (11–14%), and *Argilloecia* spp. (7–11%). The genus-level results are generally consistent with the species-level results (Fig. 3B), but show higher similarity between the Miocene and Pliocene samples than the species-level results (see below).

Species- and genus-level diversities are significantly higher in the Pliocene samples than in those from the Late Miocene (i.e., 95% confidence intervals do not overlap) (Fig. 4A, C). The NMDS result shows clear distinction in the faunal compositions between the Miocene and Pliocene samples both at the species and genus levels (Fig. 4B, D). The compositional difference between the Miocene and Pliocene faunas, however, is smaller at the genus level than at the species level (Fig. 4B, D). The genus diversity shows high linear correlation with the species diversity, and the genus diversity relative to the species diversity decreases with increasing diversity (Fig. 5).

DISCUSSION

We found a significant Pliocene diversity increase in our dataset (Fig. 4A, C), supporting the Pliocene diversity jump hypothesis. The ostracod faunal compositions, however, are substantially different between the Miocene and the Pliocene, suggesting different depositional environments between them. We, therefore, evaluate whether this diversity increase is explained by a local environmental change reflected in the ostracod faunal difference. The Miocene samples are dominated by *Neocyprideis* Apostolescu, 1956, *Lankacythere* Bhatia & Kumar, 1979, *Ajehella* Kingma, 1948, *Pistocythereis* Gou in Gou *et al.*, 1983, and *Neomonoceratina*, Kingma, 1948. *Neocyprideis* is known from very shallow, fully-marine environments in the Neogene IWP (Yasuhara *et al.*, 2018), *Lankacythere* from the continental shelf shallower than 100 m (Whatley & Zhao, 1988; Zhao & Whatley, 1989), and *Ajehella* also mainly from depths shallower than 100 m (Keij, 1979; Whatley & Zhao, 1988;



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Figure 2. Scanning electron microscopy images of selected ostracod species. *Cytherella semitalis* Brady, 1868, juvenile LV, MNT11 (A); *Cytherelloidea* aff. *leroyi* Keij, 1964, adult LV, CJR7 (B); *Neonesidea* sp., adult RV, RMB1 (C); *Pontocythere?* sp., adult LV, MNT11 (D); *Neomonoceratina macropora* Kingma, 1948, adult LV, RMB1 (E); *Argilloecia acuminata* Müller, 1894, adult LV, SDE6 (F); *Kriithe* sp., adult LV, SDE4 (G); *Agrenocythere* cf. *spinosa* Benson, 1972, adult LV, SDE6 (H); *Actinocythereis? scutigera* (Brady, 1868), adult LV, MNT11 (I); *Keijella multisulcus* Whatley & Zhao, 1988, adult LV, MNT11 (J); *Lankacythere* sp. 2, adult LV, CJR7 (K); *Pistocythereis* aff. *euplectella* (Brady, 1869), adult LV, RMB1 (L); *Bradleya* sp. 2, adult LV, SDE4 (M); *Neocyprideis* sp., adult LV, CJR7 (N); *Uroleberis* cf. *ymchengi* (Malz, 1980), juvenile LV, MNT8 (O); *Xestoleberis* sp. 5, adult LV, SDE4 (P); *Atjehella* aff. *mckenziei* Keij, 1979, juvenile LV, TLH2 (Q). Scale bars represent 0.5 mm. All lateral views.

Zhao & Whatley, 1989). *Pistocythereis* is also a shallow-water marine genus commonly known from < 100 m (Whatley & Zhao, 1988; Zhao & Whatley, 1989) and *Neomonoceratina* is abundant at depths shallower than 30–40 m (Zhao & Wang, 1988, 1990). All of the Miocene samples, thus, are deposited under shallow marine, continental shelf environments at depths of < 100 m. Some of the Miocene samples (TLH.7 and TLH.8) are characterized by a very high abundance of *Neocyprideis* and, thus, were probably

deposited under very shallow marine conditions (e.g., tropical, full-marine lagoons; see Yasuhara *et al.*, 2018). In contrast, some of the Pliocene samples (SDE.4 and SDE.6) are characterized by deep-water genera, e.g., *Kriithe* Brady, Crosskey & Robertson, 1874, *Argilloecia* Sars, 1866, *Bradleya* Hornibrook, 1952, and *Agrenocythere* Benson, 1972 (Benson, 1972; Cronin & Dwyer, 2003; Yasuhara *et al.*, 2019; Iwatani *et al.*, 2018). MNT.8 also includes some deep-water components such as *Kriithe*, *Cythereopteron* Sars, 1866, and

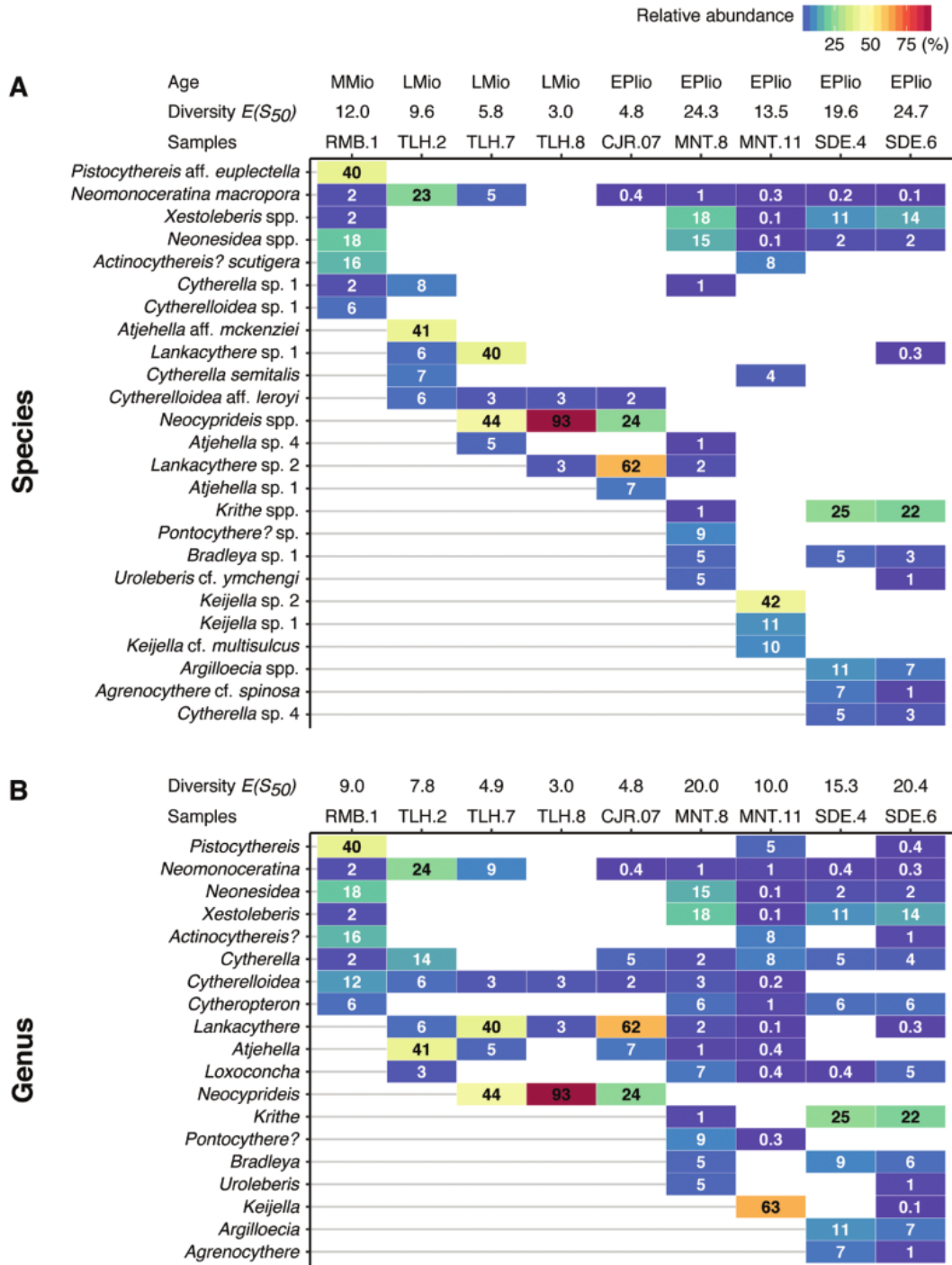


Figure 3. Summary of Neogene marine ostracod faunas in Java, Indonesia; relative abundances (%). Ostracod species constituting > 5% in a sample and species diversity [$E(S_{50})$] (A). Ostracod genera constituting > 5% in a sample and genus diversity [$E(S_{50})$] (B). MMio, Middle Miocene; LMio, Late Miocene; EPio, Early Pliocene. Relative abundance values are shown in various shades (the figure is available in color at [Journal of Crustacean Biology](https://academic.oup.com/jcr/article/39/3/244/5304204) online), and the values > 20% and < 20% are shown as black and white fonts, respectively.

Bradleya (Whatley *et al.*, 1984; Ayress *et al.*, 1999; Zhao *et al.*, 2000; Iwatani *et al.*, 2018), but their abundance is low and shallow marine ostracods including *Neonesidea* Maddocks, 1969, *Xestoleberis* Sars, 1866, *Loxococoncha* Sars, 1866, and *Pontocythere* Dubowsky, 1939 (van

Morkhoven, 1961; Maddocks, 1969; Athersuch, 1976; Athersuch & Horne, 1984; Ishii *et al.*, 2005; Sato & Kamiya, 2007; Tsurumi & Kamiya, 2007) are much more abundant, indicating a mid-lower shelf environment. CJR.07 and MNT.11 do not include

NEOGENE MARINE OSTRACODS FROM JAVA, INDONESIA

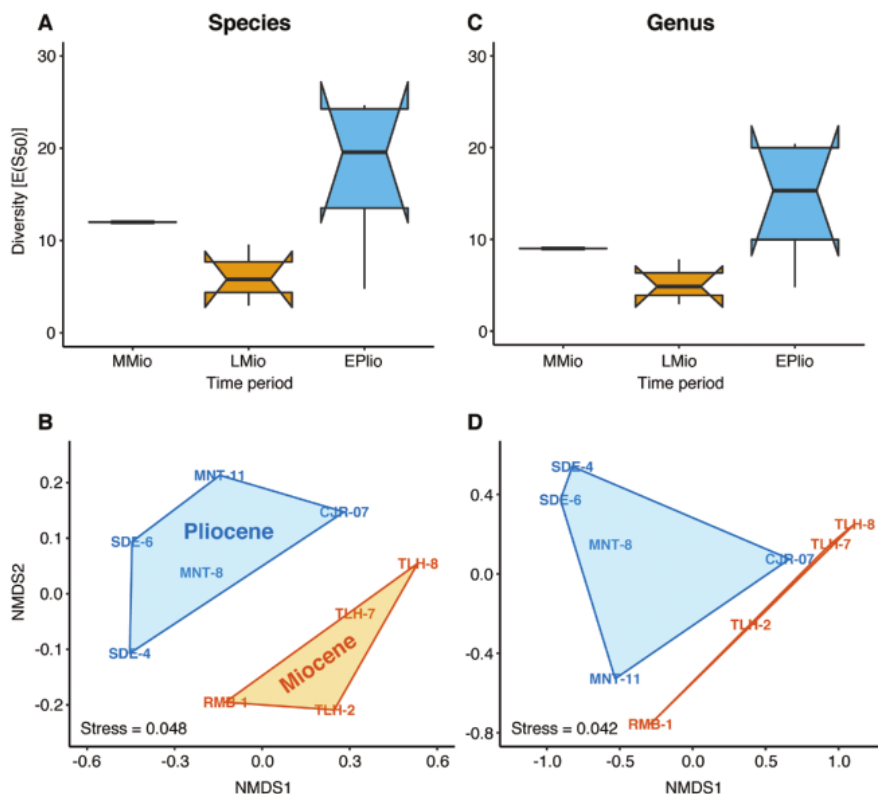


Figure 4. Neogene marine ostracod diversity and faunal composition in Java, Indonesia. Box plot showing species diversity (A); NMDS plot using species-level data (B); box plot showing genus diversity (C); NMDS plot using genus-level data (D). Notch shows 95% confidence interval of the median in the box plots. Convex hulls are shown for the Miocene and the Pliocene sample groups. MMio, Middle Miocene; LMio, Late Miocene; EPlio, Early Pliocene.

any deep-water ostracods, and are dominated by shallow marine genera, *Lankacythere* (CJR.07) and *Keijella* Ruggieri, 1967 (MNT.11) (Whatley & Zhao, 1988; Zhao & Whatley, 1989). Depositional environments of the Pliocene samples, thus, vary from deep sea (upper bathyal) to shallow marine. Furthermore, diversity in tropical shallow water is in general known to be higher than in deep water diversity (Sanders, 1968; Sanders & Hessler, 1969), and the modern continental shelf ostracod dataset of Yasuhara *et al.* (2017) shows only a modest quadratic relationship with water depth. The paleo-depth difference between our Miocene and Pliocene samples, thus, does not explain well the differences in their diversities between such samples. This result tends to support the Pliocene Diversity Jump Hypothesis, although our dataset is rather small and further collection of data is needed.

Our data showed that the Miocene and Pliocene ostracod faunas are much more similar to each other at the genus level than at the species level (Figs. 3, 4). The shallow-marine Pliocene CJR.07 and MNT.11 samples are particularly very close to the Miocene samples indicating shallow-marine environments on the genus-level NMDS plot, but not at the species-level (Fig. 4B, D). Such difference between species and genera indicates that genus is the taxon that best reflects the environment and habitat, and species is the taxon that better reflects macroevolution. The reason why data on the larger benthic foraminiferans do not show an increase in Pliocene diversity could be, at least partly, because it is genus-level data (Renema, 2007). There is a trend in that higher diversity is more underestimated at the genus level, whereas diversities of species and genera are almost the same in low-diversity ranges (Fig. 5). This issue is especially true in the tropics, because it is known that species-genus ratios are higher (i.e., more species per

genus) in the tropics than in the extratropics (Krug *et al.*, 2008). An additional reason of the discrepancy between the diversity trends of ostracods and larger benthic foraminiferans could be the difference of the diversity measurements used: data on ostracods reflect alpha (local) diversity and data on the larger benthic foraminiferans correspond to gamma (regional) diversity. Gamma diversity (in this case, total number of genera in the region in a certain time period) can be biased by the sampling intensity. The Pliocene larger benthic foraminiferan gamma diversity may be underestimated by the paucity of the Pliocene data in this region (Renema, 2007), especially given the high habitat heterogeneity of the tropical marine environments (Paulay, 1997; Schlacher *et al.*, 1998; Hoeksema, 2007).

The genus-level data is found to be less sensitive to detect diversity history on macroevolutionary time scales. Such a result, however at the same time, highlights importance and advantage of the usage of genus-level data for paleoenvironmental reconstruction, especially on secular, macroevolutionary time scales and in species-rich systems. This is because species-level data involve speciation and extinction within a same or similar habitat and a species-rich system can include many species with same or similar habitat preferences, that could be noises for the paleoenvironmental reconstruction purpose. Genus-level data is often used for ostracod-based paleoenvironmental and paleoceanographic reconstructions (Cronin *et al.*, 1996; Didić *et al.*, 2002; Alvarez Zarikian *et al.*, 2009; Iwatani *et al.*, 2018), and our result validates such a strategy.

Our Java ostracod data generally support the Pliocene Diversity Jump hypothesis. But still far less paleontological data are available for the IWP compared to the tropical western Atlantic region.

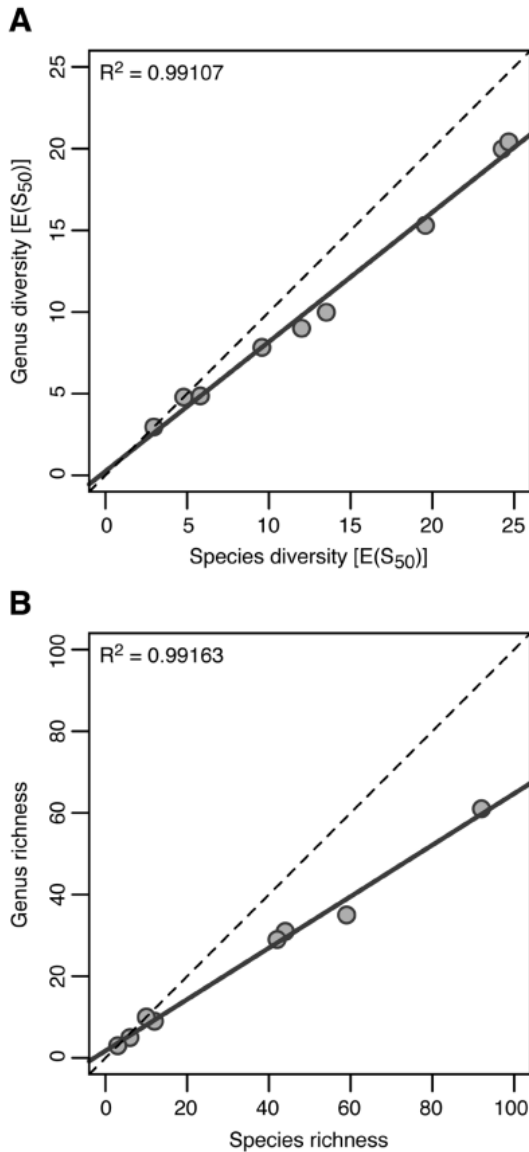


Figure 5. Comparison of species and genus diversities of Neogene Javan marine ostracods. Scatter plots of $E(S_{50})$ (A) and Richness (B). The dotted and solid lines indicate the 1:1 (slope = 1, intercept = 0) and linear regression lines, respectively.

In addition, there is no synthetic data on the tropical western Atlantic, particularly on ostracods, although classic and often local taxonomic and biostratigraphic studies exist for the Caribbean region (van den Bold, 1946, 1957a, b, 1960, 1968, 1981, 1988). Additional ostracod data and synthetic efforts are therefore needed in both the IWP and tropical western Atlantic.

The comparison between the species-level and genus-level results gives insights into macroevolutionary diversity history and paleoenvironmental reconstructions. Species-level data are more sensitive to detailed macroevolutionary diversity changes, and genus level data are more useful for paleoenvironmental and paleoceanographic reconstructions. Species-level and genus-level data could better reflect, respectively, biotic factors (also known as the “Red Queen”) and abiotic factors (the “Court Jester”) (Benton, 2009).

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