Naturalis Repository

Cenozoic dynamics of shallow-marine biodiversity in the Western Pacific

Moriaki Yasuhara, Hokuto Iwatani, Gene Hunt, Hisayo Okahashi, Tomoki Kase, Hiroki Hayashi, Toshiaki Irizuki, Yolanda M. Aguilar, Allan Gil S. Fernando, Willem Renema

Downloaded from:
https://doi.org/10.1111%2Fjbi.12880

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.

Journal of Biogeography (*J. Biogeogr.*) (2017) **44**, 567–578

Journal of Biogeography

ORIGINAL ARTICLE

Cenozoic dynamics of shallow-marine biodiversity in the Western Pacific

Moriaki Yasuhara[1]*, Hokuto Iwatani[1], Gene Hunt[2], Hisayo Okahashi[1], Tomoki Kase[3], Hiroki Hayashi[4], Toshiaki Irizuki[4], Yolanda M. Aguilar[5], Allan Gil S. Fernando[6] and Willem Renema[7]

[1]*School of Biological Sciences and Swire Institute of Marine Science, the University of Hong Kong, Kadoorie Biological Sciences Building, Pokfulam Road, Hong Kong SAR, China,* [2]*Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012, USA,* [3]*Department of Geology and Paleontology, National Museum of Nature and Science, 4-1-1 Amakubo, Tsukuba, Ibaraki 305-0005, Japan,* [4]*Department of Geoscience, Interdisciplinary Graduate School of Science and Engineering, Shimane University, 1060 Nishikawatsu-cho, Matsue 690-8504, Japan,* [5]*Marine Geological Survey, Mines and Geosciences Bureau, North Avenue, Diliman, Quezon City, Philippines,* [6]*National Institute of Geological Sciences, University of Philippines, Diliman, Quezon City, Philippines,* [7]*Naturalis Biodiversity Center, PO Box 9517, 2300 RA, Leiden, The Netherlands*

ABSTRACT

Aim Cenozoic dynamics of large-scale species diversity patterns remain poorly understood, especially for the Western Pacific, in part, because of the paucity of well-dated fossil records from the tropics. This article aims to reveal the spatiotemporal dynamics of species diversity in the Western Pacific through the Cenozoic, focusing on the tropical Indo-Australian Archipelago (IAA) biodiversity hotspot.

Location Tropical and north-western Pacific Ocean.

Methods We analysed well-preserved fossil ostracodes from the tropical Western Pacific and combined their diversity data with other published data from the region to reconstruct Cenozoic dynamics of species diversity in the tropical and north-western Pacific Ocean. We fitted generalized additive models to test for differences in richness over time and across geographical regions while accounting for sample-size variation among samples.

Results Low-, mid- and high-latitude regions all show a similar diversity trajectory: diversity is low in the Eocene and Oligocene, increases from the Early Miocene to the Plio-Pleistocene but then declines to the present day. Present-day high biodiversity in these regions was established during the Pliocene with a remarkable diversity increase at that time. Latitudinal diversity patterns are relatively flat and never show a simple decline from the tropics to higher latitudes.

Main conclusions Western Pacific Cenozoic ostracodes exhibit a spatiotemporal pattern of species diversity that is inconsistent with the commonly reported and persistent pattern of declining diversity from the tropics to the extratropics. While this inconsistency could be interpreted as evidence that ostracodes are a contrarian clade, Atlantic ostracodes display a standard latitudinal species diversity gradient. Contrasting patterns between oceans suggest an important role for regional factors (e.g. plate tectonics and temporal geomorphological dynamics) in shaping the biodiversity of the Western Pacific.

*Correspondence: Moriaki Yasuhara, School of Biological Sciences, University of Hong Kong, Kadoorie Biological Sciences Building, Pokfulam Road, Hong Kong SAR, China.
E-mails: moriakiyasuhara@gmail.com or yasuhara@hku.hk

Keywords

biodiversity hotspot, Cenozoic, Coral Triangle, Indo-Australian Archipelago, latitudinal diversity gradients, Ostracoda, temporal diversity dynamics, tropical shallow-marine biodiversity, Western Pacific

INTRODUCTION

The Indo-Australian Archipelago (IAA) biodiversity hotspot harbours the highest marine biodiversity on earth as well documented, for example, in corals, fishes, gastropods and bivalves (Crame, 2000; Bellwood *et al.*, 2005; Hoeksema, 2007; Bellwood & Meyer, 2009; Tittensor *et al.*, 2010; Jablonski *et al.*, 2013). This tropical biodiversity hotspot constitutes an important part of the western Pacific latitudinal species diversity gradient (hereafter LSDG) (Okuda *et al.*, 2004,

http://wileyonlinelibrary.com/journal/jbi
doi:10.1111/jbi.12880

2009; O'Hara *et al.*, 2011; Hoeksema, 2015). The standard LSDG is characterized by biodiversity that peaks in low latitudes instead of the mid or high latitudes and is known as the first-order biodiversity pattern on Earth (Krug *et al.*, 2009). Western Pacific biodiversity is known to be high not only in the tropical IAA region (Renema *et al.*, 2008; Tittensor *et al.*, 2010; Jablonski *et al.*, 2013) but also in adjacent mid-latitude areas [such as the southern part of the Japanese Archipelago (Fujikura *et al.*, 2010)], e.g. in bivalves, larger benthic foraminifera and coastal fishes (Renema *et al.*, 2008; Tittensor *et al.*, 2010; Jablonski *et al.*, 2013). Some contrarian taxa (Krug *et al.*, 2007), including marine macroalgae, seagrasses, sharks, cephalopods and cetaceans, even show non-standard LSDGs with a biodiversity peak at mid-latitudes (Kerswell, 2006; Tittensor *et al.*, 2010).

How and when these biodiversity patterns came to be, however, is much less well understood. Renema *et al.* (2008) investigated temporal dynamics of the IAA hotspot throughout the Cenozoic with larger benthic foraminifera. They revealed low IAA diversity in the Eocene (the centre of marine biodiversity was in the West Tethyan region at that time) and an Early Miocene [or even earlier (McMonagle *et al.*, 2011)] origin of the IAA biodiversity hotspot, which was followed by further diversity increase (Renema *et al.*, 2008). Similar results were recently shown in corals (Leprieur *et al.*, 2016). Other than larger benthic foraminifera and corals, most well-studied tropical taxa such as coral reef-associated fishes have limited fossil data due to low fossilization potential (Bellwood *et al.*, 2012). Moreover, the Cenozoic spatiotemporal dynamics of biodiversity in the broader north-western Pacific are incompletely understood because the relevant studies in this region are often based on the fossil record of organisms whose distributions are mostly restricted to the tropics (e.g. larger benthic foraminifera, corals, mangroves and tropical gastropods) (Renema *et al.*, 2008; Leprieur *et al.*, 2016). Molluscs are broadly distributed with respect to latitude and have an excellent fossil record, with numerous studies on local fossil faunas in the north-western Pacific region. However, their diversity patterns over time have not been synthesized for this region. More broadly, Cenozoic dynamics of large-scale marine biodiversity patterns in space and time remain poorly understood globally (Crame, 2001; Buzas *et al.*, 2002).

Here, we document diversity dynamics in the tropical- and north-western Pacific region through the Cenozoic. We use fossil benthic Ostracoda (Crustacea) as a model system because they are abundant even from a small amount of sediment and an important component of meiobenthic communities and because precise species-level identification is possible based on fossil specimens (i.e. hard parts) (Yasuhara *et al.*, 2015). Ostracodes occupy a wide range of epifaunal and shallow infaunal benthic habitats (Yasuhara & Cronin, 2008; Yasuhara *et al.*, 2009) in a variety of substrates (e.g. rocks, mud, sand, algae), and they represent a variety of trophic modes including deposit feeding, suspension feeding and scavenging. This model system differs from other well-studied organisms in the tropical Western Pacific region (Hoeksema, 2007) in that ostracodes have a rich fossil record and a reasonably robust taxonomy and are distributed not only in the tropics but also in the extratropics. They are also known to show a standard LSDG in the North Atlantic Ocean (Yasuhara *et al.*, 2009; Chiu *et al.*, 2016). Our main aims are to investigate when this region attained its present-day-level biodiversity, and the degree to which biodiversity in this region has been dynamic over the past 40 million years. We use relatively broad spatial bins, and consequently, we focus on the location of the peak biodiversity along latitudinal gradients rather than the precise shape of the gradient.

MATERIALS AND METHODS

Sediment samples

Cenozoic IAA sediment samples were collected from Indonesia and the Philippines (Fig. 1, Table 1, see Appendix S1 in Supporting Information). Specifically, Eocene and Early Miocene samples are from central Java Island, Indonesia; Late Miocene samples are from eastern Kalimantan Island, Indonesia; and Plio-Pleistocene samples are from Leyte Island, Philippines. Locality and age details are found in Table 1 and Appendices S1 and S2 and the references therein. Ages of the Leyte samples were determined based on planktonic foraminiferal and calcareous nannofossil biochronology (see Appendix S2). Ages of the other samples are from published sources cited in Table 1 (Reich *et al.*, 2014; Johnson *et al.*, 2015; Renema *et al.*, 2015).

Sample processing

Samples were wet-sieved through a 63- or 125-μm mesh sieve, dried and then dry-sieved using a 150-μm mesh sieve. Ostracodes were picked from > 150 μm fraction. We used > 150 μm fraction for ostracode analysis, because this size fraction is a standard for fossil ostracod research and allows us to obtain adults and late moult stage juveniles for most species (Yasuhara *et al.*, 2009). Even small-sized genera, such as *Callistocythere*, *Eucytherura*, *Hemicytherura* and *Semicytherura*, and elongate genera, such as *Pontocythere*, are included in our samples. Early moult stage juveniles (and juveniles of small species in general) can be smaller than 150 μm, but are often not preserved because their shells are usually thin and delicate. Even when present, however, they are often impossible to identify and thus the effects of mesh size on diversity estimation are likely to be negligible. Sample residues with too many ostracode specimens were divided using a sample splitter. All ostracodes in a sample or a split aliquot were picked, sorted on a cardboard slide and identified to the species level (for most genera). We considered isolated valves and articulated carapaces each as a single individual in the counts, which is a standard ostracode counting method (Yamaguchi *et al.*, 2014). Another standard

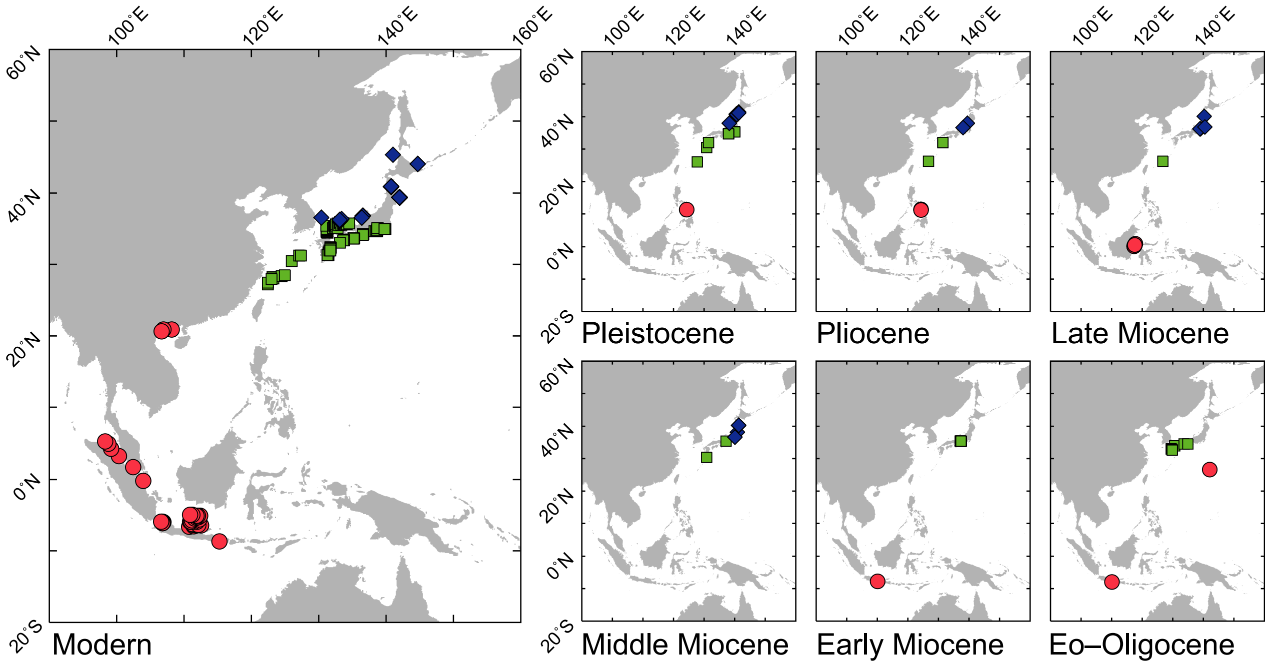

Figure 1 Locality maps of ostracod samples. Red circle: Indo-Australian Archipelago (IAA). Green square: south-western Japan (SWJP). Blue rhombus: northeastern Japan (NEJP). [Colour figure can be viewed at wileyonlinelibrary.com]

Table 1 List of samples used for this study to produce our original ostracode data. N: number of ostracode specimens. S: number of ostracode species. E, Early; L, Late; PP, Plio-Pleistocene. Geological ages determined in this paper are explained in Appendix S2.

Sample	Period	Age (Ma)	Area	Latitude (°)	Longitude (°)	N	S	References
06BA18C	E Miocene	*c.* 18.9	Java, Indonesia	7.7608 S	110.1283 E	443	27	Reich *et al.* (2014)
06BA18A	E Miocene	*c.* 18.9	Java, Indonesia	7.7608 S	110.1283 E	441	26	Reich *et al.* (2014)
06BA18B	E Miocene	*c.* 18.9	Java, Indonesia	7.7608 S	110.1283 E	445	23	Reich *et al.* (2014)
06BA18D	E Miocene	*c.* 18.9	Java, Indonesia	7.7608 S	110.1283 E	442	27	Reich *et al.* (2014)
06BA18	E Miocene	*c.* 18.9	Java, Indonesia	7.7608 S	110.1283 E	410	30	Reich *et al.* (2014)
TF110-SR42 [90 cm]	L Miocene	9.8–9.4	Kalimantan, Indonesia	0.1405 N	117.4269 E	269	21	Renema *et al.* (2015)
TF168-WR	L Miocene	8–5	Kalimantan, Indonesia	0.85696 N	117.7442 E	408	16	Renema *et al.* (2015)
TF110-WR18	L Miocene	9.8–9.4	Kalimantan, Indonesia	0.1405 N	117.4269 E	271	17	Renema *et al.* (2015)
TF517-FW03	L Miocene	9.3–8.9	Kalimantan, Indonesia	0.5678 N	117.6342 E	364	29	Renema *et al.* (2015)
TF534-NS2	L Miocene	9.3–8.9	Kalimantan, Indonesia	0.5488 N	117.6198 E	445	24	Renema *et al.* (2015)
06KW4B	Eocene	40–38	Java, Indonesia	7.9 S	110.1 E	416	14	Johnson *et al.* (2015)
06KW06	Eocene	40–38	Java, Indonesia	7.9 S	110.1 E	452	8	Johnson *et al.* (2015)
06KW05	Eocene	40–38	Java, Indonesia	7.9 S	110.1 E	371	15	Johnson *et al.* (2015)
Tinago A	E Pliocene	3.92–3.70	Leyte, Philippines	11.44273 N	124.30721 E	478	69	This paper
Tinago B	E Pliocene	3.92–3.70	Leyte, Philippines	11.44277 N	124.30708 E	316	52	This paper
Tinago C	PP	3.33–1.392	Leyte, Philippines	11.44273 N	124.30703 E	253	57	This paper
Tinago D	Pleistocene	< 0.987	Leyte, Philippines	11.44307 N	124.30637 E	202	35	This paper
Tinago F	Pleistocene	< 0.987	Leyte, Philippines	11.44163 N	124.30570 E	258	60	This paper
S-120	L Pliocene	3.33–3.18	Leyte, Philippines	11.30257 N	124.35643 E	288	72	This paper

method considers an isolated valve as one specimen and an articulated carapace as two specimens. But the difference between these two methods should be slight, because the majority of our specimens were isolated valves. We did not see a strong difference in the valve-carapace ratio among our samples. Our Miocene samples tend to have more articulated carapaces compared with the samples from other time intervals, but isolated valves are still the majority in the most of our Miocene samples.

Data and depositional environment

Modern IAA data, south-western and north-eastern Japanese data and one Eocene IAA data point were from published sources (Fig. 1; Appendix 1; see Table S1 in Appendix). We selected sites with an ostracode fauna that indicates a continental-shelf environment. For modern samples, we simply selected continental-shelf sites with < 200-m water depth. Subtle differences in habitats may add some noise to our results, but species diversity shows only a modest quadratic relationship with water depth in our modern continental-shelf data ($R^2 = 0.067$, $P = 0.0014$; see Fig. S1 in Appendix S1). Fossil ostracode faunas of our IAA samples consistently indicate a continental-shelf environment because many of the ostracode species recovered have distinct eye tubercles, which are absent in taxa limited to deeper habitats. There are no indications of brackish water environment (i.e. known brackish water ostracode taxa are not included in our IAA samples), where species diversity is usually lower compared with fully marine conditions. Thus, all of the original and published data are from similar, continental-shelf environments. Original and published data used for this study are generally from similar, fine and muddy sediments. Our IAA samples are generally calcareous sandy mud or muddy sand, and the south-western and north-eastern Japan fossil ostracode data are mainly from silt or silty sand samples. Thus, the reconstructed diversity history in this study represents that of subtidal, continental-shelf communities from soft sediments.

Definition of operational regions

We follow Renema *et al.* (2008) and Hoeksema (2007) in considering the IAA as the tropical and north-western Pacific region as far north as *c.* 20° N, which is consistent with the biogeographical province division of north-western Pacific shallow-marine ostracodes considering their Cenozoic fossil record (Whatley, 1987; Titterton & Whatley, 1988). Note that the Ogasawara (Bonin) Islands were located in the IAA region during the Eocene (Yamaguchi & Kamiya, 2009) (red dot in the Eocene–Oligocene panel of Fig. 1). The south-western Japan (SWJP) region and the northeastern Japan (NEJP) region are divided at 36° N, because this latitude is a well-known marine biogeographical boundary (Nishimura, 1981; Ogasawara, 1994) resulting from the position of the polar front and the boundary between the warm Kuroshio current and the cold Oyashio current (Gallagher *et al.*, 2009, 2015). The Kuroshio current may have existed for at least the last 16 million years (Ogasawara, 2002). In sum, the IAA, SWJP and NEJP are defined as operational latitudinal bins of low (< *c.* 20° N), mid (*c.* 20–36° N) and high latitudes (> 36° N), respectively, mainly based on modern biogeographical and oceanographic information. The boundaries of these bins are not necessarily always consistent with biogeographical boundaries throughout the Cenozoic, because biogeographical boundaries may have shifted during the Cenozoic.

Data analysis

Species diversity was measured as the number of species per sample (i.e. species richness) focusing on samples with > 200 ostracode specimens. Some Eocene and Oligocene datasets were included with lower sample sizes (see Table S1 in Appendix S1), but the lower diversity of these intervals (see Fig. S2 in Appendix S1) makes this less problematic, and is accounted for by the general additive models (GAMs) (see below). Each data point is from a single sample, except for several Eocene and Oligocene cases (see Table S1 in Appendix S1) in which we lumped several nearby (within a few kilometres) samples from a single study to increase sample size (see Table S1 in Appendix S1). Despite this lumping, species diversity remains very low in those samples. We used general additive models (GAMs) to model species richness as a linear model of the time periods, the regions and a smoothed function of sample size. The time periods and regions are included in the model in order to assess spatial and temporal variation in diversity. Sample size is used to account for differences in abundance across samples that may influence observed richness. Ideally, a subsampling approach such as rarefaction would be used to account for variation in abundance among samples, but the raw count data needed for this were not generally available for the compiled published data. Using GAMs instead assumes that sampling results in a smooth function between abundance and observed richness, and that the shape of this relationship does not change over time. One benefit of GAMs is that the user does not need to specify a function to describe the relationship between sample size and richness; the curve is instead estimated empirically using splines or similar functions (see Fig. S2).

Richness and sample size were $\log_{10}$-transformed prior to analysis. Analyses were completed using the *gam* function from the R library 'mgcv' (Wood, 2011), using restricted maximum-likelihood inference and the *gam* function's defaults for determining the degree of smoothing. Only sample size was smoothed; time periods (seven intervals: Eocene-Oligocene, Early Miocene, Middle Miocene, Late Miocene, Pliocene, Pleistocene and Modern) and regions (three regions: IAA, SWJP and NEJP) were treated as normal linear effects. The results presented focus on the model $richness \sim period * region + s(n)$, where the last term is a smooth function of sample size. This model with interactions between period and region fits the data better than an additive model ($F = 6.219$, $P = 5.94 \times 10^{-8}$), and it allows the diversity gradient to differ in different time intervals. We plotted model-predicted richness for all combinations of time period and region, projecting all to a standard sample size ($n = 200$); i.e. the richness that the GAM model predicts if 200 individuals were sampled. We used confidence limits on the predictions to guide which spatial and temporal differences were considered to be statistically significant (Table 2).

We have species abundance tables from three studies (Irizuki *et al.*, 2007; Ishida *et al.*, 2012; and the present study) that allow us to compare results from rarefaction to the GAM approach for a relatively small subset of the data ($n = 68$) from the Plio-Pleistocene and Early Miocene. Comparing richness rarefied to $n = 200$ to richness predicted by

Table 2 Predicted species richness at $n = 200$ individuals from GAMs (generalized additive models) and their 95% confidence intervals (CIs) for all combinations of time period and region. Pairwise differences are significant if CIs do not overlap. Species richness is shown on a $\log_{10}$ scale. ND, no data. SE, standard error. See Fig. 2 for abbreviations of time periods and regions.

Time period	Region	Richness	SE	Lower CI	Upper CI
Eo-Olig	IAA	0.96	0.06	0.84	1.09
EMio	IAA	1.25	0.06	1.14	1.36
MMio	IAA	ND	0.11	ND	ND
LMio	IAA	1.19	0.06	1.08	1.30
Plio	IAA	1.67	0.07	1.54	1.81
Pleist	IAA	1.62	0.08	1.46	1.79
Md	IAA	1.44	0.02	1.40	1.48
Eo-Olig	NEJP	ND	0.10	ND	ND
EMio	NEJP	ND	0.13	ND	ND
MMio	NEJP	1.44	0.03	1.37	1.50
LMio	NEJP	1.45	0.03	1.39	1.51
Plio	NEJP	1.68	0.03	1.63	1.73
Pleist	NEJP	1.66	0.02	1.62	1.70
Md	NEJP	1.46	0.02	1.42	1.50
Eo-Olig	SWJP	0.94	0.04	0.86	1.02
EMio	SWJP	1.27	0.04	1.19	1.35
MMio	SWJP	1.19	0.08	1.03	1.36
LMio	SWJP	1.36	0.05	1.25	1.47
Plio	SWJP	1.52	0.04	1.44	1.61
Pleist	SWJP	1.56	0.02	1.51	1.60
Md	SWJP	1.54	0.02	1.51	1.57

the GAM model projected to $n = 200$ shows that the two approaches yield similar sample-size corrected richnesses, and nearly the same inferred difference in richness between the Early Miocene and Plio-Pleistocene samples (see Fig. S3 in Appendix S1). In general, the sample-size corrections should only have moderate effects on the present analysis because richness-abundance plots (see Fig. S2 in Appendix S1) show only modest increases in richness with abundance over the range of abundances in the present study, mostly because sample sizes are uniformly quite high (95% of samples have $n > 200$).

Datasets and R codes used for this article are deposited at Dryad (http://dx.doi.org/10.5061/dryad.9rb13).

RESULTS

We discovered well-preserved fossil shallow-marine ostracode assemblages from Indonesia and the Philippines ranging in age from the Eocene to the Plio-Pleistocene. These samples represent the first well-dated comprehensive Cenozoic ostracode census data from the IAA region. These new Cenozoic IAA data, in conjunction with the published modern and fossil ostracode data from the north-western Pacific, allow us to infer the major features of the history of IAA and north-western Pacific biodiversity (Figs 1 & 2; see Appendix S3 for detailed preservational, taphonomic and taxonomic considerations). Analysing the raw richnesses gives results very similar to the output of the GAM models (see Fig. S4 in Appendix S1); the small differences in richness that are attributable to sampling differences are swamped by the much larger temporal and spatial differences. In addition, diversity plots with raw age and latitude (instead of time and regional bins) (see Figs S5 and S6 in Appendix S1) show consistent trends with our results shown in Fig. 2, supporting our bin-based approach.

Tropical Western Pacific diversity was very low in the Eocene-Oligocene and roughly doubled into the Early Miocene (Fig. 2). Species diversity is then relatively unchanged until the Pliocene, which has a value that is nearly double again compared to the Miocene average. The post-Palaeogene IAA diversification shown here may be related to the establishment of the Western Pacific LSDG, because LSDG dynamics are considered to be different between the greenhouse Palaeogene and icehouse Neogene (Jablonski *et al.*, 2013; Mannion *et al.*, 2014). Pleistocene diversities closely match those in the Pliocene and are followed by a modest but consistent decrease in diversity to the present day (Fig. 2).

DISCUSSION

Qualitatively similar diversity trends are found in all three regions of IAA, SWJP and NEJP. Diversities are often surprisingly similar among the three spatial bins, suggesting relatively flat latitudinal diversity gradients for ostracodes of this region. There are, however, some differences in the relative diversity of regions across time bins that add complexity to the history of this latitudinal diversity gradient (Fig. 2). During the Early Miocene, species diversity was significantly enhanced both in the tropical IAA and mid-latitude south-western Japan (Fig. 2, Table 2), possibly related to the collision of Australia with Pacific arcs and the Southeast Asian margin at *c.* 23–25 million years ago (Kuhnt *et al.*, 2004; Renema *et al.*, 2008; Hall, 2011). These enhanced low- and mid-latitude diversities probably reflect an Early Miocene origin of the IAA biodiversity hotspot [note that we define the term biodiversity hotspot as geographical area of maximal biodiversity by following Renema *et al.* (2008)] and a northern expansion of the tropical high diversity zone into mid-latitudes as seen in the present-day Western Pacific for several taxa (Renema *et al.*, 2008; Tittensor *et al.*, 2010; Jablonski *et al.*, 2013). Oligocene data are scarce, however, and we cannot rule out a somewhat earlier diversity increase, for example, after a major climatic shift at the Eocene-Oligocene boundary (Zachos *et al.*, 2001; Lyle *et al.*, 2008; Liu *et al.*, 2009), which is known to be a major extinction event (Cotton & Pearson, 2011). High-latitude diversity was already high in the Middle Miocene (Fig. 2), probably related to the formation of the Japanese Archipelago (Ogasawara, 1994); by *c.* 16 Ma present-day Japan was composed of numerous small and large islands (Ogasawara, 1994) formed as the result of enhanced tectonic activity during the Middle Miocene (Maruyama *et al.*, 1997). In the Middle and Late Miocene, we observed that high-latitude

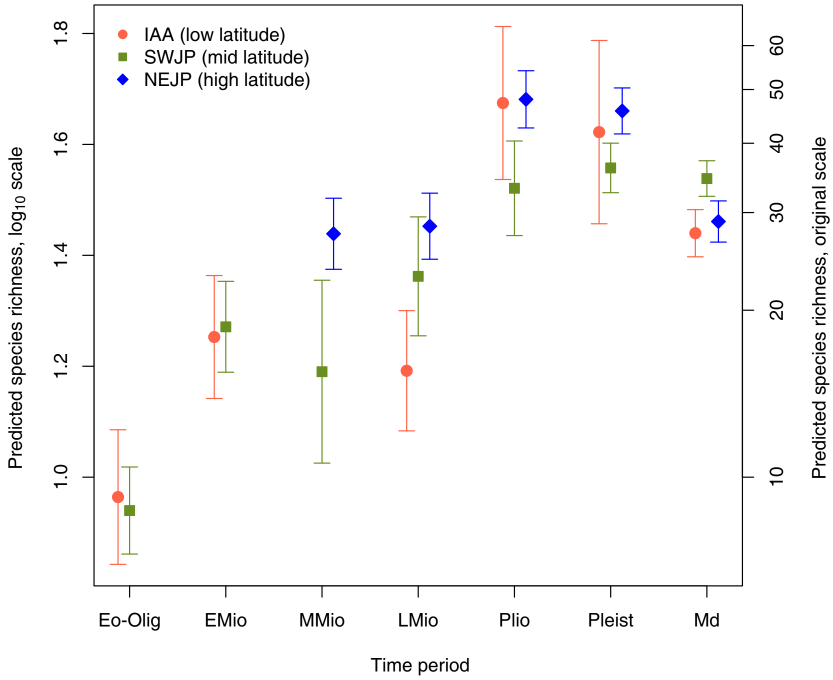

Figure 2 Ostracod diversity trajectories over time for the three regions of Indo-Australian Archipelago (IAA: low latitude), southwestern Japan (SWJP: mid latitude) and northeastern Japan (NEJP: high latitude), based on species richness from GAMs (generalized additive models). This figure shows model-predicted species richness at $n = 200$ individuals for all combinations of time period and region for which we have data (see text). Species richness is shown in $\log_{10}$ (Y axis on the left) and original (Y axis on the right) scales. Error bars show the 95% confidence interval around predicted richness. Md: Modern; Pleist: Pleistocene; Plio: Pliocene; LMio: Late Miocene; MMio: Middle Miocene; EMio: Early Miocene; Eo-Olig: Eocene–Oligocene. See Table S2 in Appendix S1 for sample sizes in each region and time period. [Colour figure can be viewed at wileyonlinelibrary.com]

diversity was generally greater than that from lower-latitude regions, suggesting a shallow but inverse LSDG (Fig. 2, Table 2). This high diversity in the mid–high latitudes could be related to the above-mentioned mid-Miocene formation of the 'Palaeo Japanese Archipelago' composed of even more numerous islands and complex coastlines compared to the present Japanese Archipelago.

One of the most remarkable features revealed here is the high species richness of Plio-Pleistocene assemblages in all regions (Fig. 2). To the extent that the relevant diversity increase took place in the Pliocene rather than Late Miocene, this pattern could be explained by a species pump model (Bellwood *et al.*, 2012). Enforced repeated upslope and downslope migrations tracking Plio-Pleistocene glacioeustatic sea-level changes to keep depth-related niche parameters (because of strong depth-preference conservatism of genera: Scarponi & Kowalewski, 2004; Holland & Zaffos, 2011) may have allowed for the diversification of species of deep-sea genera onto shelves. For example, during the time of sea-level fall when the uppermost bathyal zone was changed to lower shelf zone, some species of deep-sea genera may not have migrated downslope to keep their depth-related niche and instead may have stayed (or been left), adapted and diversified in the wide deeper shelf zone at that time (Holland & Christie, 2013). More generally speaking, some species might have been left or deviated from the enforced repeated migrations and have succeeded in obtaining a new niche often with speciation. Indeed, the Plio-Pleistocene IAA assemblages are characterized by diverse species of *Cytheropteron*, a typical deep-water genus known both from the continental shelf and the deep sea. Another possibility could be that habitat fragmentation and re-connection due to glacial-interglacial sea-level changes in archipelagos may have enhanced diversity increase through 'dynamic mosaic effects' (Bellwood *et al.*, 2012). In northeastern Japan, the formation of an enclosed Sea of Japan may also be a contributor to high Pliocene diversity, as the diverse Omma−Manganji fauna developed there (Cronin & Ikeya, 1987; Kamiya *et al.*, 2006; Amano, 2007). Interglacial expansion of warm-water (i.e. southern-origin) species northward into the Sea of Japan and subsequent glacial isolation of the Sea of Japan may have fostered speciation and resulting diversity increase (Kamiya *et al.*, 2006). If this Pliocene establishment of the modern-level high species diversity, especially in the tropical IAA, is true not only for ostracode but also for other taxonomic groups, it may suggest that the history of present-day like IAA biodiversity hotspot is unexpectedly young, i.e. *c.* 3–5 million years.

The diversity decline from the Pleistocene to the present day was stronger in the IAA and northeastern Japan than in southwestern Japan, effectively inverting the latitudinal diversity pattern from the Plio-Pleistocene (Fig. 2). This results in a significant but weak diversity peak in mid-latitudes, as is known in some other taxa (Kerswell, 2006; Tittensor *et al.*, 2010; Powell *et al.*, 2012; Chaudhary *et al.*, 2016) (Fig. 2, Table 2). This IAA diversity decline may be due to repeated glacial exposure of the Sunda Shelf during periods of large amplitude glacioeustatic sea-level changes in the late Pleistocene (Hanebuth *et al.*, 2011). Large glacioeustatic sea-level changes during the late Pleistocene may have affected diversity negatively, in contrast to the earlier Plio-Pleistocene periods with lower amplitude sea-level changes that may have affected diversity positively, as discussed above. The repeated glacial exposures may have triggered regional extinctions and prevented re-colonization of deeper, lower shelf habitats. Indeed, the ostracode genus *Krithe*, which is a typical deep-sea genus but also lives at shelf depth [> 45 m water depth in the north-western Pacific (Zhou & Ikeya, 1992; Whatley & Zhao, 1993; Zhao & Whatley, 1997)], is completely absent even in the deeper parts of the Sunda Shelf (e.g. Mostafawi, 1992).

Unlike ostracodes, larger benthic foraminifera do not show a decline in diversity from the Plio-Pleistocene to the present day (Renema, 2007). The effects of sea-level oscillations may be more severe for direct-developing ostracodes than for foraminiferans, which have a planktonic larval stage and disperse well. In addition, larger benthic foraminifera are more closely associated with coral reefs than are ostracodes, and the depth distributions of these taxa may differ. Other possibilities include the discrepancy between taxonomic scales [foraminiferal data are genus level (Renema *et al.*, 2008) but the ostracode data are for species] and shifts in spatial coverage between the Plio-Pleistocene and the modern (Fig. 1) (but see Fig. S7 in Appendix S1 suggesting relatively little spatial structuring to richness within the IAA region). For northeastern Japan, a possible explanation of the depressed modern diversity may be cooling associated with the intensification of late Quaternary glacials in high latitudes (Zachos *et al.*, 2001; Raymo *et al.*, 2004). Finally, lowered modern diversity in general may reflect an overprint of recent human-induced ecological degradation (Jackson *et al.*, 2001; Pandolfi *et al.*, 2003) related to coastal eutrophication and hypoxic dead zones (Kidwell, 2007; Diaz & Rosenberg, 2008; Yasuhara *et al.*, 2012, 2015).

We find that the Western Pacific Cenozoic biodiversity was dynamic in time and space. In the Western Pacific, all regions show increasing diversity over time and remarkable Pliocene diversity enhancement. The Pliocene diversification is also known in the eastern coast of the North American continent. But there it is found only in the tropics (in corals and molluscs) (Budd, 2000; Jackson & Johnson, 2000; Johnson *et al.*, 2008) and is not significant in the temperate region (in benthic foraminifera) (Buzas *et al.*, 2002). In the Western Pacific, diversity was never highest in the tropics and at times, higher latitude faunas were significantly more diverse than tropical faunas. In these respects, the Western Pacific seems to differ from the Western Atlantic, which shows a standard LSDG pattern throughout the Cenozoic, at least for benthic foraminifera (Buzas *et al.*, 2002). In addition, modern shallow-marine ostracodes show a species diversity decline from the tropics to higher latitudes on the eastern coast of the North American continent (Chiu *et al.*, 2016) and modern North Atlantic deep-sea ostracodes also show a standard LSDG (Yasuhara *et al.*, 2009). These differences suggest the importance of regional factors and may be explained by the complicated coastline and archipelago nature of the broad tropical and north-western Pacific which may allow for tectonic, eustatic, oceanographic, and geomorphological processes and events (Bellwood *et al.*, 2012; Leprieur *et al.*, 2016) to foster highly diverse systems, even outside of the tropics. Indeed, the Indo-Pacific (= East Indian) region is considered as 'a locus from which ostracodes have migrated out since the Miocene' (Whatley, 1987; Titterton & Whatley, 1988). Another possibility is that the Japanese Archipelago may have been an independent biodiversity hotspot (Fujikura *et al.*, 2010) (in addition to the IAA hotspot) as seen at the present day for some taxa (Kerswell, 2006; Tittensor *et al.*, 2010), although we do not have sufficient spatial coverage and resolution to evaluate this hypothesis.

Ostracodes do not show a strong IAA hotspot, in contrast to many, but not all, groups (Hoeksema, 2007; Tittensor *et al.*, 2010). Some widespread taxa such as marine macroalgae, seagrasses and cephalopods do not show particularly high IAA diversity (Kerswell, 2006; Tittensor *et al.*, 2010), which calls for further research on taxa not closely associated with coral reefs or other specifically tropical habitats. Indeed, many of the groups showing a strong IAA hotspot are mostly restricted to the tropics (coral, mangrove, larger benthic foraminifera) or are associated with coral reefs (reef fishes and tropical families of gastropods) (Hoeksema, 2007; Tittensor *et al.*, 2010), but a few widespread taxa including coastal fishes and bivalves do show a strong IAA diversity peak (Tittensor *et al.*, 2010; Jablonski *et al.*, 2013). Furthering this line of research will help to understand whether coral reef habitats are primary drivers of tropical diversification, which is still the subject of debate (Kiessling *et al.*, 2010; Jablonski *et al.*, 2013).

ACKNOWLEDGEMENTS

We thank A. Naylor for help with the Leyte samples; F. Wesselingh and R. Majima for samples; B. Zhou and K. Yamada for data; L. Wong and M. Lo for continuous support; four anonymous referees and J. A. Crame for helpful comments and constructive criticism; and M. Carine, J. A. Crame and P. Linder for editing. The work described in this article was partially supported by grants from the Research Grants Council of the Hong Kong Special Administrative Region, China (project codes: HKU 709413P, HKU 17303115), the Environment and Conservation Fund of the Hong Kong Special Administrative Region, China (project code: 19/2012), the Seed Funding Programme for Basic Research of the University of Hong Kong (project codes: 201111159140, 201311159076, 201411159017, 201511159075), and the Temminck Fellowship of the Naturalis Biodiversity Center (to MY).

REFERENCES

Amano, K. (2007) The Omma-Manganji fauna and its temporal change. *Fossils*, **82**, 6–12.

Bellwood, D.R. & Meyer, C.P. (2009) Searching for heat in a marine biodiversity hotspot. *Journal of Biogeography*, **36**, 569–576.

Bellwood, D.R., Hughes, T.P., Connolly, S.R. & Tanner, J. (2005) Environmental and geometric constraints on Indo-Pacific coral reef biodiversity. *Ecology Letters*, **8**, 643–651.

Bellwood, D.R., Renema, W. & Rosen, B.R. (2012) Biodiversity hotspots, evolution and coral reef biogeography: a review. *Biotic evolution and environmental change in Southeast Asia* (ed. by D.J. Gower, K.G. Johnson, J.E. Richardson, B.R. Rosen, L. Rüber and S.T. Williams), pp. 216–245. Cambridge University Press, Cambridge.

Budd, A.F. (2000) Diversity and extinction in the Cenozoic history of Caribbean reefs. *Coral Reefs*, **19**, 25–35.

Buzas, M.A., Collins, L.S. & Culver, S.J. (2002) Latitudinal difference in biodiversity caused by higher tropical rate of increase. *Proceedings of the National Academy of Sciences USA*, **99**, 7841–7843.

Chaudhary, C., Saeedi, H. & Costello, M.J. (2016) Bimodality of latitudinal gradients in marine species richness. *Trends in Ecology and Evolution*, **31**, 670–676.

Chiu, W.T.R., Yasuhara, M., Cronin, T.M., Hunt, G. & Gemery, L. (2016) Modern and interglacial marine ostracode species diversity patterns off eastern North America. Ocean Sciences Meeting Abstract, New Orleans.

Cotton, L.J. & Pearson, P.N. (2011) Extinction of larger benthic foraminifera at the Eocene/Oligocene boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **311**, 281–296.

Crame, J.A. (2000) Evolution of taxonomic diversity gradients in the marine realm: evidence from the composition of Recent bivalve faunas. *Paleobiology*, **26**, 188–214.

Crame, J.A. (2001) Taxonomic diversity gradients through geological time. *Diversity and Distributions*, **7**, 175–189.

Cronin, T.M. & Ikeya, N. (1987) The Omma-Manganji ostracod fauna (Plio-Pleistocene) of Japan and the zoogeography of circumpolar species. *Journal of Micropalaeontology*, **6**, 65–88.

Diaz, R.J. & Rosenberg, R. (2008) Spreading dead zones and consequences for marine ecosystems. *Science*, **321**, 926–929.

Fujikura, K., Lindsay, D., Kitazato, H., Nishida, S. & Shirayama, Y. (2010) Marine biodiversity in Japanese waters. *PLoS ONE*, **5**, e11836. doi:10.1371/journal.pone.0011836.

Gallagher, S.J., Wallace, M.W., Li, C.L., Kinna, B., Bye, J.T., Akimoto, K. & Torii, M. (2009) Neogene history of the West Pacific Warm Pool, Kuroshio and Leeuwin currents. *Paleoceanography*, **24**, PA1206, doi:10.1029/2008PA001660.

Gallagher, S.J., Kitamura, A., Iryu, Y., Itaki, T., Koizumi, I. & Hoiles, P.W. (2015) The Pliocene to recent history of the Kuroshio and Tsushima Currents: a multi-proxy approach. *Progress in Earth and Planetary Science*, **2**, 17, doi:10.1186/s40645-015-0045-6.

Hall, R. (2011) Australia–SE Asia collision: plate tectonics and crustal flow. *The SE Asian Gateway: history and tectonics of the Australia-Asia Collision (Geological Society, London, Special Publications, 355)* (ed. by R. Hall, M.A. Cottam and M.E.J. Wilson), pp. 75–109. The Geological Society of London, London.

Hanebuth, T.J.J., Voris, H.K., Yokoyama, Y., Saito, Y. & Okuno, J. (2011) Formation and fate of sedimentary depocentres on Southeast Asia's Sunda Shelf over the past sea-level cycle and biogeographic implications. *Earth-Science Reviews*, **104**, 92–110.

Hoeksema, B.W. (2007) Delineation of the Indo-Malayan centre of maximum marine biodiversity: The Coral Triangle. *Biogeography, time and place: distributions, barriers and islands* (ed. by W. Renema), pp. 117–178. Springer, Berlin.

Hoeksema, B.W. (2015) Latitudinal species diversity gradient of mushroom corals off eastern Australia: a baseline from the 1970s. *Estuarine, Coastal and Shelf Science*, **165**, 190–198.

Holland, S.M. & Christie, M. (2013) Changes in area of shallow siliciclastic marine habitat in response to sediment deposition: implications for onshore-offshore paleobiologic patterns. *Paleobiology*, **39**, 511–524.

Holland, S.M. & Zaffos, A. (2011) Niche conservatism along an onshore-offshore gradient. *Paleobiology*, **37**, 270–286.

Irizuki, T., Kusumoto, M., Ishida, K. & Tanaka, Y. (2007) Sea-level changes and water structures between 3.5 and 2.8 Ma in the central part of the Japan Sea Borderland: analyses of fossil Ostracoda from the Pliocene Kuwae Formation, central Japan. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **245**, 421–443.

Ishida, K., Yoshida, K. & Matsuoka, A. (2012) Fossil ostracode assemblages in the middle Pleistocene upper part of the Sawane Formation on Sado Island, Niigata Prefecture, central Japan and surface water freshening of the Sea of Japan. *The Journal of the Geological Society of Japan*, **118**, 476–492.

Jablonski, D., Belanger, C.L., Berke, S.K., Huang, S., Krug, A.Z., Roy, K., Tomasovych, A. & Valentine, J.W. (2013) Out of the tropics, but how? Fossils, bridge species, and thermal ranges in the dynamics of the marine latitudinal diversity gradient. *Proceedings of the National Academy of Sciences USA*, **110**, 10487–10494.

Jackson, J.B.C. & Johnson, K.G. (2000) Life in the last few million years. *Paleobiology*, **26**, 221–234.

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J. & Warner, R.R. (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science*, **293**, 629–638.

Johnson, K.G., Jackson, J.B.C. & Budd, A.F. (2008) Caribbean reef development was independent of coral diversity over 28 million years. *Science*, **319**, 1521–1523.

Johnson, K.G., Renema, W., Rosen, B.R. & Santodomingo, N. (2015) 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.

Kamiya, T., Sato, T. & Kumakiri, M. (2006) Evolution of the Ostracoda and the environmental changes of the Japan Sea. *Past, present and future environments of Pan-Japan sea region* (ed. by K. Hayakawa, N. Tang, M. Yamada, Y. Murata, K. Shiraki, T. Yamaguchi, H. Domitsu, S. Ochiai and S. Sato), pp. 109–125. Maruzen Co. Ltd, Tokyo.

Kerswell, A.P. (2006) Global biodiversity patterns of benthic marine algae. *Ecology*, **87**, 2479–2488.

Kidwell, S.M. (2007) Discordance between living and death assemblages as evidence for anthropogenic ecological change. *Proceedings of the National Academy of Sciences USA*, **104**, 17701–17706.

Kiessling, W., Simpson, C. & Foote, M. (2010) Reefs as cradles of evolution and sources of biodiversity in the Phanerozoic. *Science*, **327**, 196–198.

Krug, A.Z., Jablonski, D. & Valentine, J.W. (2007) Contrarian clade confirms the ubiquity of spatial origination patterns in the production of latitudinal diversity gradients. *Proceedings of the National Academy of Sciences USA*, **104**, 18129–18134.

Krug, A.Z., Jablonski, D., Valentine, J.W. & Roy, K. (2009) Generation of earth's first-order biodiversity pattern. *Astrobiology*, **9**, 113–124.

Kuhnt, W., Holbourn, A., Hall, R., Zuvela, M. & Käse, R. (2004) Neogene history of the Indonesian throughflow. *Continent-ocean interactions within East Asian Marginal Seas (Geophysical Monograph Series 149)* (ed. by P. Clift, W. Kuhnt, P. Wang and D. Hayes), pp. 299–320. The American Geophysical Union, Washington DC.

Leprieur, F., Descombes, P., Gaboriau, T., Cowman, P.F., Parravicini, V., Kulbicki, M., Melián, C.J., de Santana, C.N., Heine, C., Mouillot, D., Bellwood, D.R. & Pellissier, L. (2016) Plate tectonics drive tropical reef biodiversity dynamics. *Nature Communications*, **7**, 11461, doi:10.1038/ncomms11461.

Liu, Z.H., Pagani, M., Zinniker, D., DeConto, R., Huber, M., Brinkhuis, H., Shah, S.R., Leckie, R.M. & Pearson, A. (2009) Global cooling during the Eocene-Oligocene climate transition. *Science*, **323**, 1187–1190.

Lyle, M., Barron, J., Bralower, T.J., Huber, M., Lyle, A.O., Ravelo, A.C., Rea, D.K. & Wilson, P.A. (2008) Pacific ocean and Cenozoic evolution of climate. *Reviews of Geophysics*, **46**, RG2002, doi:10.1029/2005rg000190.

Mannion, P.D., Upchurch, P., Benson, R.B.J. & Goswami, A. (2014) The latitudinal biodiversity gradient through deep time. *Trends in Ecology and Evolution*, **29**, 42–50.

Maruyama, S., Isozaki, Y., Kimura, G. & Terabayashi, M. (1997) Paleogeographic maps of the Japanese islands: plate tectonic synthesis from 750 Ma to the present. *Island Arc*, **6**, 121–142.

McMonagle, L.B., Lunt, P., Wilson, M.E.J., Johnson, K.G., Manning, C. & Young, J. (2011) A re-assessment of age dating of fossiliferous limestones in eastern Sabah, Borneo: implications for understanding the origins of the Indo-Pacific marine biodiversity hotspot. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **305**, 28–42.

Mostafawi, N. (1992) Rezente Ostracoden aus dem mittleren Sunda-Schelf, zwischen der Malaiischen Halbinsel und Borneo. *Senckenbergiana lethaea*, **72**, 129–168.

Nishimura, S. (1981) *Sea and life of the Earth: an introduction to marine biogeography*. Kaimei-sha, Tokyo (in Japanese).

Ogasawara, K. (1994) Neogene paleogeography and marine climate of the Japanese Islands based on shallow-marine molluscs. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **108**, 335–351.

Ogasawara, K. (2002) Responses of Japanese Cenozoic molluscs to Pacific gateway events. *Revista Mexicana de Ciencias Geológicas*, **19**, 206–2014.

O'Hara, T.D., Rowden, A.A. & Bax, N.J. (2011) A southern hemisphere bathyal fauna is distributed in latitudinal bands. *Current Biology*, **21**, 226–230.

Okuda, T., Noda, T., Yamamoto, T., Ito, N. & Nakaoka, M. (2004) Latitudinal gradient of species diversity: multi-scale variability in rocky intertidal sessile assemblages along the Northwestern Pacific coast. *Population Ecology*, **46**, 159–170.

Okuda, T., Noda, T., Yamamoto, T., Hori, M. & Nakaoka, M. (2009) Latitudinal gradients in species richness in assemblages of sessile animals in rocky intertidal zone: mechanisms determining scale-dependent variability. *Journal of Animal Ecology*, **78**, 328–337.

Pandolfi, J.M., Bradbury, R.H., Sala, E., Hughes, T.P., Bjorndal, K.A., Cooke, R.G., McArdle, D., McClenachan, L., Newman, M.J.H., Paredes, G., Warner, R.R. & Jackson, J.B.C. (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science*, **301**, 955–958.

Powell, M.G., Beresford, V.P. & Colaianne, B.A. (2012) The latitudinal position of peak marine diversity in living and fossil biotas. *Journal of Biogeography*, **39**, 1687–1694.

Raymo, M.E., Oppo, D.W., Flower, B.P., Hodell, D.A., McManus, J.F., Venz, K.A., Kleiven, K.F. & McIntyre, K. (2004) Stability of North Atlantic water masses in face of pronounced climate variability during the Pleistocene. *Paleoceanography*, **19**, PA2008, doi:10.1029/2003PA000921.

Reich, S., Wesselingh, F. & Renema, W. (2014) A highly diverse molluscan seagrass fauna from the early Burdigalian (early Miocene) of Banyunganti (south-central Java, Indonesia). *Annalen des Naturhistorischen Museums in Wien, Serie A*, **116**, 5–129.

Renema, W. (2007) Fauna development of larger benthic Foraminifera in the Cenozoic of Southeast Asia. *Biogeography, time and place: distributions, barriers and islands* (ed. by W. Renema), pp. 179–215. Springer, Berlin.

Renema, W., Bellwood, D.R., Braga, J.C., Bromfield, K., Hall, R., Johnson, K.G., Lunt, P., Meyer, C.P., McMonagle, L.B., Morley, R.J., O'Dea, A., Todd, J.A., Wesselingh, F.P., Wilson, M.E.J. & Pandolfi, J.M. (2008) Hopping hotspots: global shifts in marine biodiversity. *Science*, **321**, 654–657.

Renema, W., Warter, V., Novak, V., Young, J.R., Marshall, N. & Hasibuan, F. (2015) Age of Miocene fossil localities in the northern Kutai Basin (East Kalimantan, Indonesia). *Palaios*, **30**, 26–39.

Scarponi, D. & Kowalewski, M. (2004) Stratigraphic paleoecology: bathymetric signatures and sequence overprint of mollusk associations from upper Quaternary sequences of the Po Plain, Italy. *Geology*, **32**, 989–992.

Tittensor, D.P., Mora, C., Jetz, W., Lotze, H.K., Ricard, D., Berghe, E.V. & Worm, B. (2010) Global patterns and predictors of marine biodiversity across taxa. *Nature*, **466**, 1098–1101.

Titterton, R. & Whatley, R.C. (1988) The provincial distribution of shallow water Indo-Pacific marine Ostracoda: origins, antiquity, dispersal routes and mechanisms. *Evolutionary biology of Ostracoda: its fundamentals and applications* (ed. by T. Hanai, N. Ikeya and K. Ishizaki), pp. 759–786. Kodansha, Tokyo.

Whatley, R. & Zhao, Q. (1993) The *Krithe* problem: a case history of the distribution of *Krithe* and *Parakrithe* (Crustacea, Ostracoda) in the South China Sea. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **103**, 281–297.

Whatley, R.C. (1987) The southern end of Tethys: an important locus for the origin and evolution of both deep and shallow water Ostracoda. *Shallow Tethys 2* (ed. by K.G. Mckenzie), pp. 461–474. A. A. Balkema, Rotterdam.

Wood, S.N. (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, **73**, 3–36.

Yamaguchi, T. & Kamiya, T. (2009) Eocene ostracodes from Hahajima Island of the Ogasawara (Bonin) Islands, northwestern Pacific, and their paleobiogeographic significance in the West Pacific. *Journal of Paleontology*, **83**, 219–237.

Yamaguchi, T., Norris, R.D. & Dockert, D.T., III (2014) Shallow-marine ostracode turnover during the Eocene-Oligocene transition in Mississippi, the Gulf Coast Plain, USA. *Marine Micropaleontology*, **106**, 10–21.

Yasuhara, M. & Cronin, T.M. (2008) Climatic influences on deep-sea ostracode (Crustacea) diversity for the last three million years. *Ecology*, **89**, S52–S65.

Yasuhara, M., Hunt, G., Cronin, T.M. & Okahashi, H. (2009) Temporal latitudinal-gradient dynamics and tropical instability of deep-sea species diversity. *Proceedings of the National Academy of Sciences USA*, **106**, 21717–21720.

Yasuhara, M., Hunt, G., Breitburg, D., Tsujimoto, A. & Katsuki, K. (2012) Human-induced marine ecological degradation: micropaleontological perspectives. *Ecology and Evolution*, **2**, 3242–3268.

Yasuhara, M., Tittensor, D.P., Hillebrand, H. & Worm, B. (2015) Combining marine macroecology and palaeoecology in understanding biodiversity: microfossils as a model. *Biological Reviews*, doi:10.1111/brv.12223.

Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K. (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, **292**, 686–693.

Zhao, Q. & Whatley, R. (1997) Distribution of the ostracod genera *Krithe* and *Parakrithe* in bottom sediments of the East China and Yellow seas. *Marine Micropaleontology*, **32**, 195–207.

Zhou, B. & Ikeya, N. (1992) Three species of *Krithe* (Crustacea: Ostracoda) from Suruga Bay, central Japan. *Transactions and Proceedings of the Palaeontological Society of Japan New Series*, **166**, 1097–1115.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Data information and supplementary figures.
Appendix S2 Geological age of the Leyte samples.
Appendix S3 Preservational, taphonomic and taxonomic considerations.

BIOSKETCH

Moriaki Yasuhara is an assistant professor in the School of Biological Sciences and the Swire Institute of Marine Science at the University of Hong Kong. He has broad interests in marine palaeoecology and macroecology, especially those using highly resolved micropalaeontological records. His recent research has focused on the spatiotemporal dynamics of large-scale biodiversity patterns, the climatic and temperature impacts on species diversity, and the controlling factor (s) of biodiversity patterns/change in shallow-marine, deep sea and pelagic ecosystems. He is also interested in microfossil-based conservation palaeobiology as well as palaeontology of the Ostracoda in general.

Author contributions: M.Y. conceived of the research; M.Y. designed the research with W.R.; T.K. M.Y., H.I., H.O., T.K., H.H., Y.M.A., A.G.S.F. and W.R. performed the research; M.Y., H.I., T.K., G.H., H.H., I.T. and W.R. interpreted the data; M.Y., G.H. and H.I. analysed the data; M.Y., G.H. and W.R. wrote most of the paper.

Editor: Alistair Crame

APPENDIX 1 Sources for published ostracode data.

Dewi, K.T. (1997) Ostracoda from the Java Sea, west of Bawean Island, Indonesia. *Marine Geological Institute Special Publication*, **4**, 1–115.

Fauzielly, L., Irizuki, T. & Sampei, Y. (2013) Spatial distribution of recent ostracode assemblages and depositional environments in Jakarta Bay, Indonesia, with relation to environmental factors. *Paleontological Research*, **16**, 267–281.

Frydl, P.M. (1982) Holocene ostracods in the southern Boso Peninsula. *Studies on Japanese Ostracoda* (ed. by T. Hanai), pp. 61–140. University of Tokyo Press, Tokyo.

Ikeya, N. & Suzuki, C. (1992) Distributional patterns of modern ostracodes off Shimane Peninsula, southwestern Japan Sea. *Reports of the Faculty of Science, Shizuoka University*, **26**, 91–137.

Ikeya, N., Zhou, B. & Sakamoto, J. (1992) Modern ostracode fauna from Otsuchi Bay, the Pacific coast of northeastern Japan. *Centenary of Japanese Micropaleontology* (ed. by K. Ishizaki and T. Saito), pp. 339–354. Terra Scientific Publishing Company, Tokyo.

Irizuki, T. (1994) Late Miocene ostracods from the Fujikotogawa Formation, northern Japan – with reference to cold water species involved with trans-Arctic interchange. *Journal of Micropalaeontology*, **13**, 3–15.

Irizuki, T. (2004) Fossil Ostracoda from the lower Pleistocene Masuda Formation, Tanega-shima Island, southern Japan. *Geoscience Reports of Shimane University*, **23**, 65–77.

Irizuki, T., Kusumoto, M., Ishida, K. & Tanaka, Y. (2007) Sea-level changes and water structures between 3.5 and 2.8 Ma in the central part of the Japan Sea Borderland: Analyses of fossil Ostracoda from the Pliocene Kuwae Formation, central Japan. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **245**, 421–443.

Irizuki, T. & Matsubara, T. (1994) Vertical changes of depositional environments of the Lower to Middle Miocene Kadonosawa Formation based on analyses of fossil ostracode faunas. *The Journal of the Geological Society of Japan*, **100**, 136–149.

Irizuki, T. & Matsubara, T. (1995) Early Middle Miocene ostracodes from the Suenomatsuyama Formation, Ninohe City, Northeast Japan and their paleoenvironmental significance. *Transactions and Proceedings of the Palaeontological Society of Japan. New series*, **177**, 65–78.

Irizuki, T., Yamada, K., Maruyama, T. & Ito, H. (2004) Paleoecology and taxonomy of Early Miocene Ostracoda and paleoenvironments of the eastern Setouchi Province, central Japan. *Micropaleontology*, **50**, 105–147.

Irizuki, T., Yamaguchi, T., Takahashi, M. & Yanagisawa, Y. (2001) Miocene temperate Ostracoda from the Tochigi and Fukushima districts, central to northeastern Japan. *14th International Symposium on Ostracoda, Guidebook of Excursions* (ed. by N. Ikeya), pp. 45–72. The Organizing Committee of ISO 2001, Shizuoka.

Ishida, K., Yoshida, K. & Matsuoka, A. (2012) Fossil ostracode assemblages in the middle Pleistocene upper part of the Sawane Formation on Sado Island, Niigata Prefecture, central Japan and surface water freshening of the Sea of Japan. *The Journal of the Geological Society of Japan*, **118**, 476–492.

Ishizaki, K. (1966) Miocene and Pliocene ostracodes from the Sendai area, Japan. *Science Reports of the Tohoku University, 2nd Series (Geology)*, **37**, 131–163.

Ishizaki, K. (1971) Ostracodes from Aomori Bay, Aomori Prefecture, northeast Honshu, Japan. *Science Reports of the Tohoku University, 2nd Series (Geology)*, **43**, 59–97.

Ishizaki, K. (1981) Ostracoda from the East China Sea. *Science Reports of the Tohoku University, 2nd Series (Geology)*, **51**, 37–65.

Iwatani, H. & Irizuki, T. (2008) Geology and fossil ostracode assemblages from the Pliocene Miyazaki Group in the northern part of the Miyazaki Plain, Southwest Japan. *Fossils*, **84**, 61–73.

Iwatani, H., Irizuki, T. & Goto, T. (2011) Temporal changes of Plio–Pleistocene Ostracoda from the Takanabe Formation, Miyazaki Group, Southwest Japan. *Paleontological Research*, **15**, 269–289.

Kamiya, T., Ozawa, H., Tsukawaki, S. & Kato, M. (1997) Ostracode fauna off Kanazawa and Oki before the heavy oil spill accident. *Status report on emergency survey and reconstruction of the polluted environment by the heavy oil spill accident in the Japan sea and studies for its reconstruction*, 76–92 (in Japanese with title translated).

Mostafawi, N., Colin, J.P. & Babinot, J.F. (2005) An account on the taxonomy of ostracodes from recent reefal flat deposits in Bali, Indonesia. *Revue de micropaléontologie*, **48**, 123–140.

Nakao, Y., Tanaka, G. & Yamada, S. (2001) Pleistocene and living marine Ostracoda in Shizuoka district, Japan. *14th International Symposium on Ostracoda, Guidebook of Excursions* (ed. by N. Ikeya), pp. 127–147. The Organizing Committee of ISO 2001, Shizuoka.

Nohara, T. & Tabuki, R. (1985) Okinawa Island (Plio-Pleistocene tropical and subtropical Ostracoda and Ostracoda of Recent coral reef). *Guidebook of Excursions* (ed. by Organizing Committee of 9th International Symposium on Ostracoda), pp. 1–27. Shizuoka University Press, Shizuoka.

Ozawa, H. (2010) Preliminary report on the middle Pleistocene ostracods from the Shichiba Formation on Sado Island in the eastern Japan Sea. *Nihon-Kaiiki Kenkyu*, **41**, 15–36.

Ozawa, H. & Domitsu, H. (2010) Early Pleistocene ostracods from the Hamada Formation in the Shimokita Peninsula, northeastern Japan: the palaeo-biogeographic significance of their occurrence for the shallow-water fauna. *Paleontological Research*, **14**, 1–18.

Ozawa, H., Ikehara, K. & Katayama, H. (1999) Recent ostracode fauna in the northeastern part of the Japan Sea, off northwestern Hokkaido. *Comprehensive study on environmental changes in the western Hokkaido coastal area and study on evaluation of marine active faults* (ed. by K.

Ikehara and Y. Okamura), pp. 103–117 (in Japanese with title translated). Geological Survey of Japan, Tsukuba.

Ozawa, H., Kamiya, T., Kato, M. & Tsukawaki, S. (2004) A preliminary report on the Recent ostracodes in sediment samples from the R.V. Tansei-maru Cruise KT01-14 in the southwestern Okhotsk Sea and the northeastern Japan Sea off Hokkaido. *Bulletin of the Japan Sea Research Institute, Kanazawa University*, **35**, 33–46.

Ozawa, H., Kamiya, T. & Tsukagoshi, A. (1995) Ostracode evidence for the paleoceanographic change of the middle Pleistocene Jizodo and Yabu Formations in the Boso Peninsula, central Japan. *The Science Reports of the Kanazawa University*, **40**, 9–37.

Ozawa, H., Nagamori, H. & Tanabe, T. (2008) Pliocene ostracods (Crustacea) from the Togakushi area, central Japan; palaeobiogeography of trans-Arctic taxa and Japan Sea endemic species. *Journal of Micropalaeontology*, **27**, 161–175.

Tabuki, R. (1986) Plio-Pleistocene Ostracoda from the Tsugaru Basin, north Honshu, Japan. *Bulletin of the College of Education, University of Ryukyus*, **29**, 27–160.

Tabuki, R. (2001) Plio-Pleistocene and Recent subtropical Ostracoda in Okinawa. *14th International Symposium on Ostracoda, Guidebook of Excursions* (ed. by N. Ikeya), pp. 21–44. The Organizing Committee of ISO 2001, Shizuoka.

Tanaka, G. & Hasegawa, Y. (2013) Miocene ostracods from the Itahana formation in the Tomioka district, Gunma Prefecture, central Japan: paleoenvironmental significance and systematics. *Paleontological Research*, **17**, 138–172.

Tanaka, G., Komatsu, T. & Phong, N.D. (2009) Recent ostracod assemblages from the northeastern coast of Vietnam and the biogeographical significance of the euryhaline species. *Micropaleontology*, **55**, 365–382.

Tanaka, G. & Nomura, S. (2009) Late Miocene and Pliocene Ostracoda from the Shimajiri Group, Kume-jima Island, Japan: biogeographical significance of the timing of the formation of back-arc basin (Okinawa Trough). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **276**, 56–68.

Tanaka, G., Zhou, B., Ikeya, N. & Hasegawa, Y. (2012) Recent ostracod assemblages from Suruga Bay, central Japan. *Bulletin of Gunma Museum of Natural History* **16**, 1–30.

Tsukawaki, S., Kamiya, T., Kato, M., Matsuzaka, T., Naraoka, H., Negishi, K., Ozawa, H. & Ishiwatari, R. (1997) Preliminary results from the R.V. Tansei-maru Cruise KT95-14 Leg 2 in the southern marginal area in the Japan Sea – Part 1: sediments, benthic foraminifers and ostracodes –. *Bulletin of the Japan Sea Research Institute, Kanazawa University*, **28**, 13–43.

Tsukawaki, S., Kamiya, T., Ozawa, H. & Kato, M. (1998) Preliminary results on the sediment samplings during the R. V. Tansei-maru Cruise KT96-17 Leg 2 in the southwestern part of the Japan Sea – sediments, benthic foraminifers and ostracodes. *Bulletin of the Japan Sea Research Institute, Kanazawa University*, **29**, 67–89.

Tsukawaki, S., Ozawa, H., Domitsu, H., Kamiya, T., Kato, M. & Oda, M. (2000) Preliminary results from the R. V. Tansei-maru Cruise KT98-17 in the southwestern marginal part of the Japan Sea – sediments, benthic and planktonic foraminifers, and ostracodes. *Bulletin of the Japan Sea Research Institute, Kanazawa University*, **31**, 89–119.

Whatley, R.C. & Watson, K. (1988) A preliminary account of the distribution of Ostracoda in recent reef and reef associated environments in the Pulau Seribu or Thousand Island Group, Java Sea. *Evolutionary biology of Ostracoda: its fundamentals and applications* (ed. by T. Hanai, N. Ikeya and K. Ishizaki), pp. 399–411. Kodansha, Tokyo.

Whatley, R.C. & Zhao, Q. (1987) Recent Ostracoda of the Malacca Straits, Part I. *Revista Española de Micropaleontología*, **19**, 327–366.

Yajima, M. (1992) Early Miocene Ostracoda from Mizunami, central Japan. *Bulletin of the Mizunami Fossil Museum*, **19**, 247–268.

Yamaguchi, T. (2004) Oligocene ostracode assemblages from the Itanoura Formation, Nishisonogi Group, Nagasaki Prefecture, southwestern Japan. *Paleontological Research*, **8**, 53–70.

Yamaguchi, T. (2006) Eocene ostracodes from the Iojima Group, Nagasaki prefecture, southwestern Japan. *Journal of Paleontology*, **80**, 902–918.

Yamaguchi, T. & Kamiya, T. (2007) Oligocene-Miocene ostracode assemblages with the genus *Palmoconcha* from Japan. *Journal of Paleontology*, **81**, 632–642.

Yamaguchi, T. & Kamiya, T. (2009) Eocene ostracodes from Hahajima Island of the Ogasawara (Bonin) Islands, northwestern Pacific, and their paleobiogeographic significance in the West Pacific. *Journal of Paleontology*, **83**, 219–237.

Yamaguchi, T., Mashiba, H. & Kamiya, T. (2012) Miocene ostracodes from the Osaki Formation, Kukinaga Group, Tanegashima, Southwest Japan, and their significance for the biogeography of the Indo-West Pacific. *Paleontological Research*, **16**, 107–123.

Yamaguchi, T., Matsubara, T. & Kamiya, T. (2005) Eocene ostracodes from the Iwaya Formation on Awajishima Island, southwestern Japan. *Paleontological Research*, **9**, 305–318.

Yamaguchi, T., Matsubara, T., Suzuki, S. & Tanaka, H. (2008) Paleogene ostracodes from Kurashiki City, Okayama Prefecture, southwestern Japan. *Paleontological Research*, **12**, 355–369.

Zhou, B. (1993) *Ostracode fauna in the Pacific off Southwest Japan*. PhD Thesis, Kyoto University.