

LETTER

Latitudinal species diversity gradient of marine zooplankton for the last three million years

Moriaki Yasuhara,^{1,2,3,4,5*} Gene Hunt,⁵ Harry J. Dowsett,⁶ Marci M. Robinson⁶ and Danielle K. Stoll⁶

Abstract

High tropical and low polar biodiversity is one of the most fundamental patterns characterising marine ecosystems, and the influence of temperature on such marine latitudinal diversity gradients is increasingly well documented. However, the temporal stability of quantitative relationships among diversity, latitude and temperature is largely unknown. Herein we document marine zooplankton species diversity patterns at four time slices [modern, Last Glacial Maximum (18 000 years ago), last interglacial (120 000 years ago), and Pliocene (~3.3–3.0 million years ago)] and show that, although the diversity-latitude relationship has been dynamic, diversity-temperature relationships are remarkably constant over the past three million years. These results suggest that species diversity is rapidly reorganised as species' ranges respond to temperature change on ecological time scales, and that the ecological impact of future human-induced temperature change may be partly predictable from fossil and paleoclimatological records.

Keywords

Biodiversity, climate changes, fossil records, latitudinal species diversity gradients, macroecology, North Atlantic, pelagic ecosystem, planktic foraminifera, temperature.

Ecology Letters (2012)

INTRODUCTION

A pattern of decreasing diversity with increasing latitude is one of the most fundamental and persistent patterns characterising life on earth (Crame 2001; Willig *et al.* 2003; Rex *et al.* 2005). In marine systems, such latitudinal species diversity gradients (LSDGs) are increasingly well documented, and recent studies have revealed that species diversity is often highly correlated with water temperature (Roy *et al.* 1998; Rutherford *et al.* 1999; Tittensor *et al.* 2010). In marine fossil records, some evidence indicates the presence of LSDGs for at least the past 270 million years (Stehli *et al.* 1969; Willig *et al.* 2003), but sparse fossil data in specific time slices have prevented detailed examinations (Thomas & Gooday 1996; Crame 2001, 2002; Yasuhara *et al.* 2009) and the temporal stability of diversity-latitude and diversity-temperature relationships is largely not known. Herein we document diversity gradients in North Atlantic zooplankton (planktic foraminifera) over the last three million years, analysed at four time slices: modern, Last Glacial Maximum (LGM: 18 000 years ago), last interglacial (LIG: 120 000 years ago), and Pliocene (~3.3–3.0 million years ago), and document quantitatively the temporal dynamics of marine LSDGs and the remarkable stability of diversity-temperature relationship through time.

Planktic foraminifera are enormously abundant in deep-sea sediments and their fossil record is probably the most complete of any marine taxon. Their taxonomy is robust because the total species richness of the group is relatively limited [~40 in the

present-day oceans (Dowsett 2007a)], and because specialists have extended great efforts to standardise identifications because of the vital role of this group in paleoceanographic, paleoclimatic and stratigraphic investigations. The Brown University Foraminiferal Database (BFD) (Prell *et al.* 1999) provided an initial understanding of global zooplankton species diversity patterns (Rutherford *et al.* 1999; Tittensor *et al.* 2010) and comprehensive fossil planktic foraminiferal data sets are available for key time slices of the last three million years. The CLIMAP (Climate: Long range Investigation, Mapping, and Prediction) data sets (CLIMAP Project Members 1976, 1984) are comprehensive foraminiferal census count data designed for time slice reconstructions of sea-surface temperature (SST) of LGM and LIG. The PRISM (Pliocene Research, Interpretation and Synoptic Mapping) foraminiferal data set (Dowsett *et al.* 1988, 2005; PRISM Project Members 1996; Robinson *et al.* 2008a) was developed for a SST time-slab reconstruction of 3.264–3.025 million years ago. These data sets provide us with a unique opportunity for detailed investigation of large-scale zooplankton species diversity patterns in the past. We concentrate here on the North Atlantic Ocean because of the quality and quantity of data available from this ocean.

MATERIALS AND METHODS

Planktic foraminiferal data are from modern BFD (<http://www.ncdc.noaa.gov/paleo/metadata/noaa-ocean-5908.html>) (Prell *et al.* 1999), LGM CLIMAP (<http://www.ncdc.noaa.gov/paleo/metadata/>

¹School of Biological Sciences, University of Hong Kong, Pok Fu Lam Road, Hong Kong SAR, China

²Swire Institute of Marine Science, University of Hong Kong, Cape d'Aguilar Road, Shek O, Hong Kong SAR, China

³Department of Earth Sciences, University of Hong Kong, Pok Fu Lam Road, Hong Kong SAR, China

⁴Center for Advanced Marine Core Research, Kochi University, Nankoku, Kochi, 783-8502, Japan

⁵Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC, 20013-7012, USA

⁶Eastern Geology and Paleoclimate Science Center, U.S. Geological Survey, Reston, VA, 20192, USA

*Correspondence: E-mails: moriakiyasuhara@gmail.com or yasuhara@hku.hk

noaa-ocean-2516.html) (CLIMAP Project Members 1976), LIG CLIMAP (<http://www.ncdc.noaa.gov/paleo/metadata/noaa-ocean-5816.html>) (CLIMAP Project Members 1984), and Pliocene PRISM (<http://geology.er.usgs.gov/eesteam/prism/>) (Dowsett *et al.* 2005, 2010; Dowsett 2007b) data sets (Fig. 1). Subspecies (including left and right coiling forms) were lumped prior to analysis but data sets without such lumping showed qualitatively similar results. After combining subspecies, data sets that we used are composed of 32 modern species from 223 sites, 32 LGM species from 101 sites, 28 LIG species from 13 sites, and 44 Pliocene species from 242 samples from 13 sites. $E(S_{200})$, species richness rarefied to 200 individuals, which is a widely used diversity index in marine ecology, was used as the diversity measure (Hurlbert 1971). All samples were processed using a 150 μm mesh size. Use of a standard mesh size is reasonable here because the size distribution of planktic foraminifera changes rather little over the interval studied here (Schmidt *et al.* 2004), and because temperature-diversity relationships are consistent between this mesh size and other mesh protocols (Al-Sabouni *et al.* 2007).

Foraminifera are widely used as a proxy for reconstructing past SSTs, and we used foraminiferal census data to estimate past SSTs for each sample for which diversity was calculated. Cold (February) SST was estimated using a planktic foraminiferal factor analytic transfer function (Dowsett & Poore 1990; Dowsett 1991) calibrated to the modern SST analysis of Reynolds & Smith (1995). This procedure first performs a factor analysis of a data matrix of the relative abundances of different foraminiferal taxa; some similar species are grouped together to allow interpretations in intervals such as the Pliocene with a somewhat different species pool. This factor analysis solution is subjected to a varimax rotation to simplify loading structure, and the resulting factor axes are interpretable as representing specific climatic and environmental faunas. For example, the first three axes represent tropical, polar, and gyre margin faunas respectively. Scores on the first five axes were calibrated to modern SST values via multiple regressions to allow prediction of cold and warm SST from assemblage factor scores (Dowsett 1991). We used cold SST here because a recent ecological hypothesis

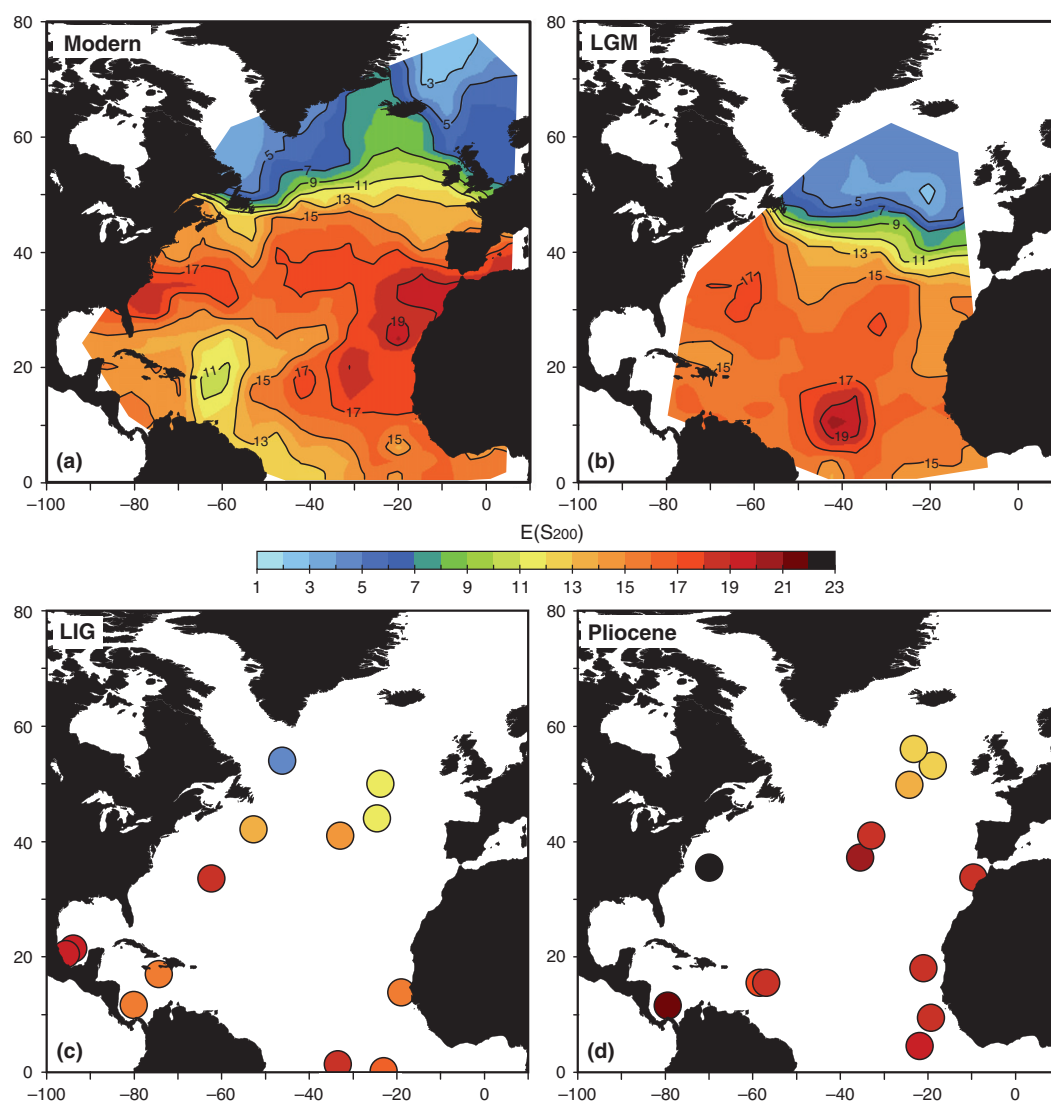


Figure 1 Planktic foraminiferal species diversity distribution in the North Atlantic Ocean. (a) Modern, (b) LGM (18 000 years ago), (c) LIG (120 000 years ago), and (d) mid-Pliocene (~3.3–3.0 million years ago). Only (a) and (b) panels are interpolated because of much better spatial coverage of the data.

suggests that tolerance to harsh conditions limits species distributions and thus may account for large-scale diversity patterns as the sum of these distributions (Currie *et al.* 2004). However, cold-month and warm-month SSTs are very highly correlated in these data ($r = 0.95$ in the modern data set), and so it is not possible to separately assess their effects in this study.

Age control and planktic foraminiferal species identifications were carefully evaluated by the leading specialists for the original paleoclimatological research projects and thus are reasonably robust in all time slices (CLIMAP Project Members 1976, 1984; Dowsett *et al.* 2005). Pliocene fossil planktic foraminifera are generally well preserved and have almost no additional taxonomic uncertainties or difficulties compared to late Pleistocene foraminifera (Dowsett & Robinson 2007). Although the Pliocene data set has a wider total temporal range than the other data sets, reconstructed diversity and temperature values are from individual sediment samples and thus of similar spatial and temporal resolution across all time intervals.

To explore the relationships between diversity and both temperature (cold SST) and latitude, we took a two-part approach. First, we used lowess smoothing to draw a curve through the relationships separately for each interval. Lowess curves are locally weighted regressions that offer a convenient means for drawing a smooth line through a cloud of points without specifying a functional relationship (see Cleveland 1979). Second, we focused on decreases in diversity and cold SST moving northwards from subtropical latitudes to the pole. The plots and the lowess curves suggest that the $E(S_{200})$ -cold SST and $E(S_{200})$ -latitude relationships were nearly linear over this range (Fig. 2). So, using least-squares regressions, we simply compared slopes and intercepts across modern, LGM, LIG and Pliocene bins.

Analyses reported herein were implemented in the R programming language (R Development Core Team 2010), using functions from the R package Vegan (Oksanen *et al.* 2010). Data sets used for this article are deposited at Dryad (<http://datadryad.org/>; <http://dx.doi.org/10.5061/dryad.dc139>).

RESULTS

North Atlantic species diversity distributions of modern, LGM, LIG and Pliocene time slices are shown in Fig. 1. Modern species diversity is highest in mid-latitudes off North America and in low- to mid-latitudes along the northwestern coast of Africa. During the LGM, this coastal African diversity hotspot largely diminishes and subtropical North Atlantic diversity is also lower, especially south of Iceland, compared to the modern diversity pattern. LGM diversity is generally lower than modern diversity at the same latitude. An exception is tropical western Atlantic, where species diversity is higher during the LGM than in the modern world. Although the number of sites is limited, LIG diversity shows similar pattern with the modern diversity, but the species diversity may be slightly higher during the LIG at similar latitudes. In the Pliocene, species diversity is generally higher compared to modern diversity of the same latitude, and rarefied diversities $[E(S_{200})]$ greater than 20 are common in the tropics.

Planktic foraminiferal diversity shows a subtropical-high with strongly decreasing values toward the polar region (Figs 1 and 2). Diversities also decrease, albeit much more shallowly, toward the tropics and the resulting diversity profiles are significantly unimodal in all time slices (Mitchell-Olds and Shaw test for unimodality: $P < 0.001$ for modern, LGM, and Pliocene, $P = 0.001$ for LIG). Species diversity is highest in the mid-Pliocene, intermediate in the modern and LIG, and lowest in the LGM time slices across most latitudes. The fitted coefficients of quadratic regressions of diversity-latitude relationships indicate lowest diversity in the LGM, intermediate diversity in the modern, and highest diversity in the Pliocene (intercepts are 0, 2.21, and 5.25 respectively); Tukey's Honest Significant Difference test indicates that all pairwise differences are significant ($P < 0.001$) (we omitted LIG from these analyses because of its small sample size).

For latitudes $> 35^\circ$ N, diversity decreases approximately linearly with increasing latitude in all data sets (Fig. 2). The slope over this

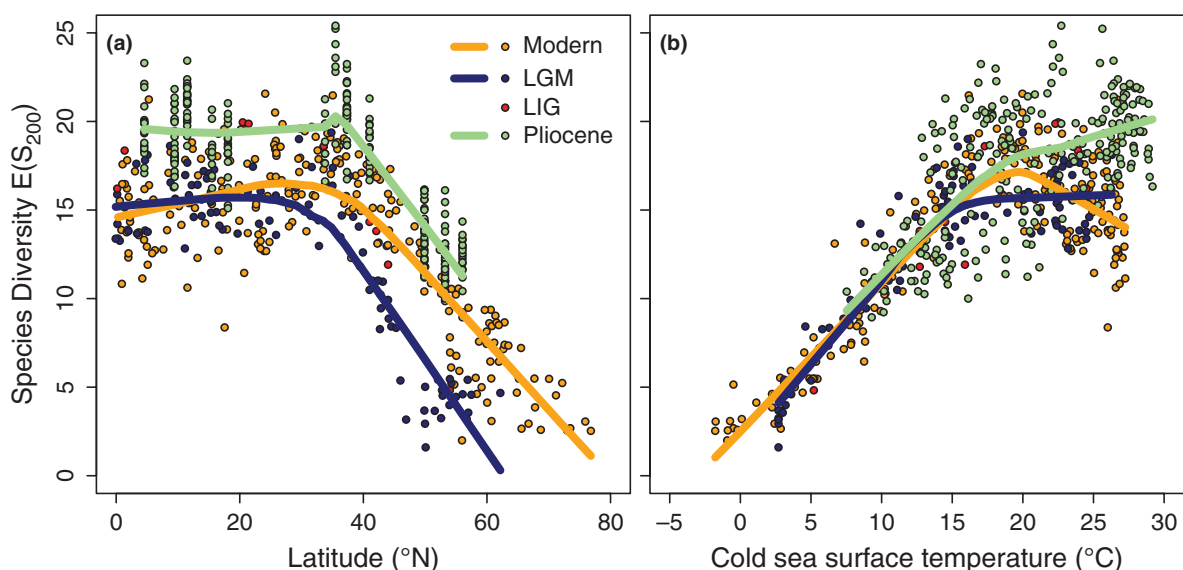


Figure 2 Species diversity patterns of the North Atlantic planktic foraminifera. (a) Latitudinal species diversity gradients. (b) Temperature (cold SST)-diversity relationship. Orange: modern. Blue: LGM. Red: LIG. Green: mid-Pliocene. Lines are lowess curves for each time slice. LIG lowess curve is not shown because of the low sample sizes. LGM, LIG, and Pliocene cold SSTs are reconstructed based on planktic foraminiferal transfer function (see Materials and Methods).

Table 1 Slope and intercepts for $E(S_{200})$ vs. latitude and temperature (cold SST) for the linear part of the curves of latitude $> 35^\circ$ N or cold SST $< 17^\circ$ C. LIG results were not used for comparison or discussion because of their small sample size (n). CI: confidence interval.

Time slices	n	Slope (95% CI)	Intercept (95% CI)
<i>E(S₂₀₀)</i> vs. latitude			
Modern	102	-0.418 (-0.451, -0.385)	32.53 (30.78, 34.29)
LIG	5	-0.613 (-0.950, -0.277)	39.69 (24.05, 55.33)
LGM	42	-0.555 (-0.638, -0.472)	34.20 (30.26, 38.14)
Pliocene	134	-0.509 (-0.552, -0.466)	39.59 (37.55, 41.62)
<i>E(S₂₀₀)</i> vs. cold SST			
Modern	94	0.921 (0.838, 1.00)	2.17 (1.33, 3.01)
LIG	5	0.819 (0.321, 1.32)	1.34 (-5.01, 7.70)
LGM	62	0.934 (0.834, 1.03)	1.74 (0.642, 2.84)
Pliocene	79	0.876 (0.664, 1.09)	2.43 (-0.466, 5.32)

range is significantly steeper in the LGM than it is in the modern world (see the confidence intervals in Table 1). Temperature-diversity curves based on cold SST are rather more consistent across all time slices than are latitude-diversity relationships (Fig. 2); the linear parts of the relationship when temperatures are below $\sim 17^\circ$ C are particularly similar as shown below. A model with separate linear regressions by time slice bin was not significantly better than a model with the same regression across all three bins of modern, LGM, and Pliocene (ANOVA, $F = 0.3759$, $P = 0.826$; for cold SST $< 17^\circ$ C again omitting the LIG bin). In contrast, the equivalent test for latitude-diversity relationships (for latitudes $> 35^\circ$ N) supports the model with different latitude-diversity relationships in each time bin ($F = 128.37$, $P < 0.001$, ANOVA). Thus, allowing that different relationships in each time bin vastly improves the diversity-latitude fit, but there is no significant gain in doing so for temperature. Furthermore, among separate regressions of modern, LGM, and Pliocene bins, the slopes and intercepts are very similar and their confidence intervals largely overlap in the $E(S_{200})$ vs. cold SST comparison, in contrast to those in the $E(S_{200})$ vs. latitude comparison (Table 1).

DISCUSSION

The presence of tropical-high, polar-low and unimodal latitudinal diversity gradients in the Pliocene, LIG, LGM and modern time slices (Figs 1 and 2) suggest that the general LSDG pattern has been persistent for the last three million years. But there are quantitative differences among the intervals with diversities highest in the mid-Pliocene, intermediate in the modern and LIG, and lowest during the LGM. These contrasts match the general state of the climate, which was warmest in the mid-Pliocene and coldest during the last glacial maximum. In addition, the slope of diversity-latitude relationship in the LGM was much steeper than it is in the modern world (for the linear part of the relationship, i.e., latitudes $> 35^\circ$ N). In contrast, temperature-diversity curves are remarkably similar across all time slices, especially for cold SST $< 17^\circ$ C.

These results show fidelity of species diversity to temperature as discussed below. The LGM latitudinal diversity gradient (for latitudes $> 35^\circ$ N) is steeper than that of the modern ocean simply because the temperature-latitude relationship was steeper during the LGM (Pflaumann *et al.* 2003); temperature-diversity relationships (for cold SST $< 17^\circ$ C) between LGM and modern time slices are

almost identical (Table 1). The relatively steep Pliocene LSDG may be influenced by the sparsity of sites in the mid-latitudinal range of $20\text{--}40^\circ$ N or related to the excess tropical diversity of the Pliocene. In sum, our result supports temperature as a consistent predictor of species diversity, not only in modern marine ecosystems (Roy *et al.* 1998; Rutherford *et al.* 1999; Tittensor *et al.* 2010) but also throughout the last three million years.

Although the SST and diversity estimates ultimately derive from the abundances of planktic foraminifera in the same samples, for several reasons it is unlikely that the relationships described here are an artefact of the methods used. First, the lumping of species before the factor analysis results in a smaller set of taxa (18 groups) than the diversity analyses (32 species). Second, the factor loadings for each axis are dominated by a small number of taxa so should be insensitive to diversity *per se*. For example, factor axes representing tropical and polar assemblages are each overwhelmingly determined by the abundance of single taxon, although it is a different taxon for each axis (Dowsett 1991). Finally, other proxy data support the overall temperature patterns inferred herein from foraminiferal data, suggesting that these reconstructions are reliable. For example, multiproxy studies using a foraminiferal transfer function, Mg/Ca ratio, and alkenone unsaturation index have been conducted to determine reliability of the PRISM sea-surface temperature reconstruction based on foraminiferal transfer function and showed good general agreement among these paleotemperature proxies in our research area of the North Atlantic Ocean (Dowsett 2007b; Robinson *et al.* 2008b; Dowsett *et al.* 2012). Furthermore, the foraminiferal transfer function is one of the well-established and widely used paleothermometry methods and shows good agreement with other geochemical methods in general (Bard 2001). Excellent spatial coverage is an important advantage of the foraminiferal transfer function over other available paleotemperature proxies. In our case, temperature data are derived from exactly the same samples as the diversity data, thus avoiding errors associated with spatial interpolation and temporal correlation.

Although the temperature-diversity relationships are similar across all intervals, at warmer temperatures Pliocene diversities are higher compared to the other intervals (Fig. 2). This diversity offset at warmer temperatures may be attributable, at least in part, to the effects of selective extinction with respect to thermal habitat. Compared to species that survived to the present day, those that have gone extinct since the Pliocene have narrower latitudinal ranges ($W = 154.5$, $P = 0.015$, Wilcoxon two-sample test) and northern range limits that are more southerly ($W = 141.5$, $P = 0.050$, Wilcoxon two-sample test) (Table S1 in Supporting Information; only species represented by > 200 specimens in PRISM data set were used). In other words, long-term Plio-Pleistocene cooling has preferentially removed species from lower latitudes. These extinctions have not been compensated for by the origination of new, warm-water species since the Pliocene and thus modern warm-water foraminiferal assemblages remain depleted relative to those from the Pliocene. Although selective extinction of species with narrower range size is consistent with recent hypotheses (Dynesius & Jansson 2000; Jocque *et al.* 2010), higher speciation rates in the tropics predicted by these hypotheses are not observed here. The preferential extinction of warm-water species since the Pliocene may also account for the steep decrease in diversity at the very highest end of the temperature range that is observed in the modern ocean but not in the other intervals, although the lack of a diversity downturn

in the LGM time slice is less certain because of the paucity of very warm temperatures during glacial periods (Pflaumann *et al.* 2003).

Paleoecology is a powerful tool as a source of direct evidence to investigate impacts of climatic changes on biodiversity in multi-decadal or longer time scales (Willis & Birks 2006; Yasuhara & Cronin 2008; Yasuhara *et al.* 2008; Willis *et al.* 2010). Consistency of temperature-diversity relationships for the last three million years suggests that species diversity can be rapidly reorganised via shifts in the geographical ranges of species, highlighting the importance of ecological mechanisms in modulating diversity gradients. Foraminiferal diversity may be limited by the number of species that can tolerate a particular thermal regime (the 'physiological tolerance hypothesis' of Currie *et al.* 2004), resulting in correlated changes to thermal and diversity gradients. Evolutionary mechanisms of negative LSDGs, such as a faster speciation rates and slower extinction rates at low latitudes (Dynesius & Jansson 2000; Allen *et al.* 2002; Jablonski *et al.* 2006; Jocque *et al.* 2010), seem to play relatively minor roles at this temporal scale. For example, modern and LGM latitudinal diversity gradients significantly differ from each other even though these two intervals share the same species pool [i.e., there are no extinctions or originations of planktic foraminifer species during the last 18 000 years (Berggren *et al.* 1995)].

Although ecological mechanisms are more important than evolutionary ones in accounting for changes in latitudinal diversity gradients over the past three million years, gradients in extinction or speciation rates may well have been important in establishing the diversity gradient prior to the Pliocene. Moreover, history has left an overprint on foraminiferal diversity patterns in the form of reduced tropical diversities as a legacy of selective extinction of warm-water taxa since the Pliocene as climate consistently cooled. The correspondence between temperature and diversity may be particularly evident in Plio-Pleistocene icehouse climates with steep latitudinal temperature gradients, and in spatially continuous systems such as the pelagic realm. Evolutionary mechanisms involving differences in speciation and extinction rates may be more important in greenhouse intervals when temperature gradients are shallower (Zachos *et al.* 2001; Amiot *et al.* 2004), and perhaps in systems with effective barriers to dispersal (Janzen 1967; Ghalambor *et al.* 2006; Jocque *et al.* 2010). Our zooplankton result is also consistent with recent study of marine invertebrates showing that organisms with planktic larva stage tend to show standard negative LSDGs (Fernández *et al.* 2009).

Steeper LGM LSDG revealed herein contrasts the pattern observed in the deep sea. The deep-sea LSDG is known to be much weakened during the LGM, at least in benthic ostracodes (Yasuhara *et al.* 2009). This discrepancy sounds reasonable from the temperature perspective, because it is known that the bulk of the deep LGM ocean was relatively homogeneous in temperature (Adkins *et al.* 2002). These facts highlight that temporal LSDGs dynamics can be quite different among ecosystems and time periods in spite of prevailing standard tropical-high, polar-low LSDGs in the modern biota.

ACKNOWLEDGEMENTS

We thank S. Berke and two anonymous referees for thoughtful and insightful comments and D. Marshall and J. Fryxell for editing. H.J. D., M.M.R. and D.K.S. thank the USGS Climate and Land Use Change Research and Development Program for continued support.

This research used samples and/or data provided by the Integrated Ocean Drilling Program (IODP).

CONFLICT OF INTEREST

There is no conflict of interest regarding this article.

AUTHOR CONTRIBUTIONS

MY and GH designed research; MY, HJD, MMR and DKS analysed the data; MY, G.H performed paleoecological modelling; HJD and MMR were responsible for foraminiferal data sets; and MY and GH wrote the paper.

REFERENCES

- Adkins, J.F., McIntyre, K. & Schrag, D.P. (2002). The salinity, temperature, and $\delta^{18}\text{O}$ of the glacial deep ocean. *Science*, 298, 1769–1773.
- Allen, A.P., Brown, J.H. & Gillooly, J.F. (2002). Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science*, 297, 1545–1548.
- Al-Sabouni, N., Kucera, M. & Schmidt, D.N. (2007). Vertical niche separation control of diversity and size disparity in planktonic foraminifera. *Mar. Micropaleontol.*, 63, 75–90.
- Amiot, R., Lecuyer, C., Buffetaut, E., Fluteau, F., Legendre, S. & Martineau, F. (2004). Latitudinal temperature gradient during the cretaceous upper campanian-middle maastrichtian: $\delta^{18}\text{O}$ record of continental vertebrates. *Earth Planet. Sci. Lett.*, 226, 255–272.
- Bard, E. (2001). Comparison of alkenone estimates with other paleotemperature proxies. *Geochim. Geophys. Geos.*, 2, 1002, doi:10.1029/2000GC000050.
- Berggren, W.A., Hilgen, F.J., Langereis, C.G., Kent, D.V., Obradovich, J.D., Raffi, I. *et al.* (1995). Late Neogene chronology: new perspectives in high-resolution stratigraphy. *Geol. Soc. Am. Bull.*, 107, 1272–1287.
- Cleveland, W.S. (1979). Robust locally weighted regression and smoothing scatterplots. *J. Am. Stat. Assoc.*, 74, 829–836.
- CLIMAP Project Members (1976). The surface of the ice-age earth. *Science*, 191, 1131–1137.
- CLIMAP Project Members (1984). The last interglacial ocean. *Quat. Res.*, 21, 123–224.
- Crame, J.A. (2001). Taxonomic diversity gradients through geological time. *Divers. Distrib.*, 7, 175–189.
- Crame, J.A. (2002). Evolution of taxonomic diversity gradients in the marine realm: a comparison of Late Jurassic and Recent bivalve faunas. *Paleobiology*, 28, 184–207.
- Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guegan, J.F., Hawkins, B. A. *et al.* (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecol. Lett.*, 7, 1121–1134.
- Dowsett, H.J. (1991). The development of a long-range foraminifer transfer function and application to late Pleistocene North Atlantic climatic extremes. *Paleoceanography*, 6, 259–273.
- Dowsett, H.J. (2007a). Paleoceanography, biological proxies: Planktic foraminifera. In: *Encyclopedia of Quaternary Science* (ed. Elias, S.A.) Elsevier, Oxford, pp. 1678–1682.
- Dowsett, H.J. (2007b). The PRISM palaeoclimate reconstruction and Pliocene sea-surface temperature. In: *Deep-Time Perspectives on Climate Change: Marrying the Signal From Computer Models and Biological Proxies. The Micropaleontological Society, Special Publications* (eds. Williams, M, Haywood, A.M., Gregory, J & Schmidt, D.N.). Geological Society of London, London, pp. 459–480.
- Dowsett, H.J. & Poore, R.Z. (1990). A new planktic foraminifer transfer function for estimating Pliocene-Holocene paleoceanographic conditions in the north Atlantic. *Mar. Micropaleontol.*, 16, 1–23.
- Dowsett, H.J. & Robinson, M.M. (2007). Mid-pliocene planktic foraminifer assemblage of the north Atlantic ocean. *Micropaleontology*, 53, 105–126.
- Dowsett, H.J., Gosnell, L.B. & Poore, R.Z. (1988). Pliocene planktic foraminifer census data from deep sea drilling project holes 366A, 410, 606, and 646B. *US Geological Survey, Open File Report*, 88-654, 1–14.

- Dowsett, H.J., Chandler, M.A., Cronin, T.M. & Dwyer, G.S. (2005). Middle Pliocene sea surface temperature variability. *Paleoceanography*, 20, PA2014, doi:10.1029/2005PA001133.
- Dowsett, H.J., Robinson, M.M., Stoll, D.K. & Foley, K.M. (2010). Mid-Piacenzian mean annual sea surface temperature: an analysis for data-model comparisons. *Stratigraphy*, 7, 189–198.
- Dowsett, H.J., Robinson, M.M., Haywood, A.M., Hill, D.J., Dolan, A.M., Stoll, D.K. *et al.* (2012). Assessing confidence in Pliocene sea surface temperatures to evaluate predictive models. *Nat. Clim. Change*, 2, 365–371.
- Dynesius, M. & Jansson, R. (2000). Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proc. Natl. Acad. Sci. USA*, 97, 9115–9120.
- Fernández, M., Astorga, A., Navarrete, S.A., Valdovinos, C. & Marquet, P.A. (2009). Deconstructing latitudinal species richness patterns in the ocean: does larval development hold the clue? *Ecol. Lett.*, 12, 601–611.
- Ghalambor, C.K., Huey, R.B., Martin, P.R., Tewksbury, J.J. & Wang, G. (2006). Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integr. Comp. Biol.*, 46, 5–17.
- Hurlbert, S.H. (1971). The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, 52, 577–586.
- Jablonski, D., Roy, K. & Valentine, J.W. (2006). Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science*, 314, 102–106.
- Janzen, D.H. (1967). Why mountain passes are higher in the tropics. *Am. Nat.*, 101, 233–249.
- Jocque, M., Field, R., Brendonck, L. & De Meester, L. (2010). Climatic control of dispersal-ecological specialization trade-offs: a metacommunity process at the heart of the latitudinal diversity gradient? *Global Ecol. Biogeogr.*, 19, 244–252.
- Oksanen, J., Blanchet, G.B., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L. *et al.* (2010). *Vegan: Community Ecology Package. R Package Version 1.17-4*. Available at: <http://CRAN.R-project.org/package=vegan>. Last accessed 21 June 2012.
- Pflaumann, U., Sarnthein, M., Chapman, M., d'Abreu, L., Funnell, B., Huels, M. *et al.* (2003). Glacial North Atlantic: sea-surface conditions reconstructed by GLAMAP 2000. *Paleoceanography*, 18, 1065, doi:10.1029/2002PA000774.
- Prell, W., Martin, A., Cullen, J. & Trend, M. (1999). *The Brown University Foraminiferal Data Base, IGBP PAGES/World Data Center-A for Paleoclimatology Data Contribution Series # 1999-027*. NOAA/NGDC Paleoclimatology Program, Boulder.
- PRISM Project Members (1996). Pliocene planktic foraminifer census data from the North Atlantic region. *U.S. Geological Survey, Open File Report*, 96–669, 1–30.
- R Development Core Team (2010). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. Available at: <http://www.R-project.org>. Last accessed 21 June 2012.
- Rex, M.A., Crame, J.A., Stuart, C.T. & Clarke, A. (2005). Large-scale biogeographic patterns in marine mollusks: a confluence of history and productivity? *Ecology*, 86, 2288–2297.
- Reynolds, R.W. & Smith, T.M. (1995). A high-resolution global sea surface temperature climatology. *J. Clim.*, 8, 1571–1583.
- Robinson, M.M., Caballero, R., Pohlman, E., Herbert, T.D., Peck, V. & Dowsett, H.J. (2008a). Mid-Pliocene planktic foraminifer census data and alkenone unsaturation indices from Ocean Drilling Program Hole 677A. *US Geological Survey Data Series*, 353. Available at: <http://pubs.usgs.gov/ds/353>. Last accessed 21 June 2012.
- Robinson, M.M., Dowsett, H.J., Dwyer, G.S. & Lawrence, K.T. (2008b). Reevaluation of mid-Pliocene North Atlantic sea surface temperatures. *Paleoceanography*, 23, PA3213, doi:10.1029/2008PA001608.
- Roy, K., Jablonski, D., Valentine, J.W. & Rosenberg, G. (1998). Marine latitudinal diversity gradients: tests of causal hypotheses. *Proc. Natl. Acad. Sci. USA*, 95, 3699–3702.
- Rutherford, S., D'Hondt, S. & Prell, W. (1999). Environmental controls on the geographic distribution of zooplankton diversity. *Nature*, 400, 749–753.
- Schmidt, D.N., Thierstein, H.R., Bollmann, J. & Schiebel, R. (2004). Abiotic forcing of plankton evolution in the Cenozoic. *Science*, 303, 207–210.
- Stehli, F.G., Douglas, R.G. & Newell, N.D. (1969). Generation and maintenance of gradients in taxonomic diversity. *Science*, 164, 947–949.
- Thomas, E. & Gooday, A.J. (1996). Cenozoic deep-sea benthic foraminifers: tracers for changes in oceanic productivity? *Geology*, 24, 355–358.
- Tittensor, D.P., Mora, C., Jetz, W., Lotze, H.K., Ricard, D., Berghe, E.V. *et al.* (2010). Global patterns and predictors of marine biodiversity across taxa. *Nature*, 466, 1098–101.
- Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003). Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annu. Rev. Ecol. Evol. Syst.*, 34, 273–309.
- Willis, K.J. & Birks, H.J.B. (2006). What is natural? The need for a long-term perspective in biodiversity conservation. *Science*, 314, 1261–1265.
- Willis, K.J., Bailey, R.M., Bhagwat, S.A. & Birks, H.J.B. (2010). Biodiversity baselines, thresholds and resilience: testing predictions and assumptions using palaeoecological data. *Trends Ecol. Evol.*, 25, 583–591.
- 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., Cronin, T.M., deMenocal, P.B., Okahashi, H. & Linsley, B.K. (2008). Abrupt climate change and collapse of deep-sea ecosystems. *Proc. Natl. Acad. Sci. USA*, 105, 1556–1560.
- Yasuhara, M., Hunt, G., Cronin, T.M. & Okahashi, H. (2009). Temporal latitudinal-gradient dynamics and tropical instability of deep-sea species diversity. *Proc. Natl. Acad. Sci. USA*, 106, 21717–21720.
- 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.

SUPPORTING INFORMATION

Additional Supporting Information may be downloaded via the online version of this article at Wiley Online Library (www.ecologyletters.com).

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organised for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

Editor, Dustin Marshall

Manuscript received 30 April 2012

First decision made 30 May 2012

Manuscript accepted 6 June 2012