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Combining marine macroecology and palaeoecology in understanding biodiversity: microfossils as a model

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ABSTRACT

There is growing interest in the integration of macroecology and palaeoecology towards a better understanding of past, present, and anticipated future biodiversity dynamics. However, the empirical basis for this integration has thus far been limited. Here we review prospects for a macroecology–palaeoecology integration in biodiversity analyses with a focus on marine microfossils [i.e. small (or small parts of) organisms with high fossilization potential, such as foraminifera, ostracodes, diatoms, radiolaria, coccolithophores, dinoflagellates, and ichthyoliths]. Marine microfossils represent a useful model system for such integrative research because of their high abundance, large spatiotemporal coverage, and good taxonomic and temporal resolution. The microfossil record allows for quantitative cross-scale research designs, which help in answering fundamental questions about marine biodiversity, including the causes behind similarities in patterns of latitudinal and longitudinal variation across taxa, the degree of constancy of observed gradients over time, and the relative importance of hypothesized drivers that may explain past or present biodiversity patterns. The inclusion of a deep-time perspective based on high-resolution microfossil records may be an important step for the further maturation of macroecology. An improved integration of macroecology and palaeoecology would aid in our understanding of the balance of ecological and evolutionary mechanisms that have shaped the biosphere we inhabit today and affect how it may change in the future.

Key words: biodiversity, macroecology, marine biology, micropalaeontology, palaeoecology, sediment core.

CONTENTS

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I. INTRODUCTION

Ecology as a discipline was largely descriptive on origination. In the early 19th century, von Humboldt recorded arguably the first macroecological (i.e. large-spatial-scale ecological) pattern, a striking latitudinal diversity gradient in the Americas (Bonebrake, 2013). In the early 20th century, ecology became more quantitative, with the analytical rigour applied to diversity patterns by Hutchinson in the 1950s paving the way for the statistical focus of macroecology that emerged in the 1980s (Brown & Maurer, 1989). Initially, the field was almost exclusively terrestrial. Marine macroecology, specifically as a highly quantitative science, is relatively new (Witman & Roy, 2009).

Palaeoecological studies have a long history, dating back to da Vinci's discussion of fossils (see Gould, 1998; Wilkinson, 2012). He already understood that marine fossils occurring from outcrops on land are '*in situ*' remains of ancient, once-living marine organisms. This was revolutionary thinking in the 16th century when people did not consider the biological origin of fossils or saw them as casualties of the biblical flood (Gould, 1998; Wilkinson, 2012). The word 'palaeoecology' has been used in a broad sense (i.e. the study of the interrelationships between ancient organisms and the palaeoenvironments in which they lived: Foote & Miller, 2007), and most commonly applied to palaeoenvironmental reconstruction using fossil species' autoecology. But, unless specified otherwise, we use the word palaeoecology here simply for (macro)ecology using fossils, i.e. studies that utilize fossil records to understand past ecosystems and biodiversity (see Yasuhara *et al.*, 2012*a*). Long before the emergence of macroecology, this approach led to the first global explorations of marine biodiversity patterns and their drivers, first for molluscs (Stehli, McAlester & Helsley, 1967), and then foramifera (Ruddiman, 1969) and corals (Stehli & Wells, 1971).

Marine macroecology and palaeoecology investigate large-scale biodiversity patterns in space and time as well as their driving forces; in recent decades both disciplines have developed rapidly (Jablonski, Roy & Valentine, 2003; Witman & Roy, 2009; Norris *et al.*, 2013). Given their complementary nature and affinity, it was suggested more than 10 years ago that the 'fields of palaeoecology and macroecology are clearly destined to be conjoined' (*cf.* Jablonski *et al.*, 2003, p. 385). Currently there is widespread interest among ecologists, palaeontologists, and evolutionary biologists in integrating these previously independent fields in biology and earth science (Harnik *et al.*, 2012; Fritz *et al.*, 2013; Mannion *et al.*, 2014; Finnegan *et al.*, 2015).

Such an integration would enhance our understanding of large-scale marine diversity dynamics. However, an empirical basis for this integration has thus far been limited (e.g. molluscs; Jablonski *et al.*, 2003, 2013). In this review, we focus on small (or small parts of) organisms with high fossilization potential (microfossils) as a useful model system (or model organisms) for integrating macroecology and palaeoecology research in the study of biodiversity dynamics, given the exceptional fossil records for this group of organisms, as discussed fully below. We argue that the establishment of this hitherto under-utilized model system will aid the empirical integration of spatial and temporal biodiversity dynamics in the marine realm.

II. MARINE MICROFOSSILS AS A MODEL SYSTEM

Micropalaeontology, or the branch of palaeontology making use of microfossils [microscopic-sized (usually $<\sim 1$ mm) fossils such as foraminifera, ostracodes, diatoms, radiolaria, coccolithophores, dinoflagellates, and ichthyoliths that have calcareous, siliceous, or organic-walled 'shells' or 'hard parts'], traditionally has had an applied focus, presumably because this field developed primarily in aid of petroleum exploration, and later served to develop microfossil proxies for palaeoclimatology and palaeoceanography. The main focus of micropalaeontology has thus revolved around biostratigraphy (determining the age of strata using fossilized remains found within the strata) and reconstruction of palaeoenvironments (such as determining physicochemical properties of past oceans) (Gregory *et al.*, 2006), rather than ecology and evolution (e.g. Ruddiman, 1969; Wei & Kennett, 1988).

Micropalaeontology is, however, a suitable resource for integrated palaeoecological and macroecological research, although this resource is currently under-utilized.

Microfossils are useful for biodiversity analyses because of their small size, high abundance, and excellent fossil record. They make quantitative palaeoecological analyses possible even with small-volume sediment subsamples. For example, a sufficient number of specimens (e.g. >100 or >200) of foraminifera or ostracodes for quantitative palaeoecology can be reasonably gathered from a $\sim 20\,\mathrm{cm}^3$ sediment core subsample. Microfossil groups cover a wide variety of ecological niches and functional traits. Protozoan foraminifera, crustacean ostracodes, and algal diatoms include both benthic and planktonic groups. However, shells of planktonic ostracodes are typically weakly calcified and rarely preserved as fossils. For this reason, ostracode fossil records are usually exclusively benthic. Benthic ostracodes and foraminifera include infaunal and epifaunal species, deposit feeders, suspension feeders, scavengers, and other functional traits. These two meiobenthic microfossil groups have contrasting dispersal potential: benthic ostracodes are direct developers and have very limited swimming capabilities, while benthic foraminifera by contrast disperse widely (Brandt *et al.*, 2007; Pawlowski *et al.*, 2007; Alve & Goldstein, 2010; Yasuhara *et al.*, 2012*b*). Planktonic microfossils include zooplankton (radiolaria and planktonic foraminifera) as well as phytoplankton (planktonic diatoms, coccolithophores, and dinoflagellates); these can be divided into functional groups, for example, based on their depth habitats and morphologies (Lazarus, 2005; Ezard *et al.*, 2011*a*). Ichthyoliths are microscopic fish remains such as teeth and scales (Sibert, Hull & Norris, 2014; Sibert & Norris, 2015). Furthermore microfossil groups play important roles in marine ecosystems: many of them are dominant primary producers (e.g. diatoms, coccolithophores) or key taxa in food webs (virtually all groups), and are major players in biogeochemical cycles in regard, for example, to carbon sequestration (e.g. planktonic foraminifera, coccolithophores) and carbon uptake (e.g. diatoms). Further details of individual microfossil groups and their biology and ecology are found, for example, in: Gooday (2001, 2003, 2014) for benthic foraminifera; Schiebel & Hemleben (2001) and Dowsett (2007) for planktonic foraminifera; Horne, Cohen & Martens (2002); Schellenberg (2007), and Mesquita-Joanes, Smith & Viehberg (2012) for ostracodes; Armbrust (2009) and Abrantes & Gil (2013) for diatoms; Anderson (2001) and Lazarus (2005, 2013) for radiolaria; Tyrrell & Young (2009) and Flores & Sierro (2013) for coccolithophores; de Vernal (2013) for dinoflagellates; Doyle & Riedel (1989) for ichthyoliths; and references therein.

Recent scientific advancements have enabled analytical marine microfossil palaeoecology to develop to the stage allowing its synthetic integration with marine macroecology. One of the most important aspects of this development has been the rapid advancement of palaeoceanography since the late 1980–1990s following its original inception in the 1950–1960s (Thomas, 2009). In the last couple of decades, reliable palaeo-proxy records of various environmental factors (such as temperature, productivity, dissolved oxygen, etc.) as well as robust dating methods to determine the accurate age of sediments (e.g. radiocarbon dating and oxygen isotope stratigraphy) have become readily available. Micropalaeontological databases have also been compiled in recent years. Some are very large (with regard to spatial, temporal, and taxonomic coverage and number of data points) yet suffer from taxonomic uncertainties and sampling biases (e.g. Neptune Database; Lazarus, 1994; Liow *et al.*, 2010), while others are relatively small but well quality-controlled (e.g. Brown University Foraminiferal Database, Modern Arctic Ostracode Database) (Prell *et al.*, 1999; Rutherford, D'Hondt & Prell, 1999; Cronin *et al.*, 2010; Yasuhara *et al.*, 2012*c,d*). Both of these two types of databases are important and suitable for palaeoecological–macroecological analyses. However, compared to the established molluscan palaeoecology field of research (e.g. Jablonski *et al.*, 2003, 2013; Kidwell, 2007), analytical microfossil-based studies addressing macroecological questions are still limited (e.g. Hunt, Cronin & Roy, 2005; Allen & Gillooly, 2006; Yasuhara *et al.*, 2009; Liow *et al.*, 2010; Ezard *et al.*, 2011*a*). In addition, an important shortcoming of microfossils, for example compared to molluscs, is insufficient knowledge of their basic biology and natural history. Yet this current weakness is balanced by some distinctive strengths of the microfossils record, such as high abundance, large spatiotemporal coverage, and good taxonomic and temporal resolution, as discussed herein.

The most important strength of utilizing marine micropalaeontology research for integrated palaeoecological and macroecological studies is the availability of long-term continuous time series derived from individual sediment cores. A marine sediment core is a cylindrical section (usually $\sim 10\,\mathrm{cm}$ diameter; varying in length from tens of centimeters to hundreds or thousands of meters) of marine sediment, that retains a much more continuous time-series record compared to often fragmentary outcrops (exposure of marine sedimentary stratum on land) where most macro- and mega-fossil specimens are derived. Cores drilled by the scientific ocean drilling projects of the Deep Sea Drilling Project (DSDP), and its successors the Ocean Drilling Program (ODP) and the Integrated Ocean Drilling Program for 2003–2013 and International Ocean Discovery Program for 2013–present (IODP) cover almost the entire ocean (Fig. 1) and the entire Cenozoic period and beyond. The DSDP, ODP, and IODP are well-organized international scientific programs which routinely obtain basic data from each core based on offshore research (such as photographic sediment images, physical properties, basic sedimentological and micropalaeontological data, biostratigraphy-based chronology, etc.) and make these data and core samples publicly available (www.iodp.org). Thus, basic, often low-resolution data are available for all DSDP, ODP, and IODP sites, and advanced, high-resolution data are available from selected sites for a subset of cores. Furthermore, numerous cores covering the late Quaternary period (the past several hundreds of thousands of years), have been obtained by various research projects, because shorter (i.e. younger) cores than the very long DSDP, ODP, and IODP cores can be taken by simpler coring devices and smaller research vessels

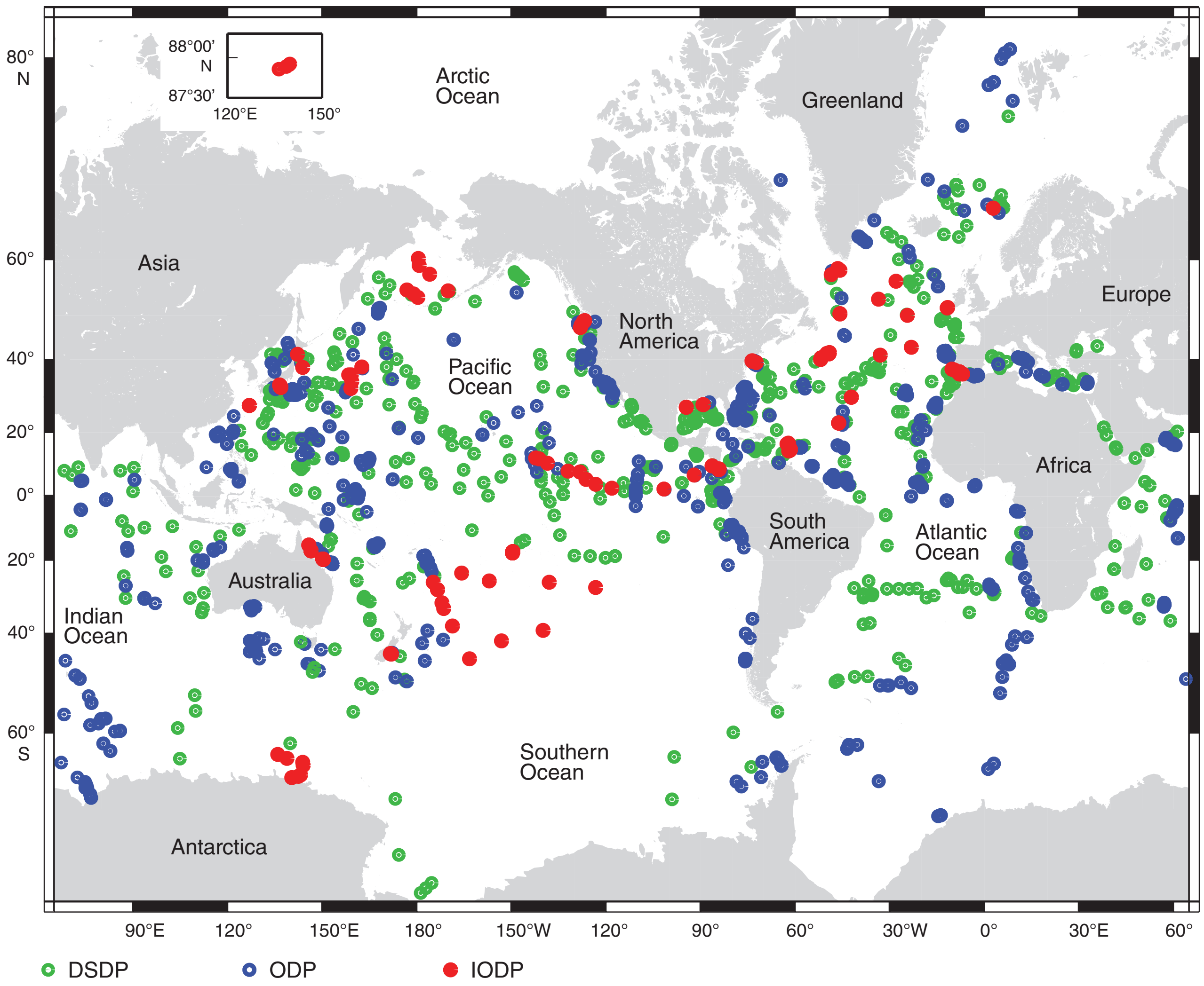

Fig. 1. Global coverage of sediment cores collected by international drilling programs. Core sites: DSDP (green dots), ODP (blue dots), and IODP (red dots) (http://iodp.tamu.edu/scienceops/maps.html).

(i.e. easier and less expensive). This time period includes glacial–interglacial climate change as well as abrupt climate change over shorter time scales (e.g. Dansgaard–Oeschger and Heinrich events) (Cronin, 2009). The unique coverage of the global oceans with microfossil samples from the DSDP, ODP, and IODP and other cores allows investigation into how marine ecosystems and biodiversity have responded to past climate changes over various time scales from decadal to multi-millennial and longer.

In summary, the advantages of using readily available microfossil samples and data and the under-utilized nature of microfossils for biodiversity dynamics motivate our focus on marine microfossils in the present review. We focus on the Cenozoic Era (the last 65 million years) because of the very good microfossil preservation and robust chronology available for this time period (e.g. Thomas & Gooday, 1996; Zachos *et al.*, 2001; Lisiecki & Raymo, 2005; Zachos, Dickens & Zeebe, 2008; Ezard *et al.*, 2011*a*; Norris *et al.*, 2013; Rohling *et al.*, 2014).

III. AFFINITY BETWEEN MACROECOLOGY AND PALAEOECOLOGY

Biodiversity research in both macroecology and palaeoecology relies on similar data types, including (*i*) count (i.e. abundance) data [these data are often called ‘census data’ in the field of micropalaeontology (e.g. Dowsett, 2007; Yasuhara *et al.*, 2012*b*), although this usage is different from the original meaning of ‘census’ or ‘demographic data’ (see e.g. Liow & Nichols, 2010; King, 2014)] or presence–absence (i.e. occurrence, encounter history, or occupancy; see e.g. Liow & Nichols, 2010; King, 2014) data of morphospecies or higher taxa; and (*ii*) environmental data from global or regional databases and palaeo-proxy records. Recent research has shown the congruence of morphologically defined units with molecular phylogenies (Jablonski & Finarelli, 2009), supporting the usage of morphospecies in general. A fossil species is a type of morphospecies using morphological characters that fossilize, and these characters often allow accurate species identification (Tsukagoshi, 1990; Hunt, 2007; Hull & Norris, 2009; Pearson & Ezard, 2013). For example, pores and fossae on ostracode valve surfaces are known as important taxonomic characters reflecting information on the underlying soft tissues (Okada, 1981, 1982*a*,*b*,1983; Keyser, 1982, 1983; Kamiya, 1989; Tsukagoshi, 1990; Hunt, 2007). Normal pores in ostracodes are canals penetrating valves and often equipped with bristles, that are known as sensory organs (Kamiya, 1989; Tsukagoshi, 1990). Each fossa bounded by skeletal ridges corresponds to an underlying epidermal cell (Okada, 1981, 1982*a*). Distribution of these pores and fossae can be taxonomically and phylogenetically informative (Tsukagoshi, 1990; Irizuki, 1996; Hunt, 2007; Hunt & Yasuhara, 2010). Because most other microfossils are unicellular organisms and thus have a simpler body plan and structure compared to metazoan ostracodes, their morphological characters may be less informative. However, recent studies have shown that detailed morphological analyses of unicellular microfossils allow identification of molecular types and sibling species (Hayward *et al.*, 2004; Aurahs *et al.*, 2011; Ishitani, Ujiié & Takishita, 2014).

Thus these macroecological and palaeoecological data enable direct comparison of present-day and past biodiversity patterns. The key difference between macroecology and palaeoecology is that the former focuses primarily on spatial patterns and the latter mainly on temporal patterns. These differences can be overcome by a 'space-for-time' substitution with the reasonable assumption that drivers of spatial diversity gradients also influence temporal changes in diversity (Blois *et al.*, 2013*b*), or by tackling research issues that can be addressed only through comparison of macroecological and palaeoecological data, i.e. large-scale data in space and time (see Section V for examples).

IV. NEED FOR THE INTEGRATION OF MACROECOLOGY AND PALAEOECOLOGY

Given the complementary nature and affinity of macroecology and palaeoecology, the critical advantage of the integration of the two fields of ecology is that this will allow analyses across the four dimensions of space and time, and thus will allow the separation of ecological and evolutionary forces structuring biodiversity (Harnik *et al.*, 2012; Yasuhara *et al.*, 2012*c*). This is particularly timely given the pressing need to understand the complex drivers of observed global changes in contemporary biodiversity, which occur against a backdrop of a rapidly changing climate and environment dominated by our own species (Worm *et al.*, 2006; Jackson, 2008; Yasuhara *et al.*, 2012*a*; Mora *et al.*, 2013).

There have been several attempts at such an integration from the palaeontological community in the 1990s (Roy *et al.*, 1996; Thomas & Gooday, 1996; Cronin & Raymo, 1997; Cannariato, Kennett & Behl, 1999). These were the pioneering fossil-based studies that addressed ecological problems: impacts of abrupt climatic changes on marine ecosystems (Roy *et al.*, 1996; Cannariato *et al.*, 1999), a deep-sea temperature–biodiversity relationship (Cronin & Raymo, 1997), and temporal dynamics of deep-sea latitudinal species diversity gradients (LSDGs) (Thomas & Gooday, 1996). However, these approaches have not yet been widely adopted among ecologists probably because of the different research histories and scientific communities between the disciplines. Macroecology derived from ecology and thus biological sciences, whereas palaeoecology in the broad sense has developed within geological and physical science, often with an applied focus on mining and fossil fuel exploration. Similarly, ecologists have indicated a need for better integration of the historical and palaeontological perspectives in ecology (Ricklefs, 1987; Cornell & Lawton, 1992). Indeed, Brown already emphasized the importance of interdisciplinary efforts including palaeontology in his foundational publications defining the field of macroecology (Brown & Maurer, 1989; Brown, 1995). More recently, efforts such as the National Center for Ecological Analysis and Synthesis (NCEAS), the National Evolutionary Synthesis Centre (NESCent), and the International Network for Scientific Investigations of Deep-Sea Ecosystems (INDEEP) have catalysed synthetic projects involving marine macroecologists and palaeoecologists (e.g. Harnik *et al.*, 2012; Mora *et al.*, 2013; Finnegan *et al.*, 2015), suggesting that the separation between macroecology and palaeoecology is beginning to dissolve (Fritz *et al.*, 2013; Mannion *et al.*, 2014). However, empirical examples of integrative macroecological and (evolutionary) palaeoecological studies are still limited.

V. INTEGRATIVE OVERVIEW OF MACROECOLOGICAL AND PALAEOECOLOGICAL DATA AND ANALYSES: CURRENT PERSPECTIVES AND FUTURE DIRECTIONS

(1) Microfossil diversity proxy and 'space-for-time' substitution

Important assumptions for macroecological and palaeoecological integration include: (*i*) the diversity of specific microfossil groups can be a proxy for biodiversity patterns across a broader range of organisms, especially those with similar ecological preferences and habitats, and (*ii*) the drivers of spatial gradients of biodiversity also drive temporal changes in biodiversity (*cf*. Blois *et al.*, 2013*b*). Recent studies generally support these two assumptions.

Biodiversity patterns can vary among taxonomic groups, but at the same time, it is also true that many different taxonomic groups, especially those with similar ecological preferences and habitats, display similar biodiversity patterns (Tittensor *et al.*, 2010; Yasuhara & Danovaro, 2014; Yasuhara *et al.*, 2014). For example, deep-sea benthic ostracode diversity may serve as a reasonable proxy for diversity of broader deep-sea benthic soft-sediment organisms (Yasuhara & Cronin, 2008). In the present-day

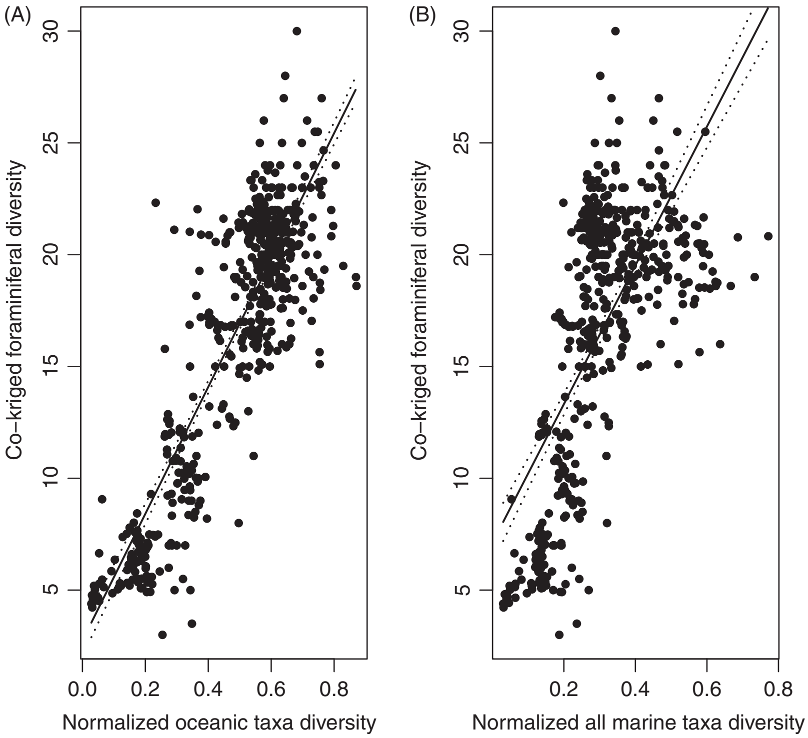

Fig. 2. Foraminifera as potential proxies for marine diversity. The figure shows the relationship between planktonic foraminiferal diversity and diversity of (A) oceanic taxa ($r = 0.87$, $P < 0.00001$) and (B) all marine taxa ($r = 0.68$, $P < 0.00001$) in the present-day ocean. Each point represents a diversity value within an equal-area grid cell, extracted from Tittensor *et al.* (2010), with taxa being weighted equally (normalized). Lines show a linear regression fit (solid line) with 95% confidence intervals (dotted lines). 'All marine taxa' here include both oceanic and coastal taxa, i.e. marine zooplankton (foraminifera and euphausiids), plants (mangroves and seagrasses), invertebrates (stony corals, squids and other cephalopods), fishes (coastal fishes, tunas and billfishes, oceanic and non-oceanic sharks), and mammals (cetaceans and pinnipeds) (only relatively well-sampled taxa were included; see Tittensor *et al.*, 2010 for details). Co-kriging is a geostatistical technique used for interpolation.

ocean, the diversity of planktonic foraminifera shows a strong correlation with total diversity of both oceanic taxa ($r = 0.87$, $P < 0.00001$) and, to a lesser degree, with all marine taxa ($r = 0.68$, $P < 0.00001$) (Fig. 2), supporting the first assumption in the previous paragraph. More empirical studies are needed to justify this assumption better, because (*i*) this planktonic foraminiferal example is, as far as we know, the only statistical (rather than qualitative) evidence for the correlation between diversities of microfossil groups and living organisms with similar ecological preferences and habitats, and (*ii*) even if specific microfossil groups are a reliable proxy for the biodiversity pattern of a broader range of living organisms, it may not mean that the same underlying mechanisms are responsible.

Comparison between present-day and Last Glacial Maximum (LGM: 20000 years ago) planktonic foraminiferal diversity patterns (Yasuhara *et al.*, 2012*c*) supports the second assumption of a 'space-for-time' substitution with respect to biodiversity drivers. Foraminiferal diversity patterns today and during the LGM display almost identical trends with sea surface temperature (Fig. 3) (Yasuhara *et al.*, 2012*c*). It is also known that temperature represents the strongest environmental predictor of spatial biodiversity patterns across all data-rich taxonomic groups in the present ocean (Tittensor *et al.*, 2010). These facts may suggest that temperature is an important driver of species diversity both spatially and temporally and both in present-day and ancient oceans.

(2) Planktonic foraminifera

Planktonic foraminifera are one of the best model systems for macroecology–palaeoecology integration studies because they feature one of the most complete and abundant fossil records. There is an almost complete record for planktonic foraminifera throughout the Cenozoic Era, for which almost all species are formally described and have known stratigraphic ranges, at least in the macroperforate clade, a monophyletic clade in planktonic foraminifera with high abundance and cosmopolitan distribution (Aze *et al.*, 2011; Ezard *et al.*, 2011*a*) (Fig. 4). Based on the known stratigraphic ranges of all species, a robust global diversity curve of macroperforate planktonic foraminifera has been reconstructed (Aze *et al.*, 2011; Ezard *et al.*, 2011*a*) (Fig. 4). The diversity of macroperforate planktonic foraminifera is driven by macroevolutionary dynamics, controlled not only by climate but also by biotic factors (Ezard *et al.*, 2011*a*). A striking feature is an abrupt cooling

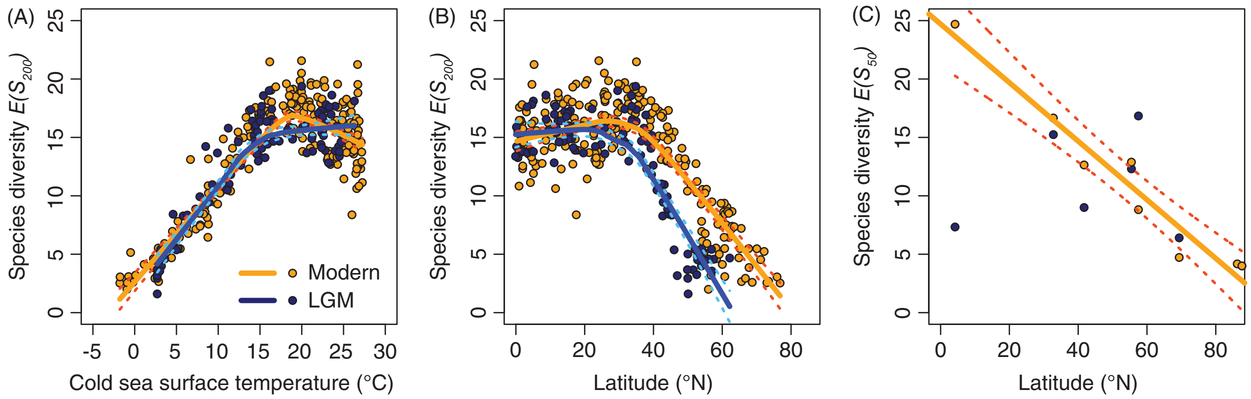

Fig. 3. A comparison of latitudinal species diversity gradients (LSDGs) between pelagic and deep-sea benthic ecosystems. (A) North Atlantic planktonic foraminiferal diversity [rarefaction $E(S_n)$] *versus* cold sea surface temperature (Yasuhara *et al.*, 2012*c*), (B) North Atlantic planktonic foraminiferal LSDGs (Yasuhara *et al.*, 2012*c*), and (C) North Atlantic deep-sea benthic ostracode LSDGs (Yasuhara *et al.*, 2009). Orange: present day; blue: Last Glacial Maximum (LGM). Solid lines: loess curves (locally weighted regression for drawing a smooth line) for each time slice (A,B); and linear regression line for present-day data (C). Dotted lines: 95% confidence intervals. North Atlantic planktonic foraminiferal data are from modern Brown University Foraminiferal Database based on core-top samples (http://www.ncdc.noaa.gov/paleo/metadata/noaa-ocean-5908.html) (Prell *et al.*, 1999) and LGM CLIMAP data set based on sediment core samples (http://www.ncdc.noaa.gov/paleo/metadata/noaa-ocean-2516.html) (CLIMAP Project Members, 1976). North Atlantic deep-sea benthic ostracode data are from core-tops (for present-day data) and sediment cores (for LGM data) (Cronin *et al.*, 1995, 1999, 2002; Yasuhara *et al.*, 2008, 2009).

coinciding with a diversity decline at the Eocene–Oligocene boundary, approximately 34 million years ago (Fig. 4A, B). Some characteristics of this diversity curve, including the late Eocene diversity peak, the diversity decline at the Eocene–Oligocene boundary, the Miocene diversification, and the post-Miocene diversity decline, are successfully reproduced by simulations using a numerical model in which the extinction probability of species is controlled by temperature and competition (De Blasio *et al.*, 2015).

At the same time, for most (if not all) microfossils, there has been almost no observed speciation and extinction during the last ~0.3 million years (e.g. Berggren *et al.*, 1995). In fact, a species lifespan is generally considered to be a few million years, much longer than the Milankovitch time scale (i.e. the time scale resolving 100000- or 41000-year orbital climatic cycles) (Cronin & Ikeya, 1990; Cronin & Schneider, 1990; Benton, 2009). Thus, on relatively short geological time scales (i.e. on the Milankovitch time scale), climate-driven changes in species ranges and/or coexistence (instead of speciation or extinction) mainly control alpha (i.e. local) diversity. In fact, the planktonic foraminiferal alpha diversity shows similar trends with palaeo-climatic changes throughout the last 0.3 million years in the subpolar North Atlantic Ocean (Fig. 5) (data from Kandiano & Bauch, 2003; Kandiano, Bauch & Müller, 2004). Furthermore, spatial alpha diversity distributions during the present day and LGM time slices correspond well to the temperature gradients (Yasuhara *et al.*, 2012*c*) (Figs 3A and 4D).

These results support a predominant role for ecological processes in shaping present-day spatial patterns of alpha diversity, although it is possible that the broad spatial patterns of diversity seen at larger scales (e.g. among regions and continents) had already been shaped by macroevolutionary processes in the deep past. Future research will enable deeper time slices in the evolutionary past, such as the Mid-Miocene Climatic Optimum and the Palaeocene–Eocene Thermal Maximum (PETM), and this may provide a better understanding of macroevolutionary dynamics and the relative importance of ecological and evolutionary processes (Fig. 4D). Phylogenetic approaches to diversification analyses will also give insights into the macroevolutionary factors that underlie large-scale diversity patterns (Weir & Schluter, 2007; Condamine, Rolland & Morlon, 2013), given a complete phylogeny of macroperforate planktonic foraminifera species of the Cenozoic Era (Aze *et al.*, 2011).

However, there is also the opposite view that evolutionary or historical processes play a predominant role shaping present-day spatial patterns of alpha diversity, because regional diversity constrains local diversity and regional diversity is shaped by evolutionary or historical processes (Ricklefs, 1987, 2008; Cornell & Lawton, 1992). In fact, benthic foraminiferal data suggested that recently evolved rare species largely shape present-day diversity patterns (Buzas & Culver, 1999, 2009). Since diversity relationships at different spatial scales are poorly understood in microfossils, this topic is an important research frontier.

(3) Temporal latitudinal species diversity gradient (LSDG) dynamics

The LSDG, Earth's 'first-order biodiversity pattern' (Krug *et al.*, 2009), is pervasive and persistent in marine systems (Willig, Kaufman & Stevens, 2003; Hillebrand, 2004; Renema *et al.*, 2008; Tittensor *et al.*, 2010), although not always centred around the equator (Tittensor *et al.*, 2010; Powell, Beresford & Colaianne, 2012; Yasuhara *et al.*, 2012*c*).

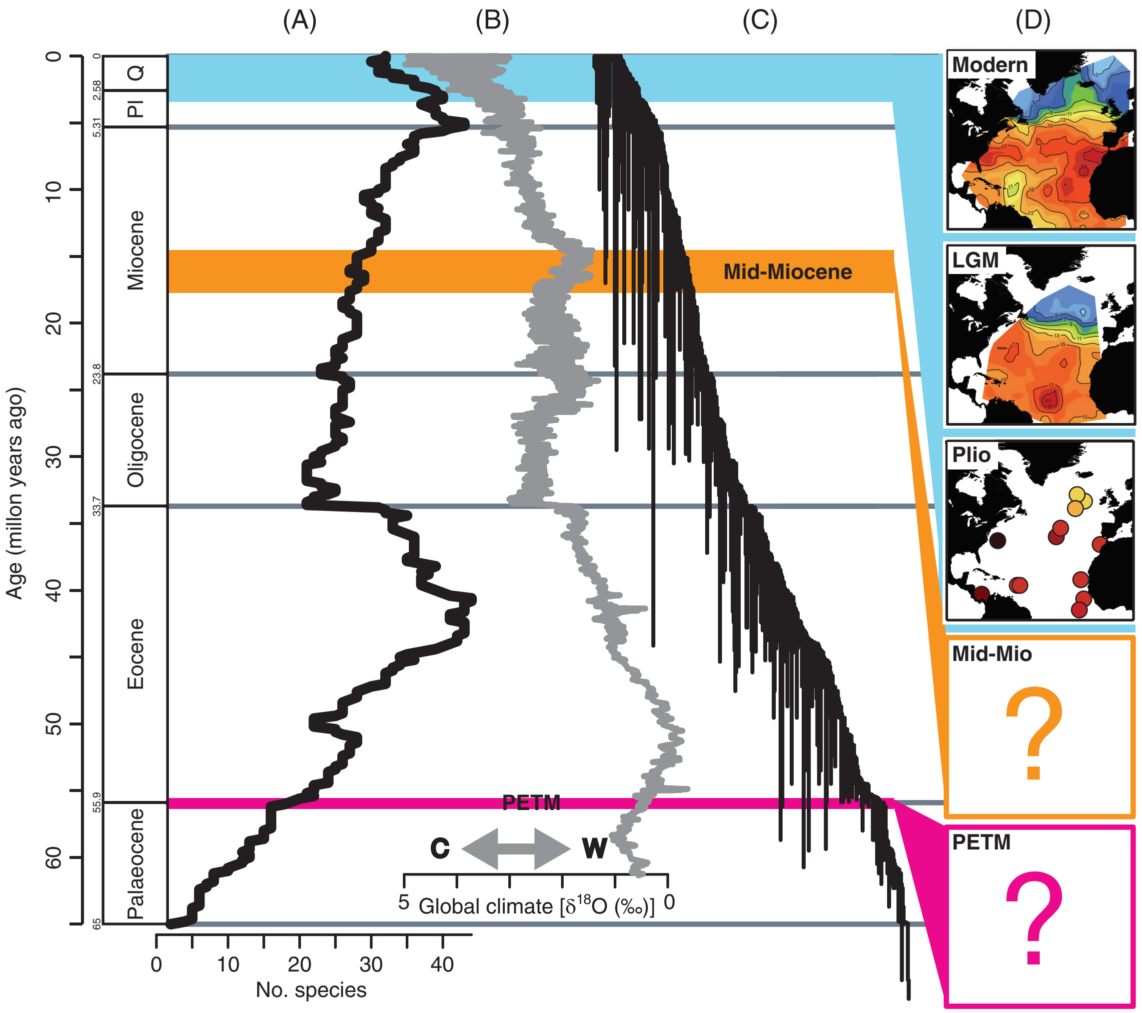

Fig. 4. Planktonic foraminiferal diversity throughout the Cenozoic. (A) Changes in global macroperforate planktonic foraminiferal diversity [black curve; using aLb (fully bifurcating lineage phylogeny = evolutionary Hennigian species) data] (Aze *et al.*, 2011; Ezard *et al.*, 2011*a*,*b*). (B) Global climate changes based on deep-sea oxygen isotope records (grey curve; ‰) (five-point running mean, Zachos *et al.*, 2001). Smaller oxygen isotope value generally indicates warmer climate condition (C, colder; W, warmer). (C) Stratigraphic ranges of all macroperforate planktonic foraminiferal species (range chart composed of black vertical lines) (Aze *et al.*, 2011; Ezard *et al.*, 2011*a*). Each black vertical line indicates duration of species. Note that last extinction and speciation of macroperforate planktonic foraminiferal species occurred ~0.3 million years ago. (D) Distribution maps of North Atlantic planktonic foraminiferal species diversity for present-day, Last Glacial Maximum (LGM), and Pliocene time slices (Yasuhara *et al.*, 2012*c*). Mid-Miocene Climatic Optimum (Mid-Mio) and Palaeocene–Eocene Thermal Maximum (PETM) diversity time slices remain unavailable, despite their importance as possible analogs of a future warmer world. Only present-day and LGM panels are interpolated because of much better spatial coverage of the data. Pl and Plio: Pliocene. Q: Quaternary.

The majority of coastal marine taxa show regular LSDGs that decrease with increasing latitude (Willig *et al.*, 2003; Tittensor *et al.*, 2010), while pelagic diversity tends to peak at broad mid-latitude bands (Worm *et al.*, 2005; Tittensor *et al.*, 2010). At least in pelagic planktonic foraminifera, this divergence may be related to a lack of higher speciation rates in the tropics and the higher extinction rates of warm-water species at low latitudes during the Plio-Pleistocene cooling (Yasuhara *et al.*, 2012*c*). However, it is not clear whether this explanation holds generally. For example, the opposite scenario has also been suggested for other taxa, i.e. future tropical diversity decline due to global warming (Mayhew, Jenkins & Benton, 2008; Whitehead, McGill & Worm, 2008; Thomas *et al.*, 2012).

The presently seen LSDGs have been persistent for the last ~20 million years or even longer (Thomas & Gooday, 1996; Renema *et al.*, 2008; Mannion *et al.*, 2014). However, late Quaternary glacial–interglacial climatic changes affected LSDG dynamics differently in different ecosystems. The pelagic zooplankton (i.e. foraminiferal) LSDG was steeper in the LGM and shallower in the present interglacial in the North Atlantic Ocean (Yasuhara *et al.*, 2012*c*) (Fig. 3). By contrast, the deep-sea benthic ostracode LSDG is distinct in the present interglacial, but was weaker or even

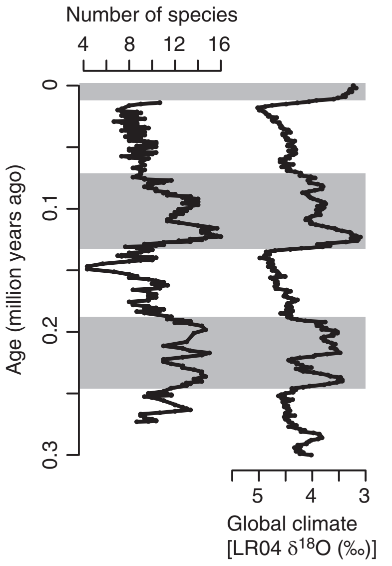

Fig. 5. Species richness and climate. Shown is the species richness of planktonic foraminifera in the subpolar North Atlantic (data from Kandiano & Bauch, 2003; Kandiano *et al.*, 2004) and global climatic (LR04 oxygen isotope curve: Lisiecki & Raymo, 2005) changes over the last 0.3 million years. Note remarkable concordance between the temporal dynamics of species richness and climate. Interglacial periods are highlighted in grey.

collapsed during glacial periods in the North Atlantic Ocean (Yasuhara *et al.*, 2009) (Fig. 3). This discrepancy can be explained by temperature control of diversity: the latitudinal surface temperature gradient was steeper in the LGM and shallower in the present interglacial (Yasuhara *et al.*, 2012*c*); and, although the latitudinal gradient of deep-water temperature is less distinct than at the surface, the regular latitudinal temperature gradient (i.e. colder temperature at higher latitudes) is still seen in the present interglacial at least within a similar depth range (e.g. ∼1000, ∼2000, or ∼3000 m) in the Atlantic Ocean (Yasuhara & Danovaro, 2014), but most of the deep LGM ocean was relatively homogeneous in temperature, suggesting the lack of a regular latitudinal temperature gradient during glacial periods (Adkins, McIntyre & Schrag, 2002; Yasuhara *et al.*, 2009, 2012*c*; Yasuhara & Danovaro, 2014). However, there are still limited time slices available for addressing LSDG dynamics. More efforts are needed for reconstructing biodiversity time slices in the geologic past, especially for deep-sea benthic foraminifera and ostracodes, because benthic time slices are more limited and incomplete (Yasuhara *et al.*, 2009) compared to planktonic time slices (Yasuhara *et al.*, 2012*c*).

(4) Changing location of ‘hotspots’ over time

Renema *et al.* (2008) provide a good example of the integrative approach not only between macroecology and palaeoecology but also between palaeoecology and molecular phylogenetics. Their study is mainly based on an overview of fossil records of larger benthic foraminifera and a reconstructed global biodiversity distribution from 56 million years ago to the present. The results clearly showed that the present ‘hotspot’ in the Indo-Australian Archipelago has been persistent throughout the last 20 million years, but not throughout the Cenozoic (the last 65 million years) (Fig. 6). Instead, during the Eocene (56–34 million years ago) there was a West Tethyan ‘hotspot’ (centred in the present Mediterranean region) (Fig. 6). Over time this ‘hotspot’ has shifted eastward to the Arabian Sea (Eocene–Miocene), and then to the present position (Fig. 6). This scenario is consistent with present-day macroecological and Cenozoic palaeoecological evidence as well as molecular data from various taxa (Renema *et al.*, 2008). One of the most important features of these three ‘hotspots’ is that each in turn marks the location of a major collision between tectonic plates (Renema *et al.*, 2008). Thus, tectonics-related processes (e.g. changes in the area and complexity of suitable shallow marine habitat; formation of islands; changes in ocean circulation and seaways; and resulting isolation, adaptation, and diversification) are likely a key driver of this kind of longitudinal diversity dynamics (Renema *et al.*, 2008). Likewise, coral distribution is well known to be correlated with plate distribution, suggesting the important role of plate-tectonics-related processes (Keith *et al.*, 2013), but it is uncertain how this has affected coral diversity (Johnson, Jackson & Budd, 2008). Thus the validity of extrapolating results from the benthic foraminiferal fossil records to other taxa, with respect to diversity, remains to be tested.

(5) Conservation applications

Recent alteration of marine ecosystems by various human activities during the Anthropocene (note that use of this term is still debated: Wilkinson *et al.*, 2014; Lewis & Maslin, 2015) is one of the most important topics in marine biology research (Jackson *et al.*, 2001; Lotze *et al.*, 2006; Worm *et al.*, 2006; Kidwell, 2007, 2015; Diaz & Rosenberg, 2008; Yasuhara *et al.*, 2012*a*; Mora *et al.*, 2013). This topic can be usefully addressed with microfossil data, because the start of the human-induced ecological degradation extends back to >100 or even >1000 years ago, far beyond the usual biological monitoring period (Lotze & Milewski, 2004; Yasuhara *et al.*, 2012*a*). It is known that rapid ecological degradation of coastal areas around the world started on average around 1800, in the wake of European industrialization and expansion (Lotze *et al.*, 2006; Worm *et al.*, 2006). But the compilation of global microfossil data has revealed further details of human-induced marine ecological degradation. Yasuhara *et al.* (2012*a*) compiled ∼150 published down-core microfossil records and determined the timing of ecological degradation (i.e. initial diversity decline, abundance change, faunal shift, etc.), showing that marine ecological degradation began significantly earlier in Europe and North America (∼1800s) compared with Asia (post-1900) due to earlier industrialization in Europe and North America (Yasuhara *et al.*, 2012*a*) (Fig. 7). The predominant cause of degradation detected in these microfossil records was nutrient enrichment and the resulting symptoms of eutrophication,

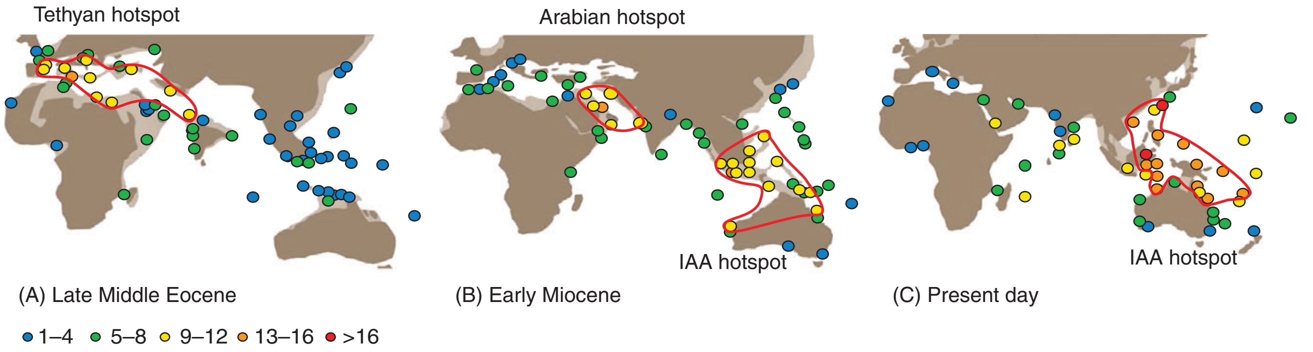

Fig. 6. Global diversity distribution of larger benthic foraminiferal genera in (A) the late Middle Eocene (42–39 million years ago), (B) the Early Miocene (23–16 million years ago), and (C) the present day. Coloured dots indicate the number of genera. Biodiversity 'hotspots' are highlighted by red lines. IAA, Indo-Australian Archipelago. From Renema *et al.* (2008) with permission from AAAS.

including hypoxia and anoxia (Yasuhara *et al.*, 2012*a*). In-depth reviews on this topic of marine ecological degradation from the micropalaeontological perspective can be found in Yasuhara *et al.* (2012*a*) and Wilkinson *et al.* (2014).

Combining this palaeoecological perspective with historical data and present-day human impact maps (Diaz & Rosenberg, 2008; Halpern *et al.*, 2008), we can provide an interesting four-dimensional (i.e. integrative macroecology–palaeoecology) perspective in conservation ecology: Europe and East Asia are similarly highly impacted regions in present-day human-impact maps (Diaz & Rosenberg, 2008; Halpern *et al.*, 2008), but the start of degradation is much earlier in Europe and the pace more rapid in Asia (Yasuhara *et al.*, 2012*a*) (Fig. 7). This modern–past difference means that conservation and management efforts solely based on biological data could miss important facets of the anthropogenic impacts. For example, a recent study comparing extinctions across fossil, historical, and modern records showed that primary drivers of extinctions differ across these eras. While direct human impacts such as exploitation and species invasion have been important drivers of extinction risk in recent human history, both fossil and possibly future extinctions may be more related to factors such as ocean warming and acidification (Harnik *et al.*, 2012).

(6) Difficulties and limitations

(*a*) *Time averaging and fossil preservation*

The difficulties and limitations of the proposed interdisciplinary integration include time averaging and fossil preservation. Palaeoecological samples are time averaged. Typically several meters of a marine sediment core span 10^3–10^5 years, and one 1–5 cm thickness sub-sample taken from such a core may represent an averaged assemblage over 10^0–10^3 years (i.e. sedimentation rate of ~1–100 cm per 1000 years or even higher in some shallow-marine sediments) (e.g. Cronin & Vann, 2003; Poirier *et al.*, 2012; Yasuhara *et al.*, 2014). Time averaging usually also causes a certain amount of spatial averaging (e.g. see Kidwell & Holland, 2002). But time averaging is not necessarily a disadvantage (Olszewski, 1999; Yasuhara *et al.*, 2012*a*), and is perhaps comparable to the spatial averaging of data into grid cells in macroecological research. It further supports our usage of microfossil taxa for biodiversity analyses that death assemblages (i.e. assemblages of dead shells preserved in surface sediment) have been shown to be reliable indicators of the diversity and community structure of the living community (Kidwell, 2001; Tomašových & Kidwell, 2010; but also see, Kidwell, 2013; Kidwell & Tomasovych, 2013 for more nuanced discussion), although less is known about this live–dead agreement in microfossils (Scott & Medioli, 1980; Whatley, 1988; also see Yasuhara *et al.*, 2012*a* and references therein).

(*b*) *Historical nature of the data*

Although reliable palaeoenvironmental proxies and robust dating methods have been developed, the historical nature of the data is still a serious challenge for several reasons. Firstly, specific palaeoenvironmental proxies and robust radiometric and oxygen-isotope chronologies are not always (readily) available. It is common that less-direct proxies (e.g. oxygen isotope ratio of benthic foraminifera shells representing a composite signal of deep-sea temperature and polar ice volume) and chronologies with lower time resolution (e.g. biostratigraphy) are available for analyses (e.g. Hannisdal, Henderiks & Liow, 2012). The noise associated with these variables may make the detection of a signal, and implied mechanisms, more difficult.

Secondly, as is also broadly true of large-scale macroecological analyses, the nature of the data prevents repeated 'experiments' (although in this case due to the temporal span of the data rather than necessarily the spatial scale). Hence it is challenging to attribute causality without being able to control variables and test effects directly. In addition, issues of statistical power for analyses may also be present. This does not mean that progress cannot be made, as great strides towards our understanding of large-scale modern-day biodiversity patterns and gradients have been made by assembling macroecological data sets. Rather, it is important to maintain the perspective that every single analysis of correlative data (with all of the issues of historical contingency and stochasticity associated) is open

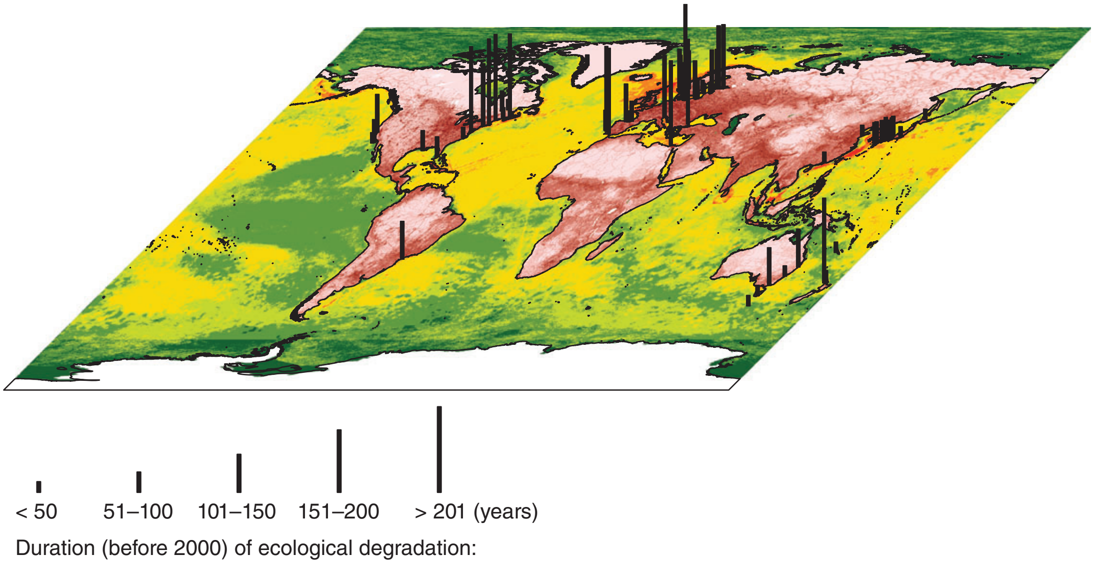

Fig. 7. Microfossils as markers of human impacts. Shown is the global distribution of human footprint [Global Human Footprint (IGHP, Version 2) of the Last of the Wild Project, Version 2 (http://sedac.ciesin.columbia.edu/data/collection/wildareas-v2) for land and Halpern *et al.* (2008) for ocean] and historical duration of marine ecological degradation (five categories) determined from published down-core micropalaeontological records (Yasuhara *et al.*, 2012*a*). Darker red colours for land and warmer colours for ocean indicate areas of higher human impact. Note that current human impact is similarly high in Europe and East Asia, but such widespread degradation occurred much earlier in Europe than in East Asia.

to alternative explanations. The power of such analyses increases as different data sets are compared or combined, providing somewhat independent tests of the same hypothesis (e.g. Tittensor *et al.*, 2010). Hence 'repeated' analyses across taxa, across differing environments, and across different time periods or regions can help to generate confidence in results should they produce similar outcomes. Bottom-up mechanistic models for these different taxa, environments, time periods, and regions can be used as independent tests by comparing their predictions. Additionally, provided that a good understanding of the true system is present, simulation studies can be used to approximate repeated experiments, or in situations where the understanding is not present, can be used to help gain insight into underlying mechanisms.

Thirdly, it is entirely possible, or more likely probable, that there could be multiple hypotheses or explanatory variables that explain observed biodiversity patterns. For example, there are many possible hypotheses to explain LSDGs (Willig *et al.*, 2003). This problem tends to be addressed in the macroecological literature through directly linking hypotheses to environmental or energetic proxies and determining the relative support for each (Currie *et al.*, 2004). We suggest that integrating macroecology and palaeoecology will provide a better chance critically to address these hypotheses through linking patterns in both space and time.

An additional wrinkle is that often multiple environmental predictors covary, making it difficult to disentangle their relative effects. This problem can be partially addressed through approaches such as multiple regression modelling, but only when the problem of multicollinearity is low to moderate. Again, integrative macroecology and palaeoecology may allow us to address this difficulty better. For example, many environmental explanatory variables (e.g. temperature, particulate organic carbon flux, etc.) can covary with water depth in present-day oceans. This is one of the major difficulties in studying possible controlling factors of marine biodiversity. But if we use deep-sea palaeoecological time-series data, we can limit such covariation problem. For example, glacial–interglacial sea-level changes of $\sim$120 m (Yokoyama *et al.*, 2000) have an almost negligible effect on explanatory variables in palaeoecological time-series studies at deep sites (i.e. $>$1000–2000 m water depths), and thus covariation between the explanatory variables due to water-depth (i.e. sea-level) change is almost negligible at the glacial–interglacial time scale. Instead, the explanatory variables do not necessarily covary in this case, because they can be controlled by different drivers. For example, in this time scale, deep-sea bottom-water temperature is largely controlled by global deep-water circulation, but particulate organic carbon flux is controlled by surface productivity that is regionally more variable than and can vary independently from bottom-water temperature (e.g. see Hunt *et al.*, 2005; Yasuhara *et al.*, 2012*b*). Similarly, comparisons of macroecological patterns on land and in the ocean can benefit from the separation of factors in one environment that covary in the other.

(*c*) *Palaeoenvironmental data derived from micropalaeontological proxies*

Another potential problem lies in the fact that palaeoenvironmental data are often derived from micropalaeontological proxies. For example, Mg/Ca ratio and δ^{18}O of foraminiferal shells and transfer functions (a method quantitatively to reconstruct environmental parameters based on multivariate analyses of microfossil assemblages) using foraminiferal faunal data are widely used as palaeo-temperature proxies and have been used with foraminiferal diversity data to test temperature–diversity relationships (Hunt *et al.*, 2005; Allen *et al.*, 2006; Yasuhara *et al.*, 2012*b*,*c*). In these cases, both environmental (e.g. palaeotemperature) and diversity data are derived from the same group of organisms, but through focusing on different aspects of their biology (e.g. chemical composition of shell or relative abundance of a small number of taxa *versus* number of species) that are not necessarily correlated (see Yasuhara *et al.*, 2012*c* for detailed discussion). In addition, faunal proxies (e.g. foraminiferal transfer functions) show good agreement with other geochemical proxies in general (e.g. Bard, 2001; MARGO Project Members, 2009; Dowsett *et al.*, 2012). Finally, many palaeoecological studies use completely independent diversity and environmental proxies, for example ostracode diversity and foraminiferal and/or sediment-based palaeoenvironmental proxies (Yasuhara *et al.*, 2009, 2014).

(*d*) *Taxonomic uncertainty of microfossils*

Taxonomic uncertainty can limit the quality of macroecological and palaeoecological inference. One of the reasons why planktonic foraminifera are a very suitable model system in integrative macroecology and palaeoecology is that they have the best alpha taxonomy among all fossils, due to their very high applied value in palaeoceanography and biostratigraphy, and relatively low, and thus manageable, species richness (~40 species in the present-day ocean) (e.g. see Dowsett, 2007). Most extant planktonic foraminiferal species are formally described, although recent molecular studies have revealed the presence of cryptic species (de Vargas *et al.*, 1999; Darling & Wade, 2008; Ujiié & Asami, 2014). Benthic foraminifera and ostracodes have much higher species richness (~10000 and ~20000 described living species for benthic foraminifera and ostracodes, respectively: Gooday, 2001; Rodriguez-Lazaro & Ruiz-Muñoz, 2012) compared to planktonic foraminifera (probably because of their higher endemism due to lower dispersal ability and higher habitat diversity in benthic environments). Still their alpha taxonomy is much better resolved than that of other meiofaunal groups (e.g. nematodes and copepods), and hence they provide suitable model systems for examining benthic biodiversity. Many other taxonomic groups have more uncertain taxonomy compared to microfossil groups, which is not surprising given that the majority of species are not yet described (Mora *et al.*, 2011).

(*e*) *Paucity of biological information for microfossils*

In addition to the taxonomic uncertainty, paucity of biological information, compared to well-known and studied taxa such as mammals and molluscs, is also a serious problem. For example, we know little about molecular phylogenetic relationships, ecological interactions, life-history traits, functional groups, habitat and feeding types of many, if not most or all, microfossil groups, especially when compared to mammals and molluscs. Although this situation has been gradually improving for molecular phylogeny of several microfossil groups (e.g. Pawlowski & Holzmann, 2002; Yamaguchi & Endo, 2003; Sims, Mann & Medlin, 2006; Ishitani *et al.*, 2012), basic biological information is often scarce (e.g. Horne *et al.*, 2002; Nomaki *et al.*, 2005, 2007, 2008; Schiebel & Hemleben, 2005; Young, Geisen & Probert, 2005; Murray, 2014). It is important to resolve the biology of microfossils better in order to bridge knowledge gaps between microfossils and well-studied living organisms, and to evaluate the use of microfossils as models. Knowledge of basic biology (e.g. life-history traits, functional groups, habitat, feeding types, ecological preference, environmental tolerance, physiology) of microfossil species and genera is highly desirable to interpret palaeoecological and macroecological patterns of microfossils better and compare them with those of macrofossils.

(*f*) *Spatial coverage and time slices*

It is still difficult to obtain a spatially integrated view of marine sediment core records. Marine palaeoecological studies using microfossils are usually based on just one or a limited number of cores for comparison (Hunt *et al.*, 2005; Yasuhara *et al.*, 2009, 2014). Although some of the examples discussed in this section provided excellent insight into certain time periods (Figs 3, 4, 6 and 7), these are rather exceptional cases. Considering (for example) latest Quaternary pollen palaeoecology – with accurate chronology and superior spatial coverage (e.g. Williams *et al.*, 2004; Blois *et al.*, 2013*a*) – as an ideal role model, further efforts towards better spatial coverage of marine palaeoecological records are warranted. For example, in the North Atlantic Ocean, excellent planktonic foraminiferal time-slice data sets are available at least for the present day and the LGM (and more limited data sets are available for the last interglacial and Pliocene) (Ruddiman, 1969; CLIMAP Project Members, 1976, 1984; Prell *et al.*, 1999; Rutherford *et al.*, 1999; Pflaumann *et al.*, 2003; Yasuhara *et al.*, 2012*c*; Dowsett *et al.*, 2013). Constructing similar time slices must be possible by using other microfossils, e.g. deep-sea benthic foraminifera and ostracodes, given excellent calcareous microfossil preservation and availability of numerous sediment cores in the North Atlantic Ocean. Sedimentation rates of deep-sea sediment cores vary depending on location, and are often lower than in lake sediment cores bearing pollen. However, the chronology of deep-sea sediment cores is similarly accurate to lake sediment cores, or even more accurate for longer time scales beyond the limit of radiocarbon dating (for the last ~50000 years), due to the fact that in addition to radiocarbon dating, accurate and well-established oxygen-isotope-based chronology and planktonic-microfossils-based biostratigraphy are available for deep-sea sediments (Berggren *et al.*, 1995; Lisiecki & Raymo, 2005; Martrat *et al.*, 2007; Zachos *et al.*, 2008). The North Atlantic Ocean could therefore be a good place for integrative macroecology–palaeoecology studies, for example to test the validity of 'space-for-time' substitution (Pickett, 1989; Blois *et al.*, 2013*b*). There is little, if any, robust evidence that directly shows 'space-for-time' substitution in microfossil biodiversity other than the planktonic foraminiferal case discussed above. Palaeoclimatologists often successfully apply present-day relationships between microfossil faunal or floral compositions and environmental parameters (e.g. temperature) to reconstruct the past environmental parameters based on microfossil faunal or floral records in sediment cores (Ikeya & Cronin, 1993; Pflaumann *et al.*, 2003; Dowsett *et al.*, 2012), and the result is usually consistent with independent reconstructions based on geochemistry (Bard, 2001; MARGO Project Members, 2009; Dowsett *et al.*, 2012). However, it is less certain whether the same is true also for relationships between microfossil biodiversity and environments (e.g. see Yasuhara & Danovaro, 2014). In addition, on-going and future efforts of massive data compilation in palaeoclimatology, e.g. PAGES 2k (PAGES 2k Consortium, 2013) and PIG2LIG-4FUTURE (El Ouahabi *et al.*, 2012), may include microfossil data usable for biodiversity analyses.

(*g*) *Use of statistical modelling in micropalaeontology*

Finally, rigorous statistical modelling approaches could be used more broadly in marine micropalaeontology to test complex hypotheses. Currently used approaches such as multivariable analyses (e.g. cluster analysis, factor analysis, detrended correspondence analysis, etc.) tend to be more descriptive (e.g. see Yasuhara *et al.*, 2012*a*). However, some micropalaeontologists have started to use statistical modelling approaches considering temporal autocorrelation to investigate climatic impact on deep-sea biodiversity (e.g. Hunt *et al.*, 2005; Yasuhara *et al.*, 2014). Furthermore, there are several recent studies with careful statistical evaluation of sampling biases and time-series analyses of large microfossil databases, although they are primarily on abundance and body size, and not on biodiversity (Hannisdal *et al.*, 2012; Reitan, Schweder & Henderiks, 2012). This approach is important because time-series microfossil records from sediment cores are not always reasonably 'continuous'. Sediment cores (especially long ones) often have sedimentation gaps known as hiatus or unconformity and sedimentation rate is not constant, and thus microfossil data are more or less unevenly distributed over time, although sedimentation gaps are usually detectable through initial and routine observation and analyses and thus not a serious problem in palaeoceanographic studies. Microfossil data (especially large databases) may be compilations of data taken by different studies with different purposes, and thus could be irregularly distributed in time with varying biases. Hence we caution against the uncritical use of aggregate microfossil data in macroecological syntheses or analyses. Another important point regarding statistics may be that sometimes multiple sediment cores are taken very close together, which will serve as potential replicates.

VI. CONCLUSIONS

(1) Both macroecology and palaeoecology have advanced significantly over the last decade, and the time seems ripe for tighter integration into a truly four-dimensional view of the ecology and evolution of our planet's biota; this appears especially feasible for the oceans. Microfossils are a useful empirical model system to bring this integration forward, given the exceptional microfossil record, with very high abundance, superior spatiotemporal coverage, a variety of functional traits, and well-resolved taxonomy.

(2) Further efforts, especially analytical and statistical comparisons of modern (i.e. macroecological) and 'deep' and 'recent' past (i.e. palaeoecological) time-slice and time-series data, and even cross-scale analyses of these data, considering both local and regional scale diversity measures, are important. Especially, more and better time slices in multiple microfossil taxa are needed, taking advantage of the global coverage of marine sediment cores, because time-slice microfossil data sets are seriously limited (Renema *et al.*, 2008; Yasuhara *et al.*, 2009, 2012*c*) compared to relatively rich time-series microfossil data (Thomas & Gooday, 1996; Cronin & Raymo, 1997; Hunt *et al.*, 2005; Ezard *et al.*, 2011*a*; Moffitt *et al.*, 2014; Yasuhara *et al.*, 2014). Furthermore, truly four-dimensional studies using many time-series data from sediment cores with regional or global coverage and considering sampling and other biases represent a promising direction. Finally, improved understanding of the basic biology of microfossils is essential to bridge the gaps better between palaeoecology and macroecology.

(3) These efforts may help to answer fundamental questions in marine biology, such as: (*i*) Why is species diversity generally high in the tropics? (*ii*) Why is longitudinal diversity variation so pronounced? (*iii*) What is the relative importance of evolutionary and ecological drivers of biodiversity? (*iv*) Is global marine diversity saturated with respect to available niches? (*v*) How and for which taxa have large-scale gradients and 'hotspots' of biodiversity changed over time? In fact, a synthesis of the fields of macroecology and palaeoecology may be the only way to get a truly holistic answer on some essential aspects of biodiversity, partly because these are shaped both by historic and present-day influences. Advancement of microfossil research in the directions reviewed here may represent a significant step towards this goal.

VII. ACKNOWLEDGEMENTS

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