Early Cenozoic evolution of the latitudinal diversity gradient

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ABSTRACT

We are beginning to appreciate that the huge radiations of both marine and terrestrial taxa in the aftermath of the K/Pg mass extinction event were concentrated largely, but not exclusively, in the low-latitude and tropical regions. This in turn means that significant latitudinal diversity gradients were developed well before the onset of global cooling at the Eocene/Oligocene boundary. Net rates of evolutionary radiations were significantly higher through the Early Paleocene – Middle Eocene interval (i.e. ~62–42 Ma) in the tropics than at the poles but this may be due as much to their retardation in the latter regions as to their acceleration in the former. At least in the marine realm, polar assemblages are characterised by the phenomenon of high dominance/low evenness, and it is thought likely that this is due to the extreme seasonality of primary production at the base of the food chain. Many modern polar marine organisms are de facto trophic generalists and occupy significantly broader ecological niches than their tropical counterparts. Although we cannot dismiss the roles of both temperature and area in promoting tropical diversity, it could well be that LDGs are just as much the product of a latitudinal gradient in the seasonality of primary productivity. Such a gradient would have operated in both greenhouse and icehouse worlds.

1. Introduction

The latitudinal gradient in taxonomic diversity forms one of the most striking features of life on Earth at the present day. For many major groups of plants and animals there are simply far more of them in the low-latitude and tropical regions than there are in the high-latitude and polar ones; such differences often amount to at least an order of magnitude at the species level (Hillebrand, 2004; Lomolino et al., 2010; Tittensor et al., 2010; Valentine and Jablonski, 2015; Worm and Tittensor, 2018). Understanding how such large disparities in the latitudinal distribution of taxa may have arisen remains a major topic at the heart of contemporary biodiversity research (Gaston, 2000; Mittelbach et al., 2007; Erwin, 2009; Krug et al., 2009; Brown, 2014; Jablonski et al., 2017; Worm and Tittensor, 2018).

One particular area of uncertainty to date has been the precise time of origin of the modern latitudinal diversity gradient (LDG). One school of thought has placed it at the Eocene/Oligocene (E/O) boundary (34 Myr ago), a time of rapid global cooling and pronounced shift in the Earth's climate state from greenhouse to icehouse (Zachos et al., 2001, 2008). At first sight this would seem to be entirely logical as many warm-temperate and tropical taxa would simply have been unable to disperse into the newly expanded cold-temperate and polar regions (Wiens and Donoghue, 2004). A previously diffuse boundary at the edge of the tropics now became much more clearly defined. Support for

an E/O origin of the modern LDG has come largely, but not exclusively, from the terrestrial realm, and a combination of molecular phylogenetic and palaeontological studies on various plants, vertebrates and insects (Hawkins et al., 2006, 2007; Archibald et al., 2010; Condamine et al., 2012; Mannion et al., 2014). There is also evidence from the deep sea fossil record that the origin of the psychrosphere (i.e. the circum-Antarctic cold water current) at this time led to a profound alteration of global circulation patterns and thermal stratification of the oceans. This in turn led to a marked reduction in the taxonomic diversity of polar deep-sea benthic taxa such as foraminifera, as well as certain phytoplankton and zooplankton (Thomas and Gooday, 1996; Wilson, 1998; Culver and Buzas, 2000; Thomas, 2007; Houben et al., 2013; Fenton et al., 2016). The E/O boundary hypothesis is linked very firmly to the concept of global climate change and thus, ultimately, to the principle that temperature directly controls standing levels of biodiversity (Brown, 2014; Clarke, 2017).

But balanced against an E/O origin for the LDG is the fact that many modern taxa, in both the terrestrial and marine realms, have their evolutionary roots in an intense Early Cenozoic radiation in the wake of the Cretaceous/Paleogene (K/Pg) mass extinction event (i.e. in the interval ~62–42 Ma) (Kafanov, 2001; Briggs, 2006; Jaramillo et al., 2006; McKenna and Farrell, 2006; Bininda-Emonds et al., 2007; Stanley, 2007; Ramirez et al., 2007; Schultz and Brady, 2008; Schuettpelz and Pryer, 2009; Meredith et al., 2011; Near et al., 2013;

Feng et al., 2017). Although this pronounced radiation, which is clearly indicated in long, time-series datasets (Flessa and Jablonski, 1996; Stanley, 2007; Alroy, 2010; Sepkoski, 2002; Huang et al., 2014), might have been spread more or less evenly across the Earth's surface, various lines of evidence suggest that it was in fact concentrated in the tropics (Jablonski, 1993, 2005a). If this is indeed the case then we may have to accept that steep, regional LDGs can form in a greenhouse world. This in turn suggests that factors other than temperature may be important in their formation.

2. Evidence for an Early Cenozoic latitudinal diversity gradient

Observational estimates of the extinction intensity at the K/Pg boundary at various global localities are generally in the range of 60–70% at the species level and 30–40% at the generic one (Stanley, 2007; Krug and Jablonski, 2012; Condamine et al., 2013; Aberhan and Kiessling, 2015). Even though there is no obvious evidence of a latitudinal bias in extinction intensity from these localities (Raup and Jablonski, 1993; Zinsmeister et al., 1989; Tobin et al., 2012; Witts et al., 2016), it is still possible that the LDG may have been significantly reduced in scale overall in the immediate aftermath of the extinction event, and then for several millions of years afterwards (Jablonski, 2005b; Stanley, 2007; Krug et al., 2009). Empirical evidence for such a reduction is in short supply but in one recent comparison of Early Cenozoic molluscan faunas between Antarctica (Seymour Island locality) and two tropical localities (US Gulf Coast and Paris Basin) it was shown that in the terminal Cretaceous stage (the Maastrichtian) there was quite a strong diversity contrast between the tropics and the pole (N.B. the very small number of rudistid bivalves in the Maastrichtian were excluded from the analyses). Nevertheless, this is reduced significantly in the initial Paleogene stage (the Danian), and especially so in the bivalves (Crame, 2019). This could be taken as a weakening of the gradient by a stronger reduction of tropical faunas in the extinction event, but further work is required to verify this pattern on smaller temporal and taxonomic scales. Work on microbiotas across the K/Pg boundary suggests that it may have taken as long as 4 Myr for taxonomic diversity levels to be restored to pre-extinction levels, with undoubtedly some variation in rates between major clades (D'Hondt, 2005).

The subsequent radiation of both bivalves and gastropods through the Paleocene and Eocene epochs has been traced between the same three localities (Beu, 2009; Crame et al., 2014, 2018; Crame, 2019). When this is done it is apparent that there is a rapid rise through the later Paleocene stages into the Early Eocene and then Middle Eocene at all three localities; indeed, this proves to be the Early Cenozoic diversity maximum in the marine realm (Piccoli et al., 1987; Dockery and Lozouet, 2003; Crame et al., 2014; Huyghe et al., 2015). This Early Cenozoic evolutionary radiation is perhaps best documented in the extensive Neogastropoda clade which is known to have expanded through the entire Cenozoic era to form one of the largest clades in shallow seas at the present day (Crame et al., 2018, and references therein). A latitudinal contrast of Middle Eocene neogastropods gives totals of approximately 437 species for the US Gulf Coast, 433 for the Paris Basin, but only 57 for Antarctica (Beu, 2009; Crame, 2019). At first sight this might be taken as simply reflecting a strong sample bias, with the Antarctic locality being much less well known than either of the two tropical ones. Nevertheless, it should be pointed out that that the Antarctic Middle Eocene gastropod fauna comprises at least 7500 individuals and of these approximately 3500 (47%) are neogastropods (Crame, 2019). In addition, of the 57 species recorded from the La Meseta Formation of Seymour Island, only 12 (21%) have individuals in excess of 50 mm; small (<20 mm) and tiny (<5 mm) taxa are reasonably well represented in this fauna (Crame et al., 2018, Suppl. Inf.). The very large Imparidentia bivalve clade (formerly Heterodonta), which includes common, shallow-water taxa such as the Cardiidae, Tellinidae, Mactridae and Veneridae, also shows a very strong Middle

Eocene diversity contrast: US Gulf Coast – 158 species; Paris Basin – 273; Antarctica – 25 (Beu, 2009; Crame, 2019).

It should be emphasised that in making these large-scale diversity comparisons it was not possible to use rarefaction or related techniques; for many of the tropical faunas accurate counts of numbers of individuals are unavailable. The US Gulf Coast locality is contained essentially within a central eastern Texas – Alabama region, but in the Middle Eocene there is a significant eastwards extension to include the upper Santee Limestone of South Carolina. Further details on the Paleocene, Early Eocene and Middle Eocene Gulf Coast localities, including estimates of the stratigraphic thicknesses of the units studied are contained in the Appendix to Crame et al. (2018) and Crame (2019). All of the various sites investigated have been comprehensively sampled, but of course this does not necessarily equate to complete sample standardisation.

Another prominent feature of the Early Cenozoic evolution of the Neogastropoda is the rapid increase in the proportion of taxa that can be assigned to modern genera. Whereas only 7% of the Maastrichtian species on the US Gulf Coast fall into this category, 44% of the Middle Eocene ones do; in Antarctica there are no modern Maastrichtian genera but the figure rises to 37% in the Middle Eocene (Crame et al., 2018). In both the tropics and the pole the pronounced evolutionary radiation is accompanied by a rapid rise of the modern neogastropod fauna.

As well as these direct latitudinal contrasts it is important to emphasise just how diverse the tropical Middle Eocene fauna of the Paris Basin as a whole is. From the Lutetian (i.e. early Middle Eocene) Calcaire Grossier Formation alone some 1550 species of gastropods and 540 species of bivalves have been recorded, and at one single outcrop at Falunière (Grignon, Yvalines) >800 species of molluscs have been collected from just one 13 m section (Cossmann and Pissarro, 1904–13; Pacaud and Le Renard, 1995; Gély, 2008; Merle, 2008; Huyghe et al., 2012). There is no obvious preservational bias between the Early, Middle and Late Eocene, and the diversity hotspot actually coincides with an interval of slight global cooling between Early and Middle Eocene climatic optima (Huyghe et al., 2012, 2015). This huge phase of Early Cenozoic diversification, which is also recorded in other Paris Basin taxa such as corals, brachiopods, decapod crustaceans and benthic foraminifera, took place on a series of very shallow-water carbonate platforms and banks, and laid the foundations for the modern hyper-diverse tropical molluscan fauna (Vermeij, 2001; Kafanov, 2001; Briggs, 2006; Harzhauser et al., 2002, 2008).

Similarly, the Bolca Lagerstätten (BL) of northern Italy has yielded a spectacular ichthyofauna of some 250+ species contained within approximately 90 families and 17 orders (Bellwood, 1996; Bellwood and Wainwright, 2006; Carnevale and Pietsch, 2009; Carnevale et al., 2014; Friedman and Carnevale, 2018; Marramà et al., 2018). Dated by calcareous nannoplankton as between 50.5 and 48.96 Ma in age, i.e. late Early Eocene (Ypresian) (Friedman and Carnevale, 2018), it reveals a major radiation of acanthomorph (i.e. spiny-rayed) teleosts in general, and various percomorph families in particular. The latter comprises a suite of grazers and herbivores, many of which bear a striking resemblance to modern coral reef taxa (Bellwood and Wainwright, 2006; Friedman and Carnevale, 2018). The taxonomic richness shown by the BL is higher than that of other Ypresian Lagerstätten (Friedman et al., 2016), and can also be linked to the initial development of modern coral reef assemblages (Bellwood, 1996; Friedman and Carnevale, 2018). The BL accumulated in a coastal area periodically affected by anoxia, probably a protected lagoonal system in close proximity to both coral reefs and seagrass beds (Carnevale and Pietsch, 2009; Carnevale et al., 2014).

Like the Calcaire Grossier Formation of the Paris Basin, the BL is also thought to have been associated with an extensive archipelago in the western Tethyan circum-tropical ocean. Although it is slightly older than the prolific faunas of the Calcaire Grossier Formation (late Early Eocene as opposed to early Middle Eocene), both would seem to have

been part of a distinct biodiversity hotspot that may have been comparable in scale to the modern Atlantic – Caribbean – East Pacific (ACEP) and Indo-West Pacific (IWP) ones (Merle, 2008; Huyghe et al., 2012; Renema et al., 2008; Friedman and Carnevale, 2018). However, it has to be stressed that the boundaries of this western Tethyan hotspot remain poorly defined. What we do know is that the Paleocene – Middle Eocene tropical belt, in both the marine and terrestrial realms, was some 40–50% larger than the present day, extending, at least intermittently, to palaeolatitudes of 55°- 65° N and S, and occasionally even higher (Wolfe, 1985; Adams et al., 1990; Greenwood and Wing, 1995; Collinson, 2000; Morley, 2007; Pross et al., 2012).

The strong high – low latitude diversity contrast seen in Early Cenozoic molluscan faunas is very probably also present in the ichthyofaunas. In this particular instance the comparisons are not between precisely contemporaneous units as the BL fauna is late Ypresian in age and the most prolific Antarctic one is slightly younger at undifferentiated Middle Eocene age (Crame et al., 2014; Douglas et al., 2014; Amenábar et al., 2019). The latter comes from the lithostratigraphic unit Telm 4 of the La Meseta Formation, Seymour Island which is essentially a condensed shell bed from which some 10,000 specimens of fish teeth, vertebrae, bone fragments, spines and otoliths have been recovered by a combination of surface collecting and dry-sieving (Reguero, 2019; Regeuro et al., 2002; Reguero et al., 2012). Such an abundant assemblage is of surprisingly low taxonomic diversity, with only approximately 35 species from 23 families being recorded. And of these some 71% are chondrichthyans, with sharks in particular being very well represented (Reguero et al., 2012). At least 21 species of shark have been identified and it is clear that taxa from many different types of habitat converged on this one locality (Long, 1992; Kriwet, 2005). In marked contrast, the BL chondrichthyans comprise only 7% of the total ichthyofauna (Marramà et al., 2018). The full ecological and evolutionary significance of the pronounced shift in the ratio of teleosts to chondrichthyans with latitude in the Early – Middle Eocene has yet to be assessed.

The precise status of LDGs in the Early Cenozoic terrestrial realm is currently uncertain. The presence of large-scale LDGs in the Eocene floras of North America (Harrington, 2004) has been challenged by the subsequent demonstration of mid-latitude diversity peaks in both plants and insects (Archibald et al., 2010), and a flat-lying LDG in Early Paleocene mammals (Rose et al., 2011; Mannion et al., 2014). Nevertheless, it is apparent from extensive sporomorph (i.e. spores and pollen) assemblages from central Colombia and western Venezuela that there was a very marked increase in equatorial diversity values between the Early Paleocene and Middle Eocene (Jaramillo and Dilcher, 2000; Jaramillo et al., 2006; Jardine et al., 2018). Indeed, this was such as to generate peak Middle Eocene values in excess of those in the present-day paratropical rainforest (Jaramillo et al., 2006). The rate of Paleocene – Eocene diversification of this equatorial rainforest exceeds that of floras on the US Gulf Coast (30°N), as well as mid-latitude floras in both hemispheres (Jardine et al., 2018; Jaramillo and Cárdenas, 2013). A comparison of Early – Middle Eocene sites between equatorial Colombia/Venezuela and temperate southern Argentina, using both palynological and megafloral records, established 572 species from the former but only 93 from the latter (Jaramillo and Cárdenas, 2013).

Although comprehensive LDGs are still at a premium, there is now a distinct impression that the Early Cenozoic global radiation of both marine and terrestrial taxa proceeded at a much higher net rate in the tropics than at the poles. This is particularly so in three major benthic marine groups that show very strong LDGs at the present day: Neogastropoda, Imparidentia bivalves, and teleost fishes (Jablonski et al., 2013; Crame et al., 2018; Rabosky et al., 2018). Each of these taxa radiated globally in the Paleocene – Middle Eocene, but a series of tropics – Antarctica comparisons indicate that they did so at a much higher net rate in the former region than the latter. A very strong latitudinal diversity contrast had developed by the Middle Eocene (~45 Ma), and this has continued through to the present day.

The precise stratigraphic, taxonomic and biogeographic status of a prolific Early Paleocene molluscan fauna from the Agatdal Formation, Nuussuaq Group, West Greenalnd (~63°N palaeolatitude) is uncertain (Kollmann and Peel, 1983; Petersen and Vedelsby, 2000; Dam et al., 2009; Grimsson et al., 2016). There are some indications that it is linked to a series of Early Paleocene (i.e. Danian – Selandian) faunas of moderately high taxonomic diversity from northern and central Europe that comprise a genuine admixture of warm- and cool-temperate elements (Schnetler, 2001; Lauridsen and Schnetler, 2014). But what is certain is that polewards of these Greenland – European faunas there was a distinct Early Paleocene (Danian) Arctic/boreal fauna in the highest northern latitudes. This can be traced from Alaska through Ellesmere Island to Svalbard and is characterised by a sparse molluscan fauna of temperate aspect (Crame, 2013, and references therein).

3. Structure of Early Cenozoic latitudinal diversity gradients

The Early Cenozoic interval of high – low latitude biotic differentiation is constrained to an approximately 20 Myr interval between 62 and 42 Ma (i.e. late Early Paleocene to late Middle Eocene). As this was almost exactly coincident with a period of global greenhouse warmth (Zachos et al., 2008), the question has to be asked whether this differentiation can be attributed to the effects of temperature alone? Early Eocene latitudinal temperature gradients were very much shallower than those of the present day, with one estimate being that there was almost no latitudinal sea surface temperature (SST) gradient at this time between subequatorial and subpolar regions (Bijl et al., 2009). Even when global cooling began in the late Middle Eocene it is still likely that latitudinal temperature gradients were less than half their present day value, and quite possibly substantially so (Pross et al., 2012; Douglas et al., 2014; Crame et al., 2018). Some clues as to what else might be contributing to the latitudinal differentiation of biotas through the Early Cenozoic have recently come to light from a detailed comparison of the structure of high- and low-latitude marine faunas.

When we look at the latitudinal diversity contrast of the very large Neogastropoda clade at the present day two things are immediately apparent: firstly, there are far fewer species at the poles than in the tropics, and secondly, those species that are present tend to be concentrated in just a few families (Fig. 1). In the Arctic, Buccinidae *s.l.* plus Conoidea (minus Conidae and Terebridae) comprises 89% of the fauna, and in the Antarctic the equivalent figure is 74%; however, in comparison, the tropical fauna comprises only 32% of these families/family groups (Crame, 2013) (Fig. 1). The two polar faunas show patterns of higher dominance/lower evenness than the tropical one and can perhaps be taken to be end-members of latitudinal gradients in species evenness in both hemispheres. This pattern is very similar to that established in the northern hemisphere for predatory gastropods as a whole (i.e. Neogastropoda + littorinimorph superfamilies Naticoidea and Tonnoidea) (Taylor and Taylor, 1977).

When relative abundance distributions (RADs) are fitted statistically to the three faunas shown in Fig. 1, using the R 'vegan' package (Oksanen et al., 2016), and the number of species occurring in each family, they show two sharply contrasting patterns: whereas the tropical fauna was best fit by the broken stick model, both the Arctic and Antarctic were closest to a Zipf distribution (Fig. 2) (Crame et al., 2018). The former of these distributions represents the comparatively even apportionment of some major environmental resource, and may perhaps be expected for a large group of species from essentially the same trophic guild (May, 1975). But the latter has a very different shape and reflects the much higher level of dominance in the polar faunas (Matthews and Whittaker, 2014) (Fig. 2).

Comparisons of polar – tropical RADs were also used by Harnik et al. (2010) in their investigation of the taxonomic structure of global marine bivalve faunas. In this they used numbers of species within the component genera of each fauna and found that the best fit for four out of five climatic zones and 26 out of 27 provinces was to the Zipf and
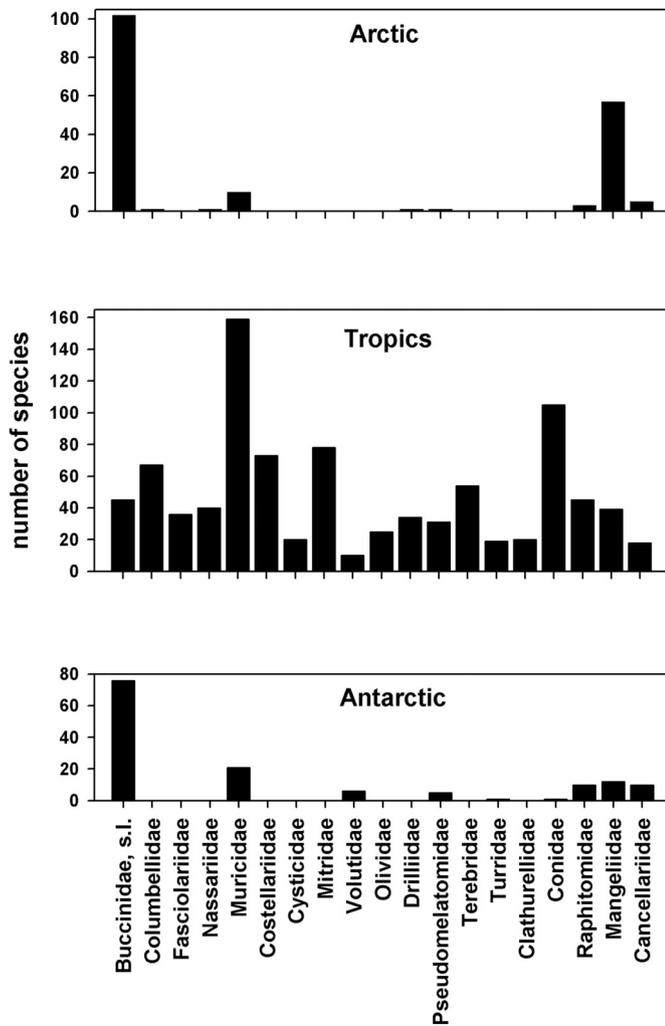
Fig. 1. Regional comparison of present day neogastropod faunas between the Arctic, Tropics and Antarctic. The histograms represent the number of species within 18 common neogastropod families. The Arctic fauna is a compilation of all shelf-depth taxa occurring north of 60°N, and the Antarctic of all shelf and bathyal taxa south of the Polar Front. The Tropics fauna is an average of six faunas: two from the Americas and four from the Indo-West Pacific province. Reproduced with slight modifications from Crame, 2013, (Fig. 1), where further details on the construction of the three faunas are given. Neogastropod family classification based on Bouchet and Rocroi (2005) and Bouchet et al. (2011).

Fig. 2. Relative abundance distributions to show the contrast between present-day polar and tropical neogastropod faunas. Relative abundance distributions (RADs) are used to examine the structure of biotic assemblages by plotting % relative abundance for each taxon (log scale, y axis) against its rank within the assemblage (x axis). They can be constructed using either the number of individuals per species, or, as in this particular instance, the number of species within a higher taxon such as a family. They are based on the principle that the abundance of a particular taxon reflects the size of its realised niche, which in turn is shaped by ecological interactions within a community or assemblage (Magurran, 2004). Sometimes referred to as dominance – diversity plots, they range in form from sub-vertical curves at one extreme (strong dominance) to sub-horizontal, sigmoidal curves at the other (strong evenness). The polar fauna (from Antarctica) fits closest to the former category and a Zipf distribution, but the tropical one is closer to the latter and a broken stick model. Redrawn from Crame et al., 2018, (Fig. 3) where further information on the composition of the respective faunas and the methods of model fitting are contained. As the two polar faunas show very similar Zipf distributions they have been amalgamated here into just one curve. It should be noted that the polar – tropical contrast seen at the present day is almost exactly repeated by a similar comparison of Middle Eocene faunas of approximately 45 Ma age.

Zipf-Mandelbrot (Z-M) family of distributions. The Z-M is influenced by two component parameter estimates: gamma, which measures the evenness of species within genera, and beta, which measures evenness within the most diverse genera; the Zipf uses only gamma, and is equivalent to a Z-M where beta = zero. Both polar provinces were found to have higher gamma values than their temperate and tropical counterparts, and thus a significantly more uneven taxonomic structure (Harnik et al., 2010).

RADs (again using the number of species per family) have also been used to compare the structure of the Antarctic Middle Eocene neogastropod fauna with those of the two Middle Eocene tropical localities, US Gulf Coast and Paris Basin (Crame et al., 2018). The result obtained is almost exactly the same as that found for modern neogastropod faunas, as the two tropical localities are best fit by a broken stick, and the Antarctic by a Zipf (Crame et al., 2018) (Fig. 2). An Early Cenozoic latitudinal gradient in species richness was also matched by a gradient in species evenness; the level of high – low latitude differentiation seen at the present day in neogastropod faunas was already established by the Middle Eocene (i.e. ~45 Myr ago) (Fig. 2).
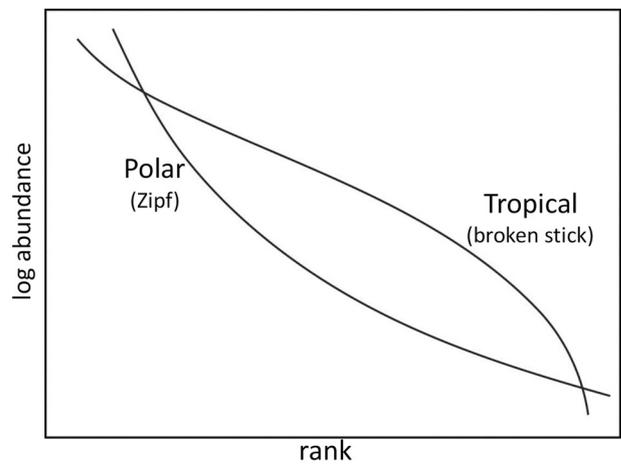
Even though we lack further examples of RADs being fitted to regional faunas, there are strong indications that other modern polar marine faunas are also characterised by the phenomenon of strong dominance/low evenness; this is particularly so in the Southern Ocean.

4. The phenomenon of higher dominance/lower evenness in modern polar biotas

An important example of high polar dominance is provided by benthic (including bentho-pelagic) fish on the Antarctic continental shelf and slope (Eastman, 2000). In total, some 213 species are known from 18 different families, but, within these, three groups are particularly prominent: Liparidae (snail fishes; 67 species), Zoarcidae (eelpouts; 23 species), and Notothenioidei (five component families; 96 species). Together, these three groups comprise 88% of the total benthic fish fauna of Antarctica, and this figure rises to 92% in the most southerly shelf seas (Eastman, 2000). Nevertheless, species richness on its own fails to reflect the overwhelming dominance of notothenioids in the Antarctic fish fauna in terms of abundance and biomass. This is estimated to be as high as 90–95%, and it is apparent that no other oceanic ecosystem is so dominated by a single taxonomic group of benthic fish (Eastman, 2000; Clarke and Johnston, 1996; Briggs, 2003).

Unfortunately, the fossil record of notothenioids is extremely poor. A partial dorsal cranium from the La Meseta Formation of Seymour Island has been assigned to the modern non-Antarctic notothenioid family Eleginopidae, and if this determination is correct then the stem group of the modern Antarctic clade could be as old as 45 Ma (i.e. Middle Eocene judging from the position of the locality on the revised geological map of Seymour Island) (Eastman and Grande, 1991; Near,

2004; Eastman, 2005). There is even some phylogenetic evidence to suggest that it could be considerably older than this (Near, 2004).

Within the marine invertebrates the dominant group on the Antarctic shelf is the peracarid crustaceans, comprising some 1350 species that are very largely assigned to either the Amphipoda or Isopoda (Arntz et al., 1997; Clarke and Johnston, 2003; Dayton, 1990; De Broyer et al., 2003; Brandt et al., 2007a). Two families, Iphimediidae and Epimeriidae, predominate within the approximately 470 amphipod shelf species (Lörz and Held, 2004), and consist of a series of predators, scavengers and necrophagous taxa on largely sedentary sponges, cnidarians, bryozoans and holothurians (De Broyer et al., 2003; De Broyer and Jazdzewski, 1996). Continental shelf isopods in turn constitute approximately 371 species, with 52% of them being assigned to just four families: Munnopsididae, Paramunnidae, Serolidae and Arcturidae (Dayton, 1990; Brandt et al., 2007a). As with the prominent amphipods, our knowledge of the ecology of these families is limited, but whereas the Arcturidae are thought to be mainly passive filter feeders, the Serolidae are known to be both active predators and scavengers (Brandt et al., 2007a, 2007b).

Although there is no Antarctic fossil record for the peracarid Crustacea, a preliminary phylogenetic analysis links the South American shelf-depth genera *Cristaserolis* and *Leptoserolis* with the Australian genus *Serolina* (Brandt, 1991, 1992). It is suggested that these taxa were only separated at the time of opening of the Tasman Gateway some 30 Myr ago (Scher et al., 2015), and before this there was a distinctive Eocene serolid isopod fauna around the shallow-water southern Gondwana margins (Brandt, 1991, 1992).

5. Significance of high dominance/low evenness in polar biotas

There is a general impression that, as high-latitude and polar organisms have to contend with more extreme and widely fluctuating environmental conditions, their constituent species have broader tolerances and less specific microhabitat requirements; selection for generalism and vagility would form an effective barrier to extinction (Chown and Gaston, 2000; Dynesius and Jansson, 2000). When diversity-dependent resources (i.e. those that can potentially be used up) are considered in the marine realm it is apparent that attenuation of trophic resources may be paramount, and in particular that caused by the extreme seasonality of primary production at the base of the food chain (Valentine, 1973, 1983; Clarke, 1988, 1990; Arntz et al., 1994; Valentine et al., 2008). It has been estimated that there is over an order of magnitude variability in primary production between the relatively stable tropics and fluctuating polar regions (Valentine and Jablonski, 2015; Krug et al., 2009), and within the latter there will be selection for organisms that can either sustain long periods of starvation, or live on material other than primary production (Valentine, 1983).

Many of the dominant benthic marine taxa in both polar regions are clearly trophic generalists (Dayton, 1990; Valentine, 1983; Valentine et al., 2008; Pearse, 1965; Arnaud, 1977). This is particularly so in the Antarctic where examples of taxa known to have very broad-based diets include the common buccinid gastropod, *Neobuccinum eatoni*, the starfish *Diplasterias brucei*, various lysaniassid amphipods, *Parbolasia corrugatus* (common nemertean), at least four species of holothurians, and three ophiuroids (Arntz et al., 1994; Pearse, 1965; Arnaud, 1970, 1977; White, 1984; McClintock, 1994). Studies in both Adélie Land and McMurdo Sound have shown that certain asteroids, echinoids, pycnogonids, isopods and amphipods are only necrophagous during the austral winter when food supplies are particularly low (Arnaud, 1977). Some benthic and bentho-pelagic notothenioid fish have been recorded as feeding on up to 16 different types of prey (Eastman, 2000; Brandt, 2000). In marked contrast, many tropical marine invertebrate species have become specialised on a much narrower range of diversity-dependent resources without the risk of extinction, and thus far more of them can be packed into any given area (Taylor et al., 1980; Kohn, 1997; Krug et al., 2009).
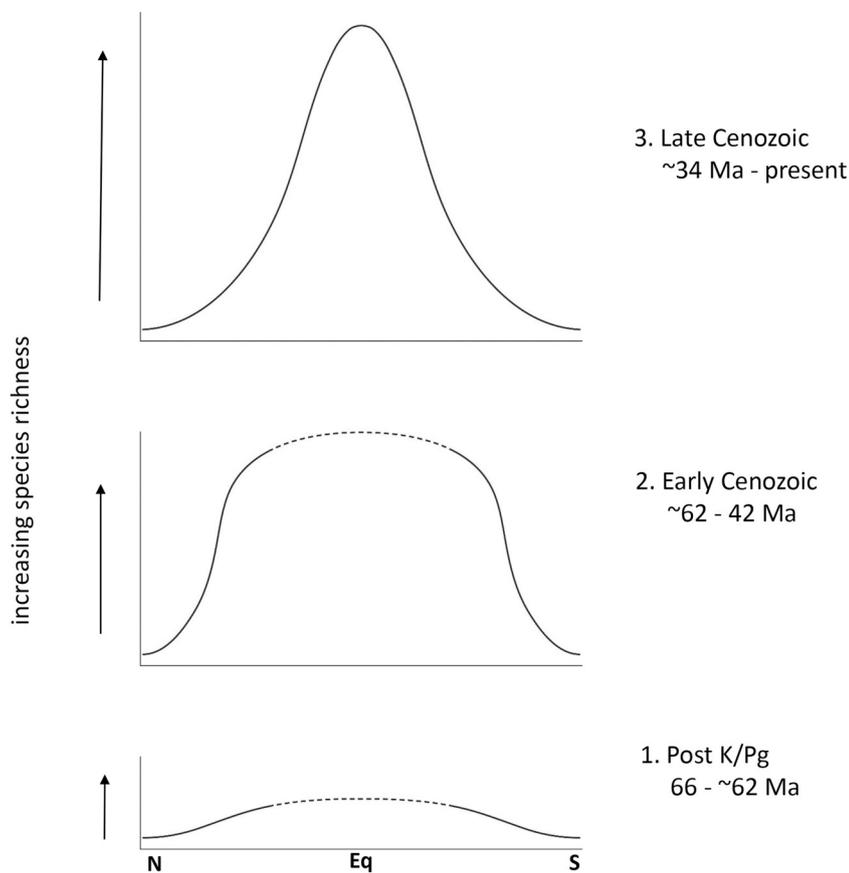
Latitudinal gradients in the species richness of predatory gastropods have already been linked to the stability of the production cycle in the eastern and western Atlantic, and eastern Pacific (Taylor and Taylor, 1977; Taylor et al., 1980; Taylor, 1981; Valentine et al., 2002). Broader feeding types, and in particular members of the Buccinidae, characterise the highest latitudes, and in the tropics neogastropod families such as the Muricidae, Mitridae, Conidae and Terebridae have much more restricted diets and frequently specialise on single prey items. The prominence of certain conoidean families, such as the Mangeliidae, in Arctic/sub-Arctic regions is linked to a preference for predation on polychaetes. These are thought to be predominantly deposit feeders and thus a predictable food resource not greatly influenced by seasonal fluctuations in the way that many suspension feeders would be (Taylor and Taylor, 1977; Taylor, 1981).

6. The link between dominance, seasonality, and the diversity of polar marine faunas

Production of diatoms and other phytoplankton at the base of the polar marine food chain is concentrated within a dense but brief summer bloom that is matched by an approximately six-fold increase in herbivorous, carnivorous and omnivorous zooplankton species (Clarke, 1988). As well as its effect on the dietary breadth of predatory taxa, a short summer season of primary production is also very probably the reason why many globally common families of suspension-feeding bivalves are either poorly represented, or completely absent, from both polar regions (Nicol, 1967; Dell, 1972; Valentine et al., 2008). Unless such bivalves have evolved the capacity to lie dormant for long periods, or utilise an alternative food resource, they would simply not be able to survive in the polar regions (Arntz et al., 1994, 1997).

When traced from south to north in the North Atlantic Ocean, both benthic and pelagic groups show a significant fall in diversity at approximately 40°N (Taylor and Taylor, 1977; Taylor et al., 1980; Angel, 1997). Whereas at latitudes <40°N warm surface waters contain low concentrations of nutrients and the phytoplankton production cycle is only weakly seasonal, at latitudes >40°N winter cooling of surface waters results in convective overturning, mixing, and resupply of nutrients back into surface waters (Angel, 1997). At 40° - 60°N there is a bimodal phytoplankton bloom (i.e. spring and autumn), and at >60°N there is a single summertime bloom. These latitudinal changes in the production cycle are thought to have a profound influence on both pelagic and benthic diversity values (Angel, 1997), and as the 40° dip in diversity is clearly marked at the family level (Taylor and Taylor, 1977), they may have done so over a considerable period of time.

The concentration of generalist and opportunist taxa in the polar regions leads us to consider whether polar – tropical diversity contrasts could be attributable, at least in part, to a latitudinal gradient in niche width or overlap? This is especially so in terms of the trophic niche where there is strong circumstantial evidence to indicate that, for essentially predatory groups such as the Neogastropoda, diets are much broader in the polar regions than the tropics. Such a concept is indeed appealing but it has to be emphasised that it has not yet been subjected to any rigorous form of testing. A rare attempt to do this was based very largely in the terrestrial realm, but could not find a positive relation between latitude and either niche breadth or the number/proportion of specialist taxa (Vázquez and Stevens, 2004). In the past, niche theory has focused primarily on the individual niche and the phenomenon of resource partitioning between potentially overlapping species. Nevertheless, this is only part of the story and we also need to consider the concept of the population niche, which centres on how populations of species are distributed within specific regions (Ricklefs, 2010). The population niche is influenced by a series of regional gradients, such as temperature, that cannot be partitioned directly by different species within a habitat. A mosaic of shifting patterns in the population niche may allow species within a clade to coexist within otherwise similar niche space (Ricklefs, 2010). Our concept of niche width is clearly

Fig. 3. Evolution of latitudinal diversity contrasts through the Cenozoic era. Stage 1 represents the immediate aftermath of the K/Pg mass extinction event when global faunas were still in a recovery phase. In all probability the LDG was greatly reduced at this time. Stage 2 represents the Early Cenozoic greenhouse world when latitudinal temperature gradients were much shallower than at the present day. However, latitudinal diversity gradients were present in the mid- to high-latitudes and the overall form of the high – low latitude diversity contrast was that of a broad, low dome. Stage 3 is set in the Late Cenozoic after the onset of global cooling at the Eocene/Oligocene boundary. The high – low diversity contrast now has the more familiar modern profile of a bell-shaped curve with a much narrower peak. It is envisaged that this is achieved by both the intensification of seasonality in the high-latitude and polar regions, and range retraction into lower latitudes. Net rate of species increase (i.e. speciation minus extinction) is significantly higher in the tropics than at the poles throughout the Cenozoic era.
Key: N – northern polar regions; S – southern polar regions; Eq – Equator.

changing, and there would seem to be considerable scope to reassess its applicability in the marine realm using taxa such as the Neogastropoda. It remains as a potentially key, but largely unproven, mechanism for generating polar – tropical diversity contrasts.

7. Synthesis: evolution of Early Cenozoic LDGs

A synopsis of how very strong latitudinal contrasts in marine benthic diversity may have evolved through the Cenozoic is presented in Fig. 3. In stage 1, 66 - ~62 Ma, there is very little direct evidence as to how steep LDGs may have been, but it is suggested that the recovery took place from a relatively flat, low diversity feature with weaker latitudinal contrasts. It is stage 2, ~62–42 Ma, where significant diversity differences between the tropics and the poles were re-established and steep LDGs produced (Fig. 3). This is where, at least in Antarctica, the modern polar fauna first becomes recognisable, but there is evidence to suggest that some of the key component clades radiated at a much slower rate than tropical counterparts; this is particularly so of very large cosmopolitan clades such as the Neogastropoda, Imparidentia bivalves and teleost fishes. On reflection, it may well be that the evolution of the modern LDG through the Early Cenozoic was due not so much to an acceleration of net evolutionary rates in the tropics as to their retardation in the high-latitude and polar regions. This in turn is linked to the marked seasonality of primary production which is essentially a time-invariant feature of both greenhouse and icehouse worlds. Seasonality leads to a preponderance of generalist taxa in the high-latitude and polar regions, and simply far fewer of these can be accommodated than in the low-latitude and tropical regions.

Although steep LDGs evolved in the interval ~62–42 Ma, their overall form was somewhat different from that of today (Fig. 3). This was the acme of the greenhouse world and we know that the tropics reached into latitudes of 50°+, and occasionally even higher. Therefore, the overall profile of the LDG in both hemispheres is more likely to

have been that of a broad dome rather than the bell-shaped curve with narrow peak of the present day (Fig. 3). The latter feature (stage 3) is seen as at least a partial retraction feature in response to the onset of global cooling at 34 Ma, but diversity is still expanding at a significantly higher rate in the tropics than in the high-latitude and polar regions.

All the indications are that in the critical greenhouse interval, ~62–42 Ma, evolutionary radiations were at a significantly higher net rate in the tropics than in the high-latitude and polar regions, and this is the fundamental process driving the evolution of the LDG through the Early Cenozoic (Jablonski et al., 2006; Mittelbach et al., 2007; Krug et al., 2009; Gillman and Wright, 2014). However, it should be emphasised that such a process is not necessarily detrimental to the long-term stability of polar biotas. There is in fact strong theoretical evidence to suggest that broad-niched polar species will have saturated all the available ecological space and are thus inherently resistant to invasion. There is very probably a high proportion of stable, incumbent taxa in the polar marine realm (Turner et al., 1996; Valentine et al., 2008).

The importance of temperature in playing at least a partial role in the Early Cenozoic evolution of LDGs should not be overlooked. Temperature can clearly influence the rate at which energy is transferred through the ecosystem, and some form of Metabloic Theory of Biodiveresity, where an increase in temperature speeds up biochemical kinetics and rates of molecular evolution, may yet be shown to have widespread applicability (Brown, 2014; Clarke, 2017). In addition, it is readily apparent that latitudinal range shifts driven by climate change are a persistent feature through time and some of these clearly have the ability to mould large-scale patterns (Jablonski et al., 2006; Condamine et al., 2012; Huang et al., 2014). The concept of tropical niche conservatism, where modern taxonomic groups originated in the extensive Early Cenozoic tropics but subsequently had little or no success in colonising the high-latitude and polar regions, may have significantly enhanced existing LDGs over the last 34 Myr (Hawkins et al., 2006, 2007; Buckley et al., 2010; Jansson et al., 2013). Furthermore, in the

very highest levels of the Seymour Island sedimentary section (informal mapping units Telm 6 & 7, also known as the Submeseta Formation) a very marked reduction in taxonomic diversity has been linked to the onset of major global cooling close to the E/O boundary (Ivany et al., 2008). Durophagous (i.e. shell-breaking) predators such as crabs, sharks and most teleost fish are almost completely absent from this interval and it is thought that this in turn led to the proliferation of dense, epifaunal, suspension feeding echinoderm communities dominated by ophiuroids and crinoids (Aronson and Blake, 2001; Aronson et al., 2007).

Nevertheless, the correspondence between temperature and taxonomic diversity change through the studied Early Cenozoic sections is not exact. At least in the marine realm, it is apparent that the really steep diversity increase occurs between the Early and Middle Eocene, just when global temperatures begin to level off and then gradually decline (Zachos et al., 2008). This may represent some sort of time-lag effect in the diversification process, or perhaps the intensity of the Middle Eocene Climatic Optimum at ~40 Ma has been underestimated (Crame et al., 2018)? And on a grander timescale it is very unlikely that the long-term decline of global temperatures from the late Middle Eocene onwards (Zachos et al., 2008) is matched by a parallel decline in global biodiversity. In the marine realm, there is compelling evidence of major later Cenozoic evolutionary radiations, including those in the very large groups such as the Neogastropoda, Imparidentia bivalves and teleost fishes (Briggs, 2003; Stanley, 2007; Norris et al., 2013; Bush and Bambach, 2015). Even in the Late Cenozoic, which has been regarded traditionally as a period of low temperatures, ice sheet extension, and extinction, it is clear that there was a pronounced phase of polar radiations linked to a major expansion of diatom-based ecosystems (at ~14 Ma) (Crampton et al., 2016; Crame, 2018). The full effect of these radiations in the benthic realm has yet to be established, but in the pelagic realm it has clearly led to the development of low diversity – high abundance assemblages showing strong dominance at each trophic level (Ducklow et al., 2007; Murphy et al., 2016). In all probability this is another area where marine taxonomic diversity levels are dictated more by food supply than temperature. The widespread assumption that temperature has been the primary driver of the LDG through deep time (Brown, 2014; Mannion et al., 2014; Worm and Tittensor, 2018) now needs to be critically re-examined.

We should also consider the effects of area on the evolution of LDGs, as the large extent of the Early Cenozoic tropics could have promoted both speciation and reduced extinction relative to smaller biomes (Rosenzweig, 1995). In a large-scale study of tree species diversity, Fine and Ree (2006) could find no correlation between the estimated area of the modern tropical forest biome and tree species richness. However, there was a good correlation with the expanded area of the Eocene tropics and this has led to the development of a time-integrated, species – area concept to explain high tropical diversity (Fine and Ree, 2006; Fine, 2015). Within the marine realm the later increase in Cenozoic diversity levels was undoubtedly influenced by the proliferation of coral reefs (Bellwood and Wainwright, 2006; Harzhauser et al., 2008; Kiessling et al., 2010; Norris et al., 2013), but this may be due as much to an increase in three-dimensional habitat complexity as to two-dimensional surface area.

8. Conclusions

- A huge global pulse of biological diversification in the wake of the K/Pg mass extinction event was concentrated in the low-latitude and tropical regions. This in turn led to the development of steep LDGs well before the onset of global cooling at 34 Ma.
- We are beginning to appreciate that, at least in the marine realm, high-latitude and polar regions are characterised not only by low taxonomic diversity but also by high dominance/low evenness. The taxonomic structure of polar communities is fundamentally different to that of tropical ones.

- The phenomenon of high dominance in polar communities is linked to the marked seasonality of primary productivity at the base of the food chain. This leads to available ecospace being dominated by comparatively few broad-niched generalists.
- The form of the Early Cenozoic LDG was very different to that of today. The tropical zone was much broader and the steep drop-off in species numbers occurred at a higher latitude.
- Both elevated temperatures and extended area could have promoted diversification in the Early Cenozoic tropics. But it is likely that the evolution of steep LDGs was also significantly enhanced by the retardation of net evolutionary rates in the high-latitude and polar regions. The seasonality of primary productivity is a time-invariant feature that would have affected both greenhouse and icehouse worlds.

Declaration of Competing Interest

The author declares that he has no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

Aberhan, M., Kiessling, W., 2015. Persistent ecological shifts in marine molluscan assemblages across the end-Cretaceous mass extinction. Proc. Natl. Acad. Sci. U. S. A. 112, 7207–7212.

Adams, C.G., Lee, D.E., Rosen, B.R., 1990. Conflicting isotopic and biotic evidence for tropical sea-surface temperatures during the Tertiary. Palaeogeogr. Palaeoclimatol. Palaeoecol. 77, 289–313.

Alroy, J., 2010. The shifting balance of diversity among major marine animal groups. Science 329, 1191–1194.

Amenábar, C.R., Montes, M., Nozal, M., Santillana, S., 2019. Dinoflagellate cysts of the La Meseta Formation (middle to late Eocene), Antarctic Peninsula: implications for biostratigraphy, palaeoceanography and palaeoenvironment. Geol. Mag. https://doi.org/10.1017/S0016756819000591.

Angel, M.V., 1997. Pelagic biodiversity. In: Ormond, R.F.G., Gage, J.D., Angel, M.V. (Eds.), Marine Biodiversity: Patterns and Processes. University Press, Cambrudge, pp. 35–68.

Archibald, S.B., Bossert, W.H., Greenwood, D.R., Farrell, B.D., 2010. Seasonality, the latitudinal gradient of diversity, and Eocene insects. Paleobiology 36, 374–398.

Arnaud, P.M., 1970. Frequency and ecological significance of necrophagy among the benthic species of Antarctic coastal waters. In: Holdgate, M.W. (Ed.), Antarctic Ecology. 1. Academic Press, London, pp. 259–266.

Arnaud, P.M., 1977. Adaptations within the Antarctic marine benthic ecosystem. In: Llano, G.A. (Ed.), Adaptations within Antarctic Ecosystems. Proceeding of the Third SCAR Symposium on Antarctic Biology. Smithsonian Institution, Washington, D.C., pp. 135–157.

Arntz, W.E., Brey, T., Gallardo, V.A., 1994. Antarctic zoobenthos. Oceanogr. Mar. Biol. Annu. Rev. 32, 241–304.

Arntz, W.E., Gutt, J., Klages, M., 1997. Antarctic marine biodiversity. In: Battaglia, B., Valencia, J., Walton, D.W.H. (Eds.), Antarctic Communities: Species, Structure and Survival. Cambridge University Press, Cambridge, pp. 3–14.

Aronson, R.B., Blake, D.B., 2001. Global climate change and the origin of modern benthic communities in Antarctica. Am. Zool. 41, 27–39.

Aronson, R.B., Thatje, S., Clarke, A., Peck, L.S., Blake, D.B., Wilga, C.D., Seibel, B., 2007. Climate change and invasibility of the Antarctic benthos. Annu. Rev. Ecol. Evol. Syst. 38, 129–154.

Bellwood, D.R., 1996. The Eocene fishes of Monte Bolca: the earliest coral reef fish

assemblage. Coral Reefs 15, 11–19.

Bellwood, D.R., Wainwright, P.C., 2006. The history and biogeography of fishes on coral reefs. In: Sale, P.F. (Ed.), Coral Reef Fishes. Dynamics and Diversity in a Complex Ecosystem. Academic Press, London, pp. 5–32.

Beu, A.G., 2009. Before the ice: biogeography of Antarctic Paleogene molluscan faunas. Palaeogeogr. Palaeoclimatol. Palaeoecol. 284, 191–226.

Bijl, P.K., Schouten, S., Sluijs, A., Reichart, G.-J., Zachos, J.C., Brinkhuis, H., 2009. Early Palaeogene temperature evolution of the Southwest Pacific Ocean. Nature 406, 776–779.

Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D., Grenyer, R., Price, S.A., Vos, R.A., Gittleman, J.L., Purvis, A., 2007. The delayed rise of present day mammals. Nature 446, 507–512.

Bouchet, P., Rocroi, J.-P., 2005. Classification and nomenclator of gastropod families. Malacologia 47, 1–397.

Bouchet, P., Kantor, Y., Sysoev, A., Puillandre, N., 2011. A new operational classification of the Conoidea (Gastropoda). J. Molluscan Stud. 77, 273–308.

Brandt, A., 1991. Zur besiedlungsgeschichte des antarktischen Schelfes am Beispiel der Isopooda (Crustacea, Malacostraca). Ber. Polarforsch. 98, 1–240.

Brandt, A., 1992. Origin of Antarctic Isopoda (Crustacea, Malacostraca). Mar. Biol. 113, 415–423.

Brandt, A., 2000. Hypotheses on Southern Ocean peracarid evolution and radiation (Crustacea, Malacostraca). Antarct. Sci. 12, 269–275.

Brandt, A., Gooday, A.J., Brandão, S.N., Brix, S., Brökeland, W., Cedhagen, T., Choudhury, M., Cornelius, N., Danis, B., De Meseal, I., Diaz, R.J., Gillan, D.C., Ebbe, B., Howe, J.A., Janussen, D., Kaiser, S., Linse, K., Malyutina, M., Pawlowski, J., Raupach, M., Vanreusel, A., 2007a. First insights into the biodiversity and biogeography of the Southern Ocean deep sea. Nature 447, 307–311.

Brandt, A., De Broyer, C., De Mesel, I., Ellingsen, K.E., Gooday, A.J., Hilbig, B., Linse, K., Thomson, M.R.A., Tyler, P.A., 2007b. The biodiversity of the deep Southern Ocean benthos. Philos. Trans. R. Soc. Lond. B 362, 39–66.

Briggs, J.C., 2003. Marine centres of origin as evolutionary engines. J. Biogeogr. 30, 1–18.

Briggs, J.C., 2006. Proximate sources of marine biodiversity. J. Biogeogr. 33, 1–10.

Brown, J.H., 2014. Why are there so many species in the tropics? J. Biogeogr. 41, 8–22.

Buckley, L.B., Davies, T.J., Ackerly, D.D., Kraft, N.J.B., Harrison, S.P., Anacker, B.L., Cornell, H.V., Damschen, E.I., Grytnes, J.-A., Hawkins, B.A., McCain, C.M., Stephens, P.R., McCain, C.M., Stephens, P.R., Wiens, J.J., 2010. Phylogeny, niche conservatism, and the latitudinal diversity gradient in mammals. Proc. R. Soc. B Biol. Sci. 277, 2131–2138.

Bush, A.M., Bambach, R.K., 2015. Sustained Mesozoic-Cenozoic diversification of marine Metazoa: a consistent signal from the fossil record. Geology 43, 979–982.

Carnevale, G., Pietsch, T.W., 2009. An Eocene frogfish from Monte Bolca, Italy: the earliest known skeletal record for the family. Palaeontology 52, 745–752.

Carnevale, G., Bannikov, A.F., Marramà, G., Tyler, J.C., Zorzin, R., 2014. 5. The Pesciara -Monte Postale *Fossil-Lagerstätte*: 2. Fishes and other vertebrates. In: Papazzoni, C.A., Giusberti, L., Carnevale, G., Roghi, G., Bassi, D., Zorzin, R. (Eds.), The Bolca Fossil-Lagerstätten: A Window into the Eocene World. Rendiconti della Società Palaeontologica Italiana 4, pp. 37–63.

Chown, S.L., Gaston, K.J., 2000. Areas, cradles and museums: the latitudinal gradient in species richness. Trends Ecol. Evol. 15, 311–315.

Clarke, A., 1988. Seasonality in the Antarctic marine environment. Comp. Biochem. Physiol. 90B, 461–473.

Clarke, A., 1990. Temperature and evolution: Southern Ocean cooling and the Antarctic marine fauna. In: Kenny, K.R., Hempel, G. (Eds.), Antarctic Ecosystems. Ecological Change and Conservation. Springer-Verlag, Berlin, pp. 9–22.

Clarke, A., 2017. Principles of Thermal Ecology: Temperature, Energy and Life. Oxford University Press.

Clarke, A., Johnston, I.A., 1996. Evolution and adaptive radiation of Antarctic fishes. Trends Ecol. Evol. 11, 212–218.

Clarke, A., Johnston, N.M., 2003. Antarctic marine benthic diversity. Oceanogr. Mar. Biol. Annu. Rev. 41, 47–114.

Collinson, M.E., 2000. Cenozoic evolution of modern plant communities and vegetation. In: Culver, S.J., Rawson, P.F. (Eds.), Biotic Responses to Global Change. The Last 145 Million Years. Cambridge University Press, pp. 223–243.

Condamine, F.L., Sperling, F.A.H., Wahlberg, N., Rasplus, J.-Y., Kergoat, G.J., 2012. What causes latitudinal gradients in species diversity? Evolutionary processes and ecological constraints on swallowtail biodiversity. Ecol. Lett. 15, 267–277.

Condamine, F.L., Rolland, J., Morlon, H., 2013. Macroevolutionary perspectives to environmental change. Ecol. Lett. 16, 72–85.

Cossmann, M., Pissarro, G., 1904–13. Monographie complete de coquilles fossils de l'Éocène des environs de Paris. In: Paris. 2 vols.

Crame, J.A., 2013. Early Cenozoic differentiation of polar marine faunas. PLoS One 8, e54139.

Crame, J.A., 2018. Key stages in the evolution of the Antarctic marine fauna. J. Biogeogr. 45, 986–994.

Crame, J.A., 2019. Paleobiological significance of the James Ross Basin. Adv. Polar. Sci. 30, 186–198.

Crame, J.A., Beu, A.G., Ineson, J.R., Francis, J.E., Whittle, R.J., Bowman, V.C., 2014. The early origin of the Antarctic marine fauna and its evolutionary implications. PLoS One 9, e114743.

Crame, J.A., McGowan, A.J., Bell, M.A., 2018. Differentiation of high-latitude and polar marine faunas in a greenhouse world. Global Ecol. Biogeog. 27, 518–537.

Crampton, J.S., Cody, R.D., Levy, R., Harwood, D., McKay, R., Naish, T.R., 2016. Southern Ocean phytoplankton turnover in response to stepwise Antarctic cooling over the past 15 million years. Proc. Natl. Acad. Sci. U. S. A. 113, 6868–6873.

Culver, S.J., Buzas, M.A., 2000. Global latitudinal species diversity gradient in deep-sea benthic foraminifera. Deep-Sea Research I 47, 259–275.

Dam, G., Pedersen, G.K., Sønderholm, M., Midtgaard, H., Larsen, L.M., Nøhr-Hansen, H., Pedersen, A.K., 2009. Lithostratigraphy of the Cretaceous – Paleocene Nuussuaq Group, Nuussuaq Basin, West Greenland. Bull. Geol. Surv. Den. Greenl. 19, 1–171.

Dayton, P.K., 1990. Polar benthos. In: Smith, W.O. (Ed.), Polar Oceanography, Part B: Chemistry, Biology and Geology. Academic Press, London, pp. 631–685.

De Broyer, C., Jazdzewski, K., 1996. Biodiversity of the Southern Ocean: towards a new synthesis for the Amphipoda (Crustacea). Bull. Mus. Civ. St. nat. Verona 20, 547–568.

De Broyer, C., Jazdzewski, K., Dauby, P., 2003. Biodiversity of the Southern Ocean: Lessons from Crustacea. In: Huiskes, A.H.L., Gieskes, W.W.C., Rozema, R.M.L., Schorno, S.M., Van der Vies, S.M., Wolff, W.J. (Eds.), Antarctic Biology in a Global Context. Backhuys, Leiden, pp. 201–214.

Dell, R.K., 1972. Antarctic benthos. Adv. Mar. Biol. 10, 1–216.

D'Hondt, S., 2005. Consequences of the Cretaceous/Paleogene mass extinction for marine ecosystems. Annu. Rev. Ecol. Evol. Syst. 36, 295–317.

Dockery III, D.T., Lozouet, P., 2003. Molluscan faunas across the Eocene/Oligocene boundary in the North American Gulf Coastal Plain, with comparisons to those of the Eocene and Oligocene of France. In: Prothero, D.R., Ivany, L.C., Nesbitt, E.A. (Eds.), From greenhouse to Icehouse. The marine Eocene – Oligocene transition. Columbia University Press, New York, pp. 303–340.

Douglas, P.M.J., Affek, H.P., Ivany, L.C., Houben, A.J.P., Sijp, W.P., Sluijs, A., Schouten, S., Pagani, M., 2014. Pronounced zonal heterogeneity in Eocene southern high-latitude sea surface temperatures. Proc. Natl. Acad. Sci. U. S. A. 111, 6582–6587.

Ducklow, H.W., Baker, K., Martinson, D.G., Quetin, L.B., Ross, R.M., Smith, R.C., Stammerjohn, S.E., Vernt, M., Fraser, W., 2007. Marine pelagic ecosystems: the West Antarctic Peninsula. Philos. Trans. R. Soc. B 362, 67–94.

Dynesius, M., Jansson, R., 2000. Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. Proc. Natl. Acad. Sci. 97, 9115–9120.

Eastman, J.T., 2000. Antarctic notothenioid fishes as subjects for research in evolutionary biology. Antarct. Sci. 12, 276–287.

Eastman, J.T., 2005. The nature of the diversity of Antarctic fishes. Polar Biol. 28, 93–107.

Eastman, J.T., Grande, L., 1991. Late Eocene gadiform (Teleostei) skull from Seymour Island, Antarctic Peninsula. Antarct. Sci. 3, 87–95.

Erwin, D.H., 2009. Climate as a driver of evolutionary change. Curr. Biol. 19, R575–R583.

Feng, Y.-J., Blackburn, D.C., Liang, D., Hillis, D.M., Wake, D.B., Cannatella, D.C., Zhang, P., 2017. Phylogenomics reveals rapid, simultaneous diversification of three major clades of Gondwanan frogs at the Cretaceous – Paleogene boundary. Proc. Natl. Acad. Sci. U. S. A. 114, E5864–E5870.

Fenton, I.S., Pearson, P.N., Dunkley Jones, T., Farnsworth, A., Lunt, D.J., Markwick, P., Purvis, A., 2016. The impact of Cenozoic cooling on assemblage diversity in planktonic foraminifera. Philos. Trans. R. Soc. B 371, 20150224.

Fine, P.V.A., 2015. Ecological and evolutionary drivers of geographic variation in species diversity. Annu. Rev. Ecol. Evol. Syst. 46, 369–392.

Fine, P.V.A., Ree, R.H., 2006. Evidence for time-integrated species-area effect on the latitudinal gradient in tree diversity. Am. Nat. 168, 796–804.

Flessa, K.W., Jablonski, D., 1996. The geography of evolutionary turnover: A global analysis of extant bivalves. In: Jablonski, D., Erwin, D.H., Lipps, J.H. (Eds.), Evolutionary Paleobiology. University of Chicago Press, pp. 376–397.

Friedman, M., Carnevale, G., 2018. The Bolca Lagerstätten: shallow marine life in the Eocene. J. Geol. Soc. Lond. 175, 569–579.

Friedman, M., Beckett, H.T., Close, R.A., Johanson, Z., 2016. The English Chalk and London Clay: Two remarkable British bony fish Lagerstätten. In: Johanson, Z., Barrett, P.M., Richter, M., Smith, M. (Eds.), Arthur Smith Woodward: His Life and Influence on Modern Vertebrate Palaeontology. 430. pp. 165–200 Geological Society, London, Special Publications.

Gaston, K.J., 2000. Global patterns in biodiversity. Nature 405, 220–227.

Gély, J.-P., 2008. La stratigraphie et la paléogeographie du Lutétien en France. In: Merle, D. (Ed.), Stratotype Lutétien. Museum National d'Histoire Naturelle Paris. Biotope Mèze, BRGM, Orléans, pp. 76–104.

Gillman, L.W., Wright, S.D., 2014. Species richness and evolutionary speed: the influence of temperature, water and area. J. Biogeogr. 41, 39–51.

Greenwood, D.R., Wing, S.L., 1995. Eocene continental climates and latitudinal temperature gradients. Geology 23, 1044–1048.

Grimson, F., Pedersen, G.K., Grimm, G.W., Zetter, R., 2016. A revised stratigraphy for the Paleocene Agatdalen flora (Nuussuaq Peninsula, western Greenland): correlating fossiliferous outcrops, macrofossils, and palynological samples from phosphoritic nodules. Acta Palaeobot. 56, 307–327.

Harnik, P.G., Jablonski, D., Krug, A.Z., Valentine, J.W., 2010. Genus age, provincial area and the taxonomic structure of marine faunas. Proc. R. Soc. B Biol. Sci. 277, 3427–3435.

Harrington, G.J., 2004. Structure of the north American vegetation gradient during the late Paleocene/early Eocene warm climate. Evol. Ecol. Res. 6, 33–48.

Harzhauser, M., Piller, W.E., Steininger, F.F., 2002. Circum-Mediterranean Oligo-Miocene biogeographic evolution – the gastropods' eye view. Palaeogeogr. Palaeoclimatol. Palaeoecol. 183, 103–133.

Harzhauser, M., Mandic, O., Piller, W., Reuter, M., Kroh, A., 2008. Tracing back the origin of the Indo-Pacific mollusc fauna: basal Tridacninae from the Oligocene and Miocene of the Sultanate of Oman. Palaeontology 51, 199–213.

Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo, C.A., Soeller, S.A., 2006. Post-Eocene climate change,niche conservatism, and the latitudinal diversity gradient of New World birds. J. Biogeogr. 33, 770–780.

Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo, C.A., Soeller, S.A., 2007. Climate, niche conservatism, and the global bird diversity gradient. Am. Nat. 170, S16–S27.

Hillebrand, H., 2004. On the generality of the latitudinal diversity gradient. Am. Nat. 163, 195–211.

Houben, A.J.P., Bijl, P.K., Pross, J., Bohaty, S.M., Passchier, S., Stickley, C.E., Röhl, U., Sugisaki, S., Tauxe, L., van der Flierdt, T., Olney, M., Sangiorgi, F., Sluijs, A., Escutia, C., Brinkhuis, H., the Expedition 318 Scientists, 2013. Reorganization of Southern Ocean plankton ecosystem at the onset of Antarctic glaciation. Science 340, 341–344.

Huang, S., Roy, K., Jablonski, D., 2014. Do past climate states influence diversity dynamics and the present-day latitudinal diversity gradient? Global Ecol. Biogeog. 23, 530–540.

Huyghe, D., Merle, D., Lartaud, F., Cheype, E., Emmanuel, l., 2012. Middle Lutetian climate in the Paris Basin: implications for a marine hotspot of paleobiodiversity. Facies 58, 587–604.

Huyghe, D., Lartaud, F., Emmanuel, L., Merle, D., Renard, M., 2015. Palaeogene climate evolution in the Paris Basin from oxygen stable isotope (δ^{18}O) compositions of marine molluscs. J. Geol. Soc. Lond. 172, 576–587.

Ivany, L.C., Lohmann, K.C., Hasiuk, F., Blake, D.B., Glass, A., Aronson, R.B., Moody, R.M., 2008. Eocene climate record of a high southern latitude continental shelf: Seymour Island, Antarctic Peninsula. Bull. Geol. Soc. Am. 120, 659–678.

Jablonski, D., 1993. The tropics as a source of evolutionary novelty: the post-Palaeozoic fossil record of marine invertebrates. Nature 364, 142–144.

Jablonski, D., 2005a. Evolutionary innovations in the fossil record: the intersection of ecology, development, and macroevolution. J. Exp. Biol. 304B, 504–519.

Jablonski, D., 2005b. Mass extinctions and macroevolution. Paleobiology 31, 192–210.

Jablonski, D., Roy, K., Valentine, J.W., 2006. Out of the Tropics: Evolutionary dynamics of the latitudinal diversity gradient. Science 314, 102–106.

Jablonski, D., Belanger, C.L., Berke, S.K., Huang, S., Krug, A.Z., Roy, K., Tomasovych, A., Valentine, J.W., 2013. Out of the tropics, but how? Fossils, bridge species, and thermal ranges in the dynamics of the marine latitudinal diversity gradient. Proc. Natl. Acad. Sci. U. S. A. 110, 10487–10494.

Jablonski, D., Huang, S., Roy, K., Valentine, J.W., 2017. Shaping the latitudinal diversity gradient: New perspectives from a synthesis of paleobiology and biogeography. Am. Nat. 189, 1–12.

Jansson, R., Rodriguez-Castañeda, G., Harding, L.E., 2013. What can multiple phylogenies say about the latitudinal diversity gradient? A new look at the tropical conservatism, out of the tropics, and diversification hypotheses. Evolution 67 (6), 1741–1755.

Jaramillo, C., Cárdenas, A., 2013. Global warming and neotropical rainforests: a historical perspective. Annu. Rev. Earth Planet. Sci. 41, 741–766.

Jaramillo, C.A., Dilcher, D.L., 2000. Microfloral diversity patterns of the late Paleocene – Eocene interval in Colombia, northern South America. Geology 28, 815–818.

Jaramillo, C., Rueda, M.J., Mora, G., 2006. Cenozoic plant diversity in the Neotropics. Science 311, 1893–1896.

Jardine, P.E., Harrinton, G., Sessa, J.A., Daškova, J., 2018. Drivers and constraints on floral latitudinal diversification gradients. J. Biogeogr. 45, 1408–1419.

Kafanov, A.I., 2001. Cenozoic *Papyridea* (Bivalvia: Cardiidae) and the problem of diversification of the epicontinental tropical marine biotas. Bull. Russ. Far East Malac. Soc. 5, 5–38.

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

Kohn, A.J., 1997. Why are coral reef communities so diverse? In: Ormond, R.F.G., Gage, J.D., Angel, M.V. (Eds.), Marine Biodiversity: Patterns and Processes. Cambridge University Press, pp. 201–215.

Kollmann, H.A., Peel, J.S., 1983. Paleocene gastropods from Nûgssuaq, West Greenland. Grønl. Geol. Unders. 146, 1–115.

Kriwet, J., 2005. Additions to the Eocene selachian fauna of Antarctica with comments on Antarctic selachian diversity. J. Vertebr. Paleontol. 25, 1–7.

Krug, A.Z., Jablonski, D., 2012. Long-term origination rates are reset only at mass extinctions. Geology 40, 731–734.

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

Lauridsen, B.W., Schnetler, K.I., 2014. A catalogue of Danian gastropods from the Baunekule Facies, Faxe Formation. Denmark. Bull. Geol. Surv. Den. Greenl. 32, 1–117.

Lomolino, M.V., Riddle, B.R., Whittaker, R.J., Brown, J.H., 2010. Biogeography, fourth ed. Sinauer, Sunderland, MA.

Long, D.J., 1992. An Eocene wrasse (Perciformes: Labridae) from Seymour Island. Antarct. Sci. 4, 235–237.

Lörz, A.-N., Held, C., 2004. A preliminary molecular and morphological phylogeny of the Antarctic Epimeriidae and Iphimediidae (Crustacea, Amphipoda). Mol. Phylogenet. Evol. 31, 4–15.

Magurran, A.E., 2004. Measuring Biological Diversity. Blackwell, Oxford.

Mannion, P.D., Upchurch, P., Benson, R.B.J., Goswami, A., 2014. The latitudinal diversity gradient through deep time. Trends Ecol. Evol. 29, 42–50.

Marramà, G., Carnevale, G., Engelbrecht, A., Claeson, K.M., Zorzin, R., Fornasiero, M., Kriwet, J., 2018. A synoptic review of the Eocene (Ypresian) cartilaginous fishes Chondrichthyes: Holocephali, Elasmobranchii of the Bolca Konservat-Lagerstätte, Italy. Pal. Zeitschr. 92, 283–313.

Matthews, T.J., Whittaker, R.J., 2014. Fitting and comparing competing models of the species abundance distribution: assessment and prospect. Front. Biogeog. 6, 67–82.

May, R.M., 1975. Patterns of species abundance and diversity. In: Cody, M.L., Diamond, J.M. (Eds.), Ecology and Evolution of Communities. Belknap Press, Cambridge, MS, pp. 81–120.

McClintock, J.B., 1994. Trophic biology of Antarctic shallow-water echinoderms. Mar. Ecol. Prog. Ser. 111, 191–202.

McKenna, D.D., Farrell, B.D., 2006. Tropical forests are both evolutionary cradles and museums of leaf beetle diversity. Proc. Natl. Acad. Sci. U. S. A. 103, 10947–10951.

Meredith, R.W., Janečka, J.E., Gatesy, J., Ryder, O.A., Fisher, C.A., Teeling, E.C., Goodbla, A., Eizirik, E., Simão, T.L.L., Stadler, T., Rabosky, D.L., Honeycutt, R.L.,

Flynn, J.J., Ingram, C.M., Steiner, C., Williams, T.L., Robinson, T.J., Burk-Herrick, A., Westerman, M., Ayoub, N.A., Springer, M.S., Murphy, W.J., 2011. Impacts of the Cretaceous terrestrial revolution and KPg extinction on mammal diversification. Science 334, 521–524.

Merle, D., 2008. Le Lutétien du basin de Paris: Un example de point-chaud de la paléobiodiversité In: Merle, D. (Ed.), Stratotype Lutétien. Museum National d'Histoire Naturelle Paris. Biotope Mèze, BRGM, Orléans, pp. 76–104.

Mittelbach, G.G., Schemske, D.W., Cornell, H.V., Allen, A.P., Brown, J.M., Bush, M.B., Harrison, S.P., Hurlbert, A.H., Knowlton, N., Lessios, H.A., McCain, C.M., McCune, A.R., McDade, L.A., McPeek, M.A., Near, T.J., Price, T.D., Ricklefs, R.E., Roy, K., Sax, D.F., Schluter, D., Sobel, J.M., Turelli, M., 2007. Evolution and the latitudinal diversity gradient: Speciation, extinction and biogeography. Ecol. Lett. 10, 315–331.

Morley, R.J., 2007. Cretaceous and Tertiary climate change and the past distribution of megathermal rainforests. In: Bush, M.B., Flenley, J.R. (Eds.), Tropical Rainforest Responses to Climatic Change. Springer, Berlin, pp. 1–31.

Murphy, E.J., Cavanagh, R.D., Drinkwater, K.F., Grant, S.M., Heymans, J.J., Hofmann, E.E., Hunt Jr., G.L., Johnston, N.M., 2016. Understanding the structure and functioning of polar pelagic ecosystems to predict the impacts of change. Proc. R. Soc. B 283, 20161646.

Near, T.J., 2004. Estimating divergence times of notothenioid fishes using a fossil-calibrated molecular clock. Antarct. Sci. 16, 37–44.

Near, T.J., Dornburg, A., Kuhn, K.L., Eastman, J.T., Pennington, J.N., Patarnello, T., Zane, L., Fernández, D.A., Jones, C.D., 2013. Ancient climate change, antifreeze, and the evolutionary diversification of Antarctic fishes. Proc. Natl. Acad. Sci. U. S. A. 109, 3434–3439.

Nicol, D., 1967. Some characteristics of cold-water marine pelecypods. J. Paleontol. 41, 1330–1340.

Norris, R.D., Kirtland Turner, S., Hull, P.M., Ridgwell, A., 2013. Marine ecosystem responses to Cenozoic global change. Science 341, 492–498.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., Wagner, H., 2016. vegan: Community Ecology Package. R package version 2 4–0.

Pacaud, J.M., Le Renard, J., 1995. Révision des Mollusques paléogènes du basin de Paris. IV – Liste systématique actualisée. Cossmanniana 3, 151–187.

Pearse, J.S., 1965. Reproductive periodicities in several contrasting populations of *Odontaster validus*, a common Antarctic asteroid. In: Llano, G.A. (Ed.), Ant. Res. Ser. Biology of the Antarctic Seas II. American Geophysical Union, Washington, D.C, pp. 39–85.

Petersen, G.H., Vedelsby, A., 2000. An illustrated catalogue of the Paleocene Bivalvia from Nuussuaq, Northwest Greenland: their paleoenvironments and the paleoclimate. Steenstrupia 25, 25–120.

Piccoli, G., Sartori, S., Franchino, A., 1987. Benthic molluscs of shallow Tethys and their destiny. In: McKenzie, K.G. (Ed.), Shallow Tethys. 2. Balkema, Rotterdam, pp. 332–373.

Pross, J., Contreras, L., Bijl, P.K., Greenwood, D.R., Bohaty, S.M., Schouten, S., Bendle, J.A., Röhl, U., Tauxe, L., Raine, J.I., Huck, C.E., van der Flierdt, T., Jamieson, S.R., Stickley, C.E., van de Schootbrugge, B., Escutia, C., Brinkhuis, H., Integrated Ocean Drilling Program Expedition 318 Scientists, 2012. Persistent near-tropical warmth on the Antarctic continent during the early Eocene epoch. Nature 488, 73–77.

Rabosky, D.L., Chang, J., Title, P.O., Cowman, P.F., Sallan, L., Friedman, M.F., Kaschner, K., Garilao, C., Near, T.J., Coll, M., Alfaro, M., 2018. An inverse latitudinal gradient in speciation rate for marine fishes. Nature 559, 392–398.

Ramirez, R., Gravendeel, B., Singer, R.B., Marshall, C.R., Pierce, N.E., 2007. Dating the origin of the Orchidaceae from a fossil orchid with its pollinator. Nature 448, 1042–1045.

Raup, D.M., Jablonski, D., 1993. Geography of end-Cretaceous marine bivalve extinctions. Science 260, 971–973.

Regeuro, M.A., Marenssi, S.A., Santillana, S.N., 2002. Antarctic Peninsula and South America (Patagonia) Paleogene terrestrial faunas and environments: biogeographic relationships. Palaeogeogr. Palaeoclimatol. Palaeoecol. 179, 189–210.

Reguero, M.A., 2019. Antarctic paleontological heritage: late Cretaceous – Paleogene vertebrates from Seymour (Marambio) Island, Antarctic Peninsula. Adv. Polar. Sci. 30, 328–355.

Reguero, M.A., Marenssi, S.A., Santillana, S.N., 2012. Weddellian marine/coastal vertebrates diversify from a basal horizon (Ypresian, Eocene) of the *Cucullaea* 1 Allomember, La Meseta Formation, Seymour (Marambio) Island, Antarctica. Rev. Peru. Boll. 19, 275–284.

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

Ricklefs, R.E., 2010. Evolutionary diversification, coevolution between populations and their antagonists, and the filling of niche space. Proc. Natl. Acad. Sci. U. S. A. 107, 1265–1272.

Rose, P.J., Fox, D.L., Marcot, J., Badgley, C., 2011. Flat latitudinal gradient in Paleocene mammal richness suggests decoupling of climate and biodiversity. Geology 39, 163–166.

Rosenzweig, M.L., 1995. Species Diversity in Space and Time. Cambridge University Press.

Scher, H.D., Whittaker, J.M., Williams, S.E., Latimer, J.C., Kordesch, W.E.C., Delaney, M.L., 2015. Onset of Antarctic Circumpolar Current 30 million years ago as Tasmanian Gateway aligned with westerlies. Nature 523, 580–583.

Schnetler, K.I., 2001. The Selandian (Paleocene) mollusc fauna from Copenhagen, Denmark: the Poul Harder 1920 collection. Bull. Geol. Surv. Den. 37, 1–85.

Schuettpelz, E., Pryer, K.M., 2009. Evidence for a Cenozoic radiation of ferns in an angiosperm-dominated canopy. Proc. Natl. Acad. Sci. U. S. A. 106, 11200–11205.

Schultz, T.R., Brady, S.G., 2008. Major evolutionary transitions in ant agriculture. Proc. Natl. Acad. Sci. U. S. A. 105, 5435–5440.

Sepkoski, J.J., 2002. A compendium of fossil marine animal genera. Bull. Am. Paleont. 363, 1–563.

Stanley, S.M., 2007. An analysis of the history of marine animal diversity. Paleobiology, Suppl. 33, 1–55.

Taylor, J.D., 1981. The evolution of predators in the late Cretaceous and their ecological significance. In: Forey, P.L. (Ed.), The Evolving Biosphere. British Museum (Natural History), London, Cambridge University Press, Cambridge, pp. 229–240.

Taylor, J.D., Taylor, C.N., 1977. Latitudinal distribution of predatory gastropods on the eastern Atlantic shelf. J. Biogeogr. 4, 73–81.

Taylor, J.D., Morris, N.J., Taylor, C.N., 1980. Food specialization and the evolution of predatory prosobranch gastropods. Palaeontology 23, 375–409.

Thomas, E., 2007. Cenozoic mass extinctions in the deep sea: what perturbs the largest habitat on Earth? Geol. Soc. Am. Spec. Pap. 424, 1–23.

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., Vanden Berghe, E., Worm, B., 2010. Global patterns and predictions of marine biodiversity across taxa. Nature 466, 1098–1103.

Tobin, T.S., Ward, P.D., Steig, E.J., Olivero, E.B., Hilburn, I.A., Mitchell, R.N., Diamond, M.R., Raub, T.D., Kirschvink, J.L., 2012. Extinction patterns, $\delta^{18}O$ trends, and magnetostratigraphy from a southern high-latitude Cretaceous – Paleogene section: Links with Deccan volcanism. Palaeogeogr. Palaeoclimatol. Palaeoecol. 350–352, 180–188.

Turner, J.R.G., Lennon, J.J., Greenwood, J.J.D., 1996. Does climate cause the global biodiversity gradient? In: Hochberg, M.E., Clobert, J., Barbault, R. (Eds.), Aspects of the Genesis and Maintenance of Biological Diversity. Oxford University Press, pp. 199–220.

Valentine, J.W., 1973. Evolutionary Paleoecology of the Marine Biosphere. Prentice-Hall, Englewood Cliffs, N.J.

Valentine, J.W., 1983. Seasonality: Effects in marine benthic communities. In: Tevesz, M.J.S., McCall, P.L. (Eds.), Biotic Interactions in Recent and Fossil Benthic Communities. Plenum Press, New York, pp. 121–156.

Valentine, J.W., Jablonski, D., 2015. A twofold role for global energy gradients in marine biodiversity trends. J. Biogeogr. 42, 997–1005.

Valentine, J.W., Roy, K., Jablonski, D., 2002. Carnivore/non-carnivore ratios in northeastern Pacific marine gastropods. Mar. Ecol. Prog. Ser. 228, 153–163.

Valentine, J.W., Jablonski, D., Krug, A.Z., Roy, K., 2008. Incumbency, diversity, and latitudinal gradients. Paleobiology 34, 169–178.

Vázquez, D.P., Stevens, R.D., 2004. The latitudinal gradient in niche breadth. Am. Nat. 164, E1–19.

Vermeij, G.J., 2001. Community assembly in the sea. Geologic history of the living shore biota. In: Bertness, M.D. (Ed.), Community Assembly in the Sea. Sinauer, pp. 39–60.

White, M.G., 1984. Marine benthos. In: Laws, R.M. (Ed.), Antarctic Ecology. 2. Academic Press, London, pp. 421–461.

Wiens, J.J., Donoghue, M.J., 2004. Historical biogeography, ecology and species richness. Trends Ecol. Evol. 19, 639–644.

Wilson, G.D.F., 1998. Historical influences on deep-sea isopod diversity in the Atlantic Ocean. Deep-Sea Res. II 45, 279–301.

Witts, J.D., Whittle, R.J., Wignall, P.B., Crame, J.A., Francis, J.E., Newton, R.J., Bowman, V.C., 2016. Macrofossil evidence for a rapid and severe Cretaceous – Paleogene mass extinction in Antarctica. Nat. Comms. 7, 11738.

Wolfe, J.A., 1985. Distribution of major vegetation types during the Tertiary. In: Sundquist, E.T., Broeker, W.S. (Eds.), The Carbon Cycle and Atmospheric CO_2: Natural Variations Archean to Present. Geophys, Monogr. AGU, pp. 357–375.

Worm, B., Tittensor, D.P., 2018. A Theory of Global Biodiversity. Princeton University Press.

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

Zachos, J.C., Dickens, G.R., Zeebe, R.E., 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. Nature 451, 279–283.

Zinsmeister, W.J., Feldmann, R.M., Woodburne, M.O., Elliot, D.H., 1989. Latest Cretaceous/earliest Tertiary transition on Seymour Island, Antarctica. J. Paleontol. 63, 731–738.