

A twofold role for global energy gradients in marine biodiversity trends

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ABSTRACT

Explanations for major biodiversity patterns have not achieved a consensus, even for the latitudinal diversity gradient (LDG), but most relate to patterns of solar energy influx into Earth systems, and its effects on temperature (as biochemical activity rates are temperature sensitive) and photosynthesis (which drives nearly all of the productivity that fuels ecosystems). Marine systems break some of the confounding correlations among temperature, latitude and biodiversity that typify the terrestrial systems that have dominated theoretical discussions and large-scale analyses. High marine diversities occur not only in warm shallow seas where productivity may be either low or high, depending on regional features, but also in very cold deep-sea regions, indicating that diversity is promoted by stability in temperature and in trophic resources (nutrients and food items), and more specifically by their interaction, rather than by high mean values of either variable. The common association of high diversity with stable but low to moderate annual productivity suggests that ecological specialization underlies the similarly high diversities in the shallow tropics and deep sea. Recent work on shallow-marine bivalves is consistent with this view of decreasing specialization in less stable habitats. Lower diversities in shallow seas are associated with either high thermal seasonality (chiefly in temperate latitudes) or highly seasonal trophic supplies (at any latitude), which exclude species that are adapted to narrow ranges of those variables.

Keywords

Continental shelves, deep sea, latitudinal diversity gradient, productivity, seasonality, stability, temperature.

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INTRODUCTION

The energy that sustains most life on Earth today radiates from the Sun as photons, quanta of thermal energy that provide a (nearly) stable energy flux. As the Earth is a spinning spheroid, more solar radiation arrives near the Earth's equator than near the poles, forming a latitudinal energy gradient (LEG) within each polar hemisphere. But as Earth's declination is near 23.5° to the incoming photon stream, the LEG exhibits a significant seasonal cycle. Today, macroscopic life in terrestrial biomes and in the shallow sea is an order of magnitude more diverse in terms of species numbers, and appears to be more richly organized, in equatorial regions than in polar ones (Hillebrand, 2004; Mittelbach *et al.*, 2007; Schemske *et al.*, 2009). This latitudinal diversity gradient (LDG), peaking in low latitudes and declining

towards each pole (for example Fig. 1), is thus positively correlated with the LEG. Here we suggest that marine systems break the correlations among latitude, temperature and diversity that typify terrestrial settings, and so allow renewed consideration of factors that govern the origin and maintenance of large-scale diversity patterns. Most strikingly, deep-sea benthic habitats are cold but species-rich, and thus fall outside the temperature–productivity–diversity relationships that characterize both shallow-sea and terrestrial systems (e.g. Valentine, 2009 on shallow seas; Gillman *et al.*, 2014 on terrestrial systems). Clearly, any comprehensive theory of biodiversity must account for high diversity on both the tropical west Pacific shelves and bathyal seafloors. At first glance it is difficult to imagine two more different marine biomes, but we argue that their commonalities are key.

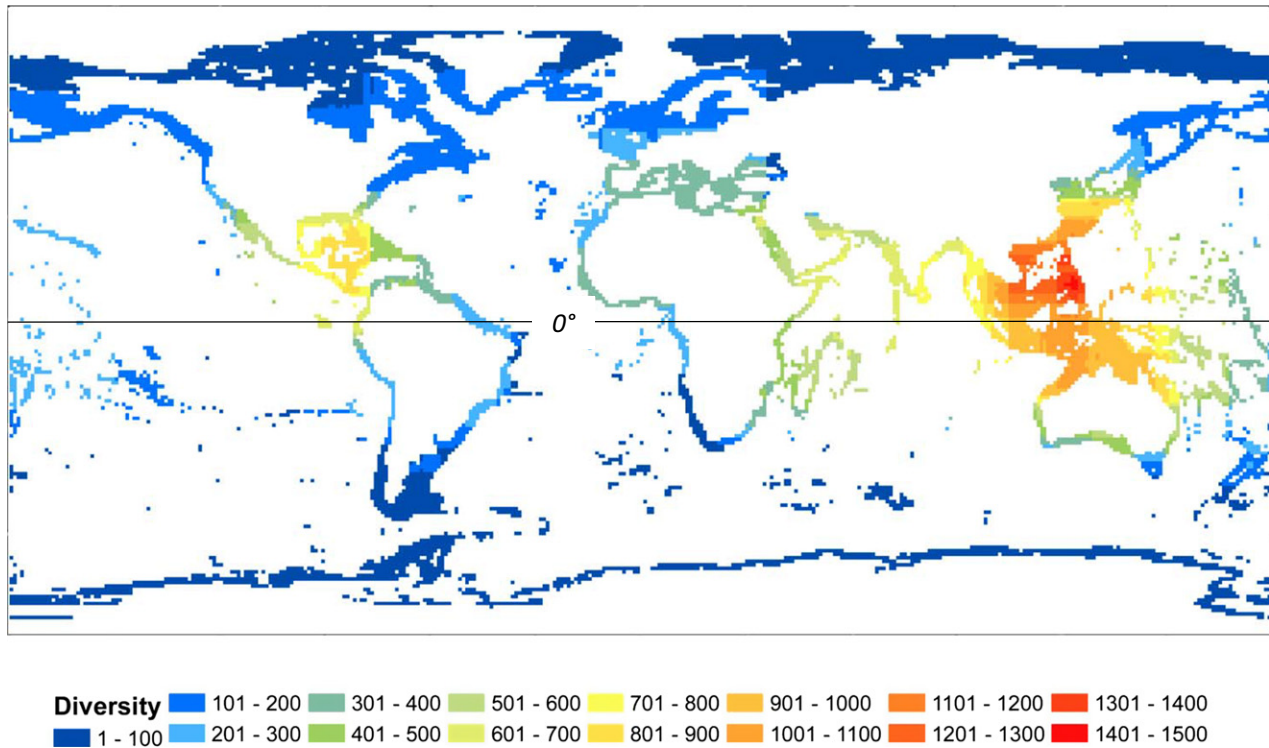


Figure 1 Bivalve species diversity at shelf depths in the world ocean (< 200 m) found in grid cells of 1°. Although based on a single class, species collecting records for this group have been taxonomically standardized, and their global diversity trends are representative of standing benthic invertebrate diversity trends reported for shelf faunas in general. Note latitudinal gradients along coastlines, and longitudinal gradients in the tropics; both of those gradients are related to variations in seasonality of trophic resources and of sea-surface temperatures (see text). After Belanger *et al.* (2012).

THE TWO PRIMARY BIOTIC EFFECTS OF THE LEG

Today solar energy has two important effects on the evolution and distribution of life that must date from deep in geological history. One effect is the pattern of radiant heating of the biosphere, for the metabolic activities of organisms are sensitive to temperature. The second is the support of oxygenic photosynthesis, which fuels productivity and thus energy flux through most ecosystems. Both of these features, thermal and photochemical, are clearly of basic importance in the evolution and distribution of multicellular organisms, and each has been hypothesized to be the primary factor in the origin and maintenance of the LDG. The same pattern of incoming solar energy drives both effects, but each fosters different biotic patterns. These differences arise largely because the chief contributions of each to the functioning of the biosphere (heat and primary production) are distributed differently within Earth systems. In the shallow sea, temperature is highest at low latitudes but productivity is highest at the higher mid-latitudes. Each climate zone and each marine province is characterized by a different combination of temperature and productivity (Tittensor *et al.*, 2010; Belanger *et al.*, 2012), and the interaction of those factors is likely to be important in understanding the major effects of the LEG

on the LDG. For convenience we refer to adaptation to those factors in terms of niches, thermal and trophic, respectively.

Marine temperatures and diversity

Temperature is clearly implicated in the regulation of modern marine diversity. Marine thermal patterns are basic to the processes associated with oceanic circulation, and themselves help drive the oceanic currents that transport heat across the globe. Temperature acts as a major limiting factor on species distributions, partly by setting time-dependent temperature limits for vital functions and by coordinating the many different chemical reaction rates that control metabolism; the evolutionary processes that respond to these factors produce species' tolerances and optima (see Brown, 2014). Diversity patterns observed in the shallow sea (habitats from the intertidal zone to near 200 m in depth, encompassing the continental shelves) suggest a close fit between climate and diversity in both space and time (Erwin, 2009). Indeed, correlation of both species and genus diversities to sea-surface temperatures (SSTs) in the modern shallow sea is stronger than for any other physical variable yet tested (Tittensor *et al.*, 2010; Belanger *et al.*, 2012), linking the shallow LDGs in some way to thermal aspects of the LEG and their climatic consequences. The geographical

boundaries between the biotic provinces of the world's continental shelves are also strongly tied to regions of marked change in annual SSTs (Belanger *et al.*, 2012), indicating that marine provinciality and thus thermal niche boundaries are primarily related to the geography of marine thermal structure, or to a common cause. Finally, solar radiation ensures that surface water layers, where undisturbed by upwelling currents, are warmer and less dense than deeper waters, with minor exceptions chiefly owing to salinity (Stutut *et al.*, 2012). The shallow ocean thus becomes stratified, most effectively so where SSTs are highest and the temperature – and therefore density difference – between surface and deeper waters is greatest. This stratification promotes stability within the shallow water column, inhibiting vertical water motion and tending to stabilize productivity in the euphotic zone (the upper regions of the water column in which light penetration is sufficient for production, a characteristic of the shallow sea).

At the Earth's surface the LEG is characterized not only by the latitudinal gradient of radiation intensity, but by a gradient in the seasonality of that radiation, low in the tropics but increasing from tropical into middle latitudes, where broader thermal niches are required to weather the seasonal changes. At still higher latitudes seasonality in marine SST narrows again, the lower temperature is capped at freezing, and narrower (but cooler) thermal niches are again permitted.

In today's oceans, with extensive north–south continental coastlines creating barriers to east–west circulation, the warmer lateral limbs of the ocean gyres that bracket the equator occur along the western boundaries of the ocean basins (Stommel, 1948). Shelves and islands washed by those western boundary currents and their offshoots, in which the thermocline is deep and the upper water column relatively stable, are the regions of highest metazoan diversity in today's shallow seas, most strikingly in the tropical West Pacific (Fig. 1). It is thus possible to argue (as in Brown, 2014 and references therein) that latitudinal diversity is explained by climatic control of thermal kinetics, that the faster biochemical reactions at warmer temperatures create high levels of metabolism and may involve high mutation rates that could drive higher evolutionary rates and permit high levels of diversity accumulation. Brown epitomizes this situation as 'the Red Queen runs faster when she is hot'. It is not clear why the accumulation of diversity follows, however, rather than, for example, a corresponding ramping up of negative ecological interactions to damp speciation or elevate extinction rates.

Many hypotheses for the causes of the LDG have involved biogeographical responses to mean annual temperature and its seasonality. One of the more interesting and enduring of those suggestions was championed by Stevens (1989), who dubbed it Rapoport's rule. Stevens posited that as terrestrial and marine species must have increasingly larger thermal niches in more variable higher latitudes, they should also tend to have wider latitudinal ranges there. Thus in lower

latitudes, where species have narrower thermal niches, more species may be supported within a given region because their smaller latitudinal ranges reduce overlaps between species and permit higher regional diversities without increasing species densities and therefore competition. However, in the shallow sea, this predicted pattern was not found for bivalve and gastropod species (Roy *et al.*, 1994, 1998), and results are mixed for teleost fishes (Rohde *et al.*, 1993; Mora & Robertson, 2005; Fortes & Absalão, 2010). Furthermore, although the marine seasonal temperature range at high poleward latitudes is actually narrower than in temperate latitudes, diversity also declines along the LDG there towards the poles.

An important missing element in the formulation of Rapoport's rule is the actual pattern of shallow-sea temperatures. The relationship between marine temperature range varies nonlinearly with latitude (Jablonski *et al.*, 2013; Tomašových *et al.*, 2015). Latitudinal variation in SSTs is very low near the equator, especially along coastlines bathed in western boundary currents. As a result, many species in tropical waters have narrow thermal but broad latitudinal ranges, because the narrow temperature ranges to which they are adapted are latitudinally widespread there. Accordingly, tropical species commonly have wider latitudinal ranges than temperate ones and Rapoport's rule breaks down (see Gaston & Chown, 1999), although the relationships between water temperature variation and thermal niche width with latitude that led Stevens to define the rule (i.e. tropical species tolerate a narrower range of temperature than do temperate ones) evidently do hold for those regions. Clearly, Rapoport's rule only works well where latitudinal temperature seasonality varies linearly with latitude.

Marine productivity and diversity

Photosynthetic productivity has also been suggested as a major factor in regulating marine biodiversity (Valentine, 1971, 2009), although both temperature and diversity map more closely to the LEG than does productivity (Belanger *et al.*, 2012). Global marine production relies primarily on micro-phytoplankton (which show an LDG today; Fuhrman *et al.*, 2008), and is supplemented by eukaryotic phytoplankton and, on the shelves, by benthic production (Bauer *et al.*, 2013). However, productivity is sensitive not only to radiation from the LEG but to nutrient input, ultimately from the land but associated with the introduction of nutrient-rich waters into the euphotic zone. In stable marine water columns capped by warm SSTs, as in much of the tropics, nutrients are depleted by phytoplanktonic assimilation, and by the sinking of organic detritus from the food chain, including debris from the phytoplankton and faecal pellets from the pelagic fauna. The shallow tropical waters, thermally stratified and thus relatively stable, are often relatively nutrient poor, and productivity is therefore low but also tends to be relatively stable. The sinking organic material passes through a region where light is too weak to sustain production and then continues to the deep sea (see below).

Where the water column is capped by cool water, however, as in upwelling regions in the tropics or in temperate latitudes, and/or where waters are turbulent in the euphotic zone, nutrients are commonly introduced and support productivity that is seasonal or otherwise variable in responding to nutrient supply, depending on the associated hydrography (Cullen *et al.*, 2002; Li, 2009). Such variation grades latitudinally with seasonality and may also underlie some of the strong longitudinal variations in diversity within the tropics: high but seasonal productivity is accompanied by relatively low diversity in the upwelling zones of tropical west South America and tropical west Africa, and the monsoonal tropical Indian Ocean (Fig. 1). The combined effects of the seasonality of solar energy outside the tropics, increasing with latitude, and the episodic nature of upwelling at any latitude, creates a positive correlation between seasonal variation and mean annual values in productivity, but one that is not linearly related to latitude (Valentine, 2009). For our purposes, the chief message here is that steady primary production is more likely to favour the accumulation of high diversity in benthic metazoan communities than is pulse production, even when the pulses sum to higher annual values.

In high-latitude settings, winter productivity in shallow seas drops far below its spring and summer intensities, which draw on nutrients that accumulated during times of low solar input. When solar energy rises in the spring, this rich nutrient resource supports intense phytoplankton blooms, which in turn support very large seasonal populations of assimilators. Thus productivity can be seasonally high at extratropical latitudes where it supports a large biomass of assimilators, and either moderately low or high in tropical latitudes, depending on local stability of production, each in large regions of the shallow sea. Episodic spikes in primary production can be so strong that phytoplankton blooms overwhelm consumers and create anoxic bottom conditions as seen in the 'dead zones' of the world ocean. The effects of local or regional disturbances on diversity can be somewhat ameliorated by metacommunity effects, i.e. restoration of depleted areas by recolonization from the species pool of that biotic region (Witman *et al.*, 2004; Lessard *et al.*, 2012).

Generalizing from these patterns, we can consider a rule based on trophic niches (i.e. feeding specializations), stating simply that more species can be packed into an ecosystem wherein trophic niches are narrow. One obstacle in evaluating such an argument is that quantifying the distribution of trophic breadth within regional metazoan faunas requires detailed knowledge among large numbers of species that differ significantly in feeding techniques, habitat overlap with trophic resources, type and range of prey preferences, and so forth. By contrast, ocean temperature data are abundantly available and apply to all species within large, thermally homogeneous regions, making thermal niches far easier to explore. Our working hypothesis is that more stable conditions apparently favour narrow niches for both niche types. (For other mechanisms potentially linking niche breadth to the LDG, see Vasquez & Stevens, 2004.)

Marine diversity and functional patterns in Bivalvia

We have been exploring the LDG by concentrating on one major marine metazoan clade, the molluscan class Bivalvia, in the global shallow sea. Bivalves are diverse, widespread, relatively well known, show diversity patterns that are highly representative of the benthic fauna as a whole, and have a fossil record that is significantly better than the average clade, permitting many elements of the history of their LDGs to be investigated. Like many other marine groups, the bivalves are under-sampled today and in the geological record in their tropical West Pacific diversity maximum (Bouchet *et al.*, 2002; Knowlton *et al.*, 2010; Valentine *et al.*, 2013), but improved sampling will only strengthen the relationships described here. As the clade is dominated by various types of suspension feeders it must tend to be sensitive to patterns of phytoplankton productivity within the euphotic zone. However, the clade does include other functional groups, including carnivores, detritivores and chemosymbiotic forms, and its species participate in essentially all of the more important shallow-sea communities.

Following the mass extinctions at the close of the Cretaceous Period *c.* 66 Ma, bivalve diversities rebounded strongly at both genus and species levels, with most of the increases coming from younger lineages, chiefly in the tropics (Crame, 2000, 2001; Krug *et al.*, 2009; Jablonski *et al.*, 2013). During the Cenozoic, especially the Neogene, many tropical bivalve lineages spread poleward, even as high latitudes cooled and local extinctions and range terminations produced the present bivalve LDGs (Jablonski *et al.*, 2006, 2013). The latitudinal diversity patterns of the functional groups among the bivalve faunas along each of the four major north–south coastlines in both hemispheres (Berke *et al.*, 2014), provides eight samples of the outcomes of this history. Despite a *c.* 90% reduction in species diversity between tropical and polar zones, few functional groups are entirely lost, even in polar oceans, and as the more species-rich groups lose more species, functional evenness increases dramatically poleward. Viewed another way, the bivalve LDG shows a massive drop in the number of species and higher taxa that can persist near the poles, but far less decline in the number of potential ways for a bivalve to make a living.

Origination rates vary significantly among functional groups in the tropics, and are positively related to the highly uneven diversities among those groups in low-latitude provinces (Berke *et al.*, 2014). Thus, congeneric species in the tropics evidently partitioned their habitats into niches that permit co-occurrence despite their functional similarities. The data are not yet available to test this view thoroughly, but we note that sibling species in tropical marine molluscs often appear to differentiate among microhabitats rather than showing strict allopatry, although functional shifts can also occur (see Bennett *et al.*, 2011; González & Giribet, 2012; and references therein). High-latitude species evidently occupy wider ranges of habitats, and are phenotypically more variable than tropical species (Clarke, 1978). Local separation

might also occur via trophic specialization, but trophic niches have been little studied in marine bivalves; metagenomic analysis of the stomach contents of sympatric species within a single functional group (see Hata *et al.*, 2014 on cichlid fishes) would be a valuable approach to this problem.

Our interpretation of these findings on functional diversity and evenness, and hints on other aspects of marine ecology, is that as species, and thus clades, expanded out of the tropics, broader functional ranges were required, both thermally and trophically. Thus, functional overlaps or redundancies increased within some lineages, affecting more species in the more diverse genera. Proceeding into high latitudes, the diversity within the larger functional groups declined the most, implying that as some of their low-latitude niche dimensions expanded there was a decline in the number of species that could be accommodated within groups of functionally similar species, such as those within genera. This in turn implies that aspects of the environment deteriorated poleward for more specialized species. Despite the evidence that lineages (genera) expanded latitudinally from the tropics towards the poles, there is no sign that higher-latitude bivalve species diversities increased as the poles cooled; presumably the new arrivals filled vacancies opened by extinction. In contrast to terrestrial clades that were largely excluded from high northern latitudes by continental glaciations (e.g. Hewitt, 2000), the highest regional extinction rates for marine bivalves over the past 5 Myr have been at mid-latitudes (Valentine *et al.*, 2008). The most obvious hypothesis is that high-latitude bivalve species diversity had been near a steady state, as survival in that difficult environment maintained a stochastic balance between the extinction of previous residents and appearances of new species, chiefly by invasion from temperate latitudes. Perhaps species invasion occurs more rapidly than *in situ* speciation, and might preserve or even enlarge functional differences among species, rather than multiplying similarly adapted forms.

DEEP-SEA ENVIRONMENTS AND FAUNAS

Benthic faunas were once thought to be absent from the deep sea, but animals inhabit all depths, from the bathyal habitats of the continental slope and rise (c. 200–3000 m) through the vast abyssal plain (c. 3000–6000 m) to the hadal zone of the deep-sea trenches (c. 6000–10,000 m). As the deep sea lacks photosynthetic productivity, most of its trophic energy is provided by organic debris derived from surface waters or from rivers, some of it dissolved, but the supply is highly attenuated as it is dispersed and sinks from the ocean margins. Despite almost uniformly low temperatures and low energy flux from shallow-water phytoplankton, alpha diversity is high in much of the deep sea, especially the bathyal zone, where it may commonly exceed shallow-water diversities at similar latitudes (see Hessler & Sanders, 1967; McClain *et al.*, 2009; Menot *et al.*, 2010; Ramirez-Llodra *et al.*, 2010; Rex & Etter, 2010; and in a rare tropical comparison, Bouchet *et al.*, 2009; and for a representative

comparative plot see Fig. 2). This pattern supports the view that the stability of trophic resources, even at these relatively low levels, is critical, and is sufficient to generate and sustain high alpha diversities. The deep-sea benthos is adapted to those conditions – species tend to be small-bodied and to feed low in the trophic pyramid (McClain *et al.*, 2012), indicating that they have a broad range of trophic suppliers. The total standing diversity in the deep sea remains uncertain, in part because the beta diversities are reported to be very high in some situations and groups, and low in others (Rex & Etter, 2010; Brault *et al.*, 2013). The heterogeneity of regional habitat conditions in shallow water is not matched in the deep sea, and whether global invertebrate diversity is higher in deep or shallow water is still arguable.

The fall of large fish and whale carcasses, or clumps of seaweed or land plants, provide spotty delivery of some trophic resources to the deep sea, and even support some specialized consumers, but such windfall communities do not contribute significantly to deep-sea diversity. Further, some spectacular diversity hotspots are fuelled, not from photosynthesis, but from chemosynthetic reactions that draw chiefly on methane-rich fluids along hydrothermal vents, as along ridges, and from seeps along continental slopes (Van Dover, 2000). The body sizes and local biomass of these animals are impressive, but, again, their diversities are far lower than those of the widespread level-bottom faunas ultimately fueled from photosynthesis in the shallow sea.

The deep sea, then, presents a situation where, judging just from the high levels of alpha diversity, the Red Queen would seem to be positively galloping, but she is very cold indeed: bathyal temperatures are predominantly below 4 °C

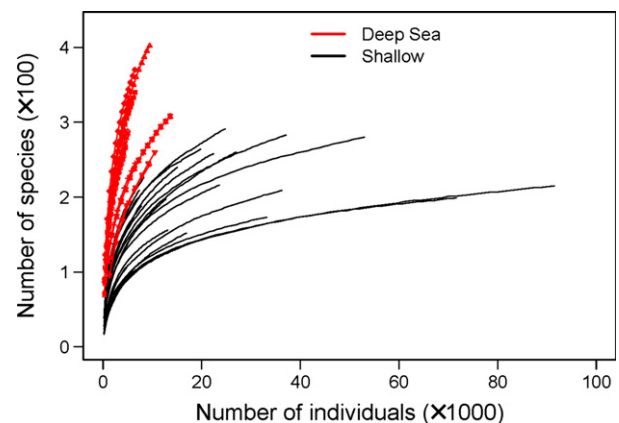


Figure 2 A classic comparison between shallow-sea and deep-sea benthic diversity of the invertebrate fauna, as sampled by identical methods (by benthic sled) at approximately the same latitude. Shallow-sea samples are from George's Bank (simple black lines) and deep-sea samples are from the adjacent bathyal zone off southern New England (red lines with symbols). The samples thus contrast shallow- and deep-water diversities over relatively short distances, and clearly show that the deeper are consistently higher. This seminal analysis, first undertaken by Hessler & Sanders (1967), was reconstructed from original data provided by Ron Etter, University of Massachusetts, Boston.

(Locarnini *et al.*, 2013). On the other hand she has a very stable but reasonably strict diet – although not necessarily the near-starvation rations sometimes inferred (Danovaro *et al.*, 2014).

Some seasonality does occur in detrital nutrient supplies to deep-sea regions (e.g. Sun *et al.*, 2006), but it is damped with respect to surface seasonality, especially at lower latitudes (Smith *et al.*, 2006), perhaps accounting for the deep-sea LDG observed in the North Atlantic, where sampling is most extensive (Rex & Etter, 2010). Thus, in respect to resource stability (high) and species diversity (high), much of the cold deep sea most closely resembles the warm shallow tropics, of all places. As the deep sea must still be greatly under-sampled relative to shallow waters, the known richness of bathyal faunas may be expected to climb significantly. In some parts of the abyssal zone, diversity declines, the density of individuals decreases, and the fauna chiefly represents depth-range extensions of bathyal zone species: the trophic supply may finally become too sparse at deep abyssal depths to support very many metazoan populations at densities that permit successful reproduction (Rex & Etter, 2010; Brault *et al.*, 2013). The diversity declines in some abyssal plains but not others might be examined as potential indicators of resource thresholds required for high diversity even under stable conditions, but other factors may be involved (Jamieson *et al.*, 2010).

In his classic paper, Sanders (1969) suggested that high deep-sea diversity derived from a combination of environmental stability, and its maintenance over sufficient time to permit the competitive interactions to drive the evolution of high levels of niche differentiation (the ‘stability-time hypothesis’). As the bulk of deep-sea diversity does depend on trophic supplies from photosynthesis in the euphotic zone, it is fair to consider it as ultimately dependent on the LEG. However, the extent to which deep invertebrate diversity patterns show a marked LDG in all longitudes, or whether it is as pervasive phylogenetically, is still uncertain.

A PROVISIONAL EXPLANATION OF THE MARINE LDG

Several important requirements for the evolution and maintenance of a shallow-sea LDG are not satisfied by citing any single feature, but seem more satisfactory when combined. That shallow tropical waters accommodate high levels of species diversity within many lineages, coupled with the out-of-the-tropics dynamic, indicates that origination rates are relatively high (as documented in the fossil record, e.g. Jablonski *et al.*, 2006, 2013; Kiessling *et al.*, 2010), and that tropical adaptive zones can commonly be subdivided into many functional categories, and these into niches in which occupancy is sustainable over geological time-scales. The relatively high speciation rates inferred for many tropical settings imply that those lineages can be sustained on an increasingly smaller share of the available trophic resources, which are commonly relatively low and would shrink per capita as

diversities rise. These settings are in regions where euphotic zones are most warm and stable and least seasonal, and we propose that the stability in those factors permit the evolution of narrow niches, both thermal and trophic, and permit small populations to persist (as well as large ones), indeed low per-capita productivity may favour species that are demographically capable of persisting at small population sizes in many settings. For trophic niches, niche subdivision rather than tolerance to overlap seems more likely in stable conditions (e.g. in general terms; Chase, 2011), although as suggested above such subdivision may be accomplished by habitat rather than by prey specialization (e.g. at low trophic levels), and under some circumstances predation may mediate coexistence of some prey species (Stanley, 2008; Wollrab *et al.*, 2013). Major variations in trophic supplies on seasonal scales tend to disfavour less competitive lineages and small populations subject to stochastic extinctions during low-supply seasons, but produce larger populations among more generalized lineages when supplies are growing. Thus, favoured by both higher thermal kinetics and stable productivity, tropical faunas have the highest diversities in the shallow sea. However, in upwelling and monsoonal regions, even tropical euphotic zones tend to be seasonal and less stable with respect to productivity. In mid-latitudes, where the environment is more seasonal, speciation is less exuberant, fewer species are accommodated, and extinction rates are evidently highest (Berke *et al.*, 2014). The marine fossil record suggests that resources freed by those regional extinctions are most commonly used, not in promoting the origin of new species, but in permitting the spread of lineages from the tropics.

Within this framework, specific clades and biomes will differ in how controls sum or interact. For example, mean and seasonality in moisture will enter into the equation for terrestrial plants and the animals that depend on them (e.g. Whittaker *et al.*, 2003; O’Brien, 2006; Krefl & Jetz, 2007). Further, some clades, usually embedded within larger clades showing more conventional LDGs, exhibit an inverse gradient, with diversity minima in the tropics, evidently for intrinsic biological reasons (Kindlmann *et al.*, 2007; Krug *et al.*, 2007), and even clades that do show ‘normal’ LDGs may respond differently to different aspects of environmental variability, as in the greater impact of thermal seasonality versus annual temperature in small versus large terrestrial mammals, respectively (see discussion in Whittaker *et al.*, 2003).

Finally, large-scale diversity patterns cannot be understood strictly in terms of present-day environmental controls: history matters (Ricklefs, 2007; Krug *et al.*, 2009; Jetz & Fine, 2012; Jablonski *et al.*, 2013; and many others). Just as mass extinctions can disrupt global LDGs, regional events can perturb LDGs locally, as seen along the Chilean shelf, where Plio-Pleistocene changes in climate and upwelling intensity evidently flattened the LDGs of marine clades (Rivadeneira & Marquet, 2007). The regional amplitude of Pleistocene climate changes may also disrupt climate–diversity relationships

on land (e.g. Jansson & Davies, 2008; Sandel *et al.*, 2011) and sea (e.g. Pellissier *et al.*, 2014). Nevertheless, present-day conditions allow accumulation of biological diversity in an LDG pattern, in similar ways for the vast majority of clades, even though the levels themselves are in flux as environments change through time.

The richness of today's deep-sea biota certainly contributes significantly to a theory of biodiversity, for it seems to be telling us that trophic stability is a crucial factor. Temperature is surely also important, but we suggest that its chief roles lie in establishing stable conditions in euphotic zones and in setting the geographical ranges of taxa, and perhaps in affecting the rate at which successful speciation occurs. The deep sea and the polar seas are both cold, but, crucially, the polar seas are trophically less stable. The multiplication of niches (i.e. local diversity regulation through time) would then stem from biotic interactions in some form, from competition and predation to positive feedbacks from ecosystem engineering, whether in warm shallow or cold deep water, although the regulatory tempo may vary with temperature. Thus we suggest that weaving together the major environmental effects of the physics associated with radiant heating and the biology associated with photosynthesis, both generated through the LEG, leads to an improved explanation for the origin, historical patterns within, and persistence of the LDG. This explanation, although not fully tested in many aspects, can account for the diversity maxima that occur in two of the seemingly most disparate marine environments on the planet: the warm shallow tropics and the cold deep sea.

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BIOSKETCHES

James W. Valentine is interested in the evolutionary origins of morphological novelties, and the macroevolution of ecogeographic units (species' populations, communities, provinces, etc.).

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