

Opinion

Bimodality of Latitudinal Gradients in Marine Species Richness

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The paradigm for the latitudinal gradient in species richness is that it is unimodal with a tropical peak. For 27 published studies, and global datasets of 65 000 recent and 50 000 fossil marine species, we found that almost all datasets were significantly bimodal with a dip in species richness near the equator. The locations of mid-latitude peaks varied between taxa and were higher in the northern hemisphere where the continental shelf is greatest. Our findings support hypotheses of tropical species evolving in response to temperature variation near the edges of the tropics and available high-productivity habitat. They suggest that the equator may already be too hot for some species and that the modes may move further apart due to climate warming.

Latitudinal Gradients in Species Richness

The general latitudinal pattern is that species richness decreases from the lower to the higher latitudes [1]. Such a pattern is considered unimodal, with a peak at the equator. This appears to be the case for almost all terrestrial plants and animals [2,3]. It has also usually been applied to marine species' distributions [4,5]. However, a unimodal peak of species richness was reported between 10° and 20° north for a range of marine taxa [6]. Of 18 global-scale studies on latitudinal gradients in marine species, 9 have reported one or more taxa as unimodal, 9 as not unimodal, and 2 as bimodal (Table 1). In general, bimodality has been reported in only three ecologically contrasting taxa – planktonic Foraminifera (Atlantic Ocean only), benthic razor clams (Mollusca, Solenidae), and deep-sea brittle stars (Ophiuroidea) (globally) – with a dip near the equator [7–9].

Two hypotheses for why species richness varies with latitude, Rapoport's rule and the Mid-Domain Effect (MDE), assume a unimodal distribution of species against latitude. Rapoport's rule proposes that the latitudinal gradient arose because the geographic range of species increases with latitude [10]. The MDE states that if the ranges of the species were shuffled randomly between geographic boundaries (domains), a peak comprising maximum species richness would tend to appear at the centre of the domain [11]. If the gradient is not unimodal, these hypotheses would be rejected and/or need significant reformulation.

Latitudinal Gradients Revisited

For this opinion article, we reexamined 27 published studies and extracted data from the graphs of 13 of them (Table 1). These data were the total number of species known for each latitude (i.e., gamma diversity). The geographic distribution of 65 000 species was obtained from the Ocean Biogeographic Information System (OBIS) [12]. From these data, the total number of species for each 5° latitudinal band (i.e., gamma diversity) were analyzed as examples: bony fish (2600 species), gastropods (1036 species), hydrozoans (237 species), ophiuroids (69 species), red algae (183 species), shark and rays (132 species), sponges (184 species), stony corals

Trends

The latitudinal gradient in species richness is generally assumed to be unimodal.

We show it is bimodal with a dip near the equator for marine species.

Mid-latitude temperature variation and available productive habitat may drive speciation.

Climate warming is likely to move the modes further apart.

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Table 1. Studies Showing the Latitudinal Gradients in Marine Species Richness

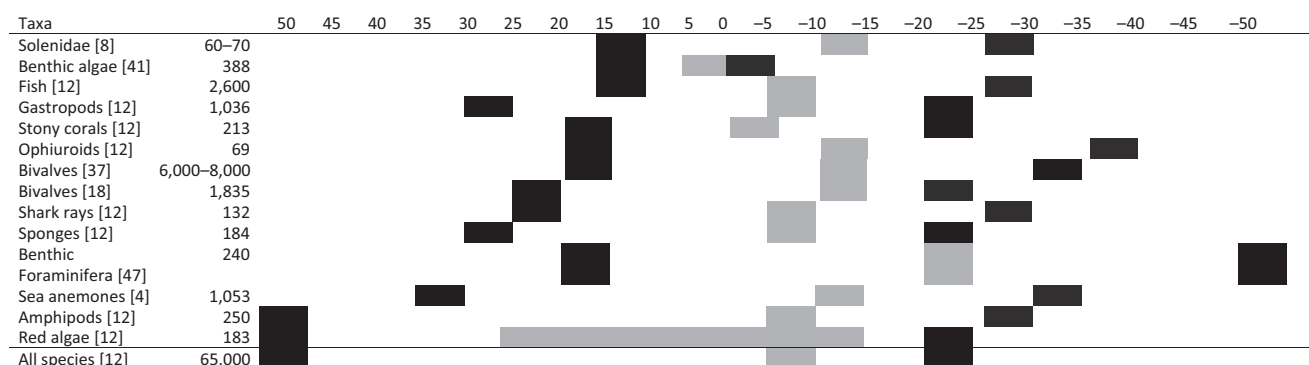
Marine Taxa	Region	Author's Interpretation	Present-Study Interpretation
Coastal fishes [27]	California (north hemisphere 30°S to –60°N)	Peaked in 32°N	Asymmetric
Seaweeds, 1277 species [28]	Atlantic coasts North and South America (50°S to 0°N)	Unimodal	Asymmetric
Bivalves, shallow water, 930 species [29]	Northeastern Pacific shelf from 5°S to 70°N	Not unimodal	Asymmetric in north
Bryozoa [30]	North Atlantic	Peaked between 15° N and 30°N	Asymmetric; less at the equator
Corals and fishes, 727 and 1766 species [31]	Indo-Pacific region (40°N to 40°S)	Unimodal	Unimodal within region
Reef fishes, 1970 species [32]	Indian and Pacific Ocean (40°N to 30°S)	Unimodal	Unimodal
Mollusks, 629 species [33]	Pacific South American shelf	Asymmetric	Asymmetric
Planktonic Foraminifera [7]	Atlantic Ocean	Bimodal	Bimodal
Benthic mollusks [34]	East Pacific North to South America	Asymmetric	Asymmetric
Seaweeds, 1700–2400 species [35]	Global	Unimodal	Asymmetric bimodal
Bivalves, 600 genera, 14 families (shallow) [18]	Global	Unimodal	Asymmetric bimodal
Planktonic Foraminifera, 33 species and six subspecies [36]	Global	Not unimodal	Asymmetric bimodal
Bivalves [37]	Global coastal	Asymmetric	Asymmetric bimodal
Benthic epifaunal invertebrates, ten phyla, with sponges, cnidarians, ascidians [38]	Global	Unimodal	Asymmetric bimodal
Tuna and bill fish diversity [39]	Global	Not unimodal	Asymmetric bimodal
Tintinnid planktonic ciliates [40]	Global	Not unimodal	Asymmetric bimodal
Benthic microalgae, 1069 genera; Bryopsidales, 388 species [41]	Global	Bryopsidales unimodal; other algae not unimodal	Algae bimodal
Planktonic bacteria [42]	Global	Unimodal	Asymmetric bimodal
Copepods [43]	Global	Asymmetric	Asymmetric bimodal
Thirteen primarily coastal, 11 567 species [44]	Global	Coastal unimodal in tropics, oceanic peaked in mid-latitudes	Bimodal
Predicted mammals, 115 species [45]	Global	Not unimodal	Asymmetric bimodal
Sharks, 507 species [46]	Global	Not unimodal	Asymmetric bimodal
Sea anemones, 1053 species [4]	Global	Not unimodal	Asymmetric bimodal
Foraminifera and copepods [19]	Global	Unimodal	Bimodal
Razor clams, 60–70 species [8]	Global	Asymmetric bimodal	Asymmetric bimodal
Brachiopoda since 530 Mya, 4394 genera [17]	Global	Unimodal	Asymmetric bimodal for modern fauna
Ophiuroidea, 2099 species [9]	Global	Unimodal <200 m, bimodal >200 m depth	Asymmetric bimodal overall

(213 species), and amphipods (250 species). For all OBIS data, species richness was plotted as the mean and standard error of the number of species present in 5° latitude–longitude cells (i.e., alpha diversity) in their respective band [13]. Thus, these data show how variable richness is in each latitude. The geographic distribution of fossilized marine species was also analyzed. The fossil species data, taxonomic classification, and geographic location in Paleozoic (245–544 Mya), Mesozoic (65–245 Mya), and Cenozoic (0–65 Mya) eras were downloaded from the Paleobiology database [14]. The marine species were selected by matching the records at genus, family, and order level, where applicable with the World Register of Marine Species [15]. The final list comprised 23 106 species from the Paleozoic, 15 882 species from the Mesozoic, and 11 181 species from the Cenozoic. Visual Basic Script macros and MySQL were used to perform the calculations and manage the datasets. To test whether the gradients were unimodal or bimodal, we performed the Kernel density estimation test [16].

At a global scale, we found that all 18 global studies showed asymmetric bimodality (Table 1). In all cases where we could fit a kernel density estimation, the latitudinal gradient in species richness was bimodal. In 12 of these cases, there was a dip in species richness near the equator between -5° and -15° latitude (Figure 1). However, the peaks in richness were more variable: 10 peaks between -20° and -30° and 12 from $+10^{\circ}$ to $+35^{\circ}$ latitude. All global latitudinal species richness gradients were asymmetric (Figures 1 and S2, S3, and S4 in the supplemental information online). Most cases had higher species richness peaks in the northern than in the southern hemisphere. Exceptions were stony corals and bony and cartilaginous fish (Figure S4).

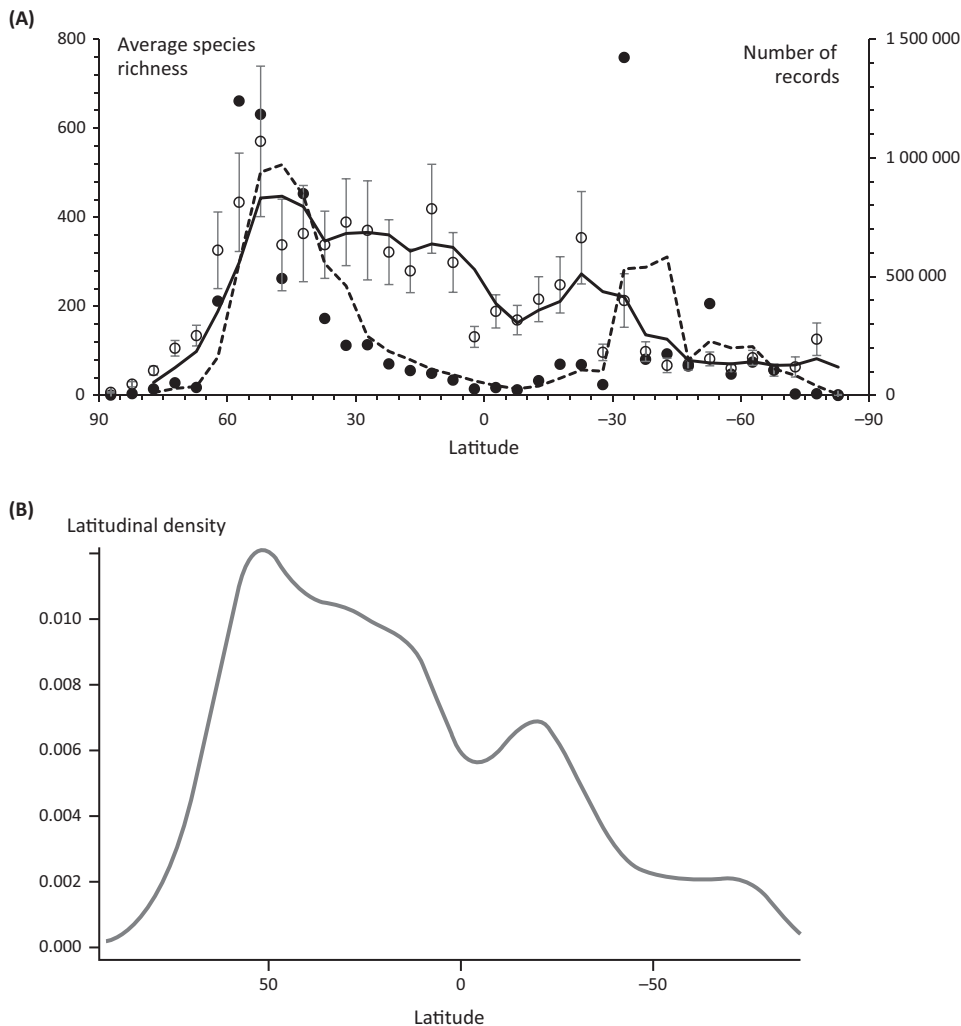
For all of the species richness data from OBIS, the mean richness (alpha diversity) dipped between -5° and -10° and peaked at $+50^{\circ}$ to $+55^{\circ}$ and -20° to -25° . The highest peak was in the northern hemisphere, coincident with most sampling records (Figure 2). However, the error bars were also widest up to $+60^{\circ}$ north. While there are fewer samples in the tropics (-25° to $+25^{\circ}$), both high (edges of tropics) and low (equator) numbers of species were recorded there (Figure 2).

Fossil species richness also showed significant latitudinal gradients. Species richness in the Paleozoic peaked between -10° and -20° , while in the Mesozoic and Cenozoic it peaked between $+35^{\circ}$ and $+45^{\circ}$. A secondary peak was observed in the Mesozoic and the Cenozoic between -30° and -40° and -40° and -50° , respectively (Figure S5). However, no secondary peak was observed in the Paleozoic. Similarly, brachiopod genus richness was unimodal with latitude until recent times [17].



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Figure 1. The Locations of the Dips (Gray) and Peaks (Black) in Species Richness with Latitude as Found Using the Kernel Density Estimation Test (Figure S4). All cases represent total species richness (gamma diversity) for that latitude band except for the last, which is the mean species richness for all 5° cells in that latitude (i.e., alpha diversity) [4,8,12,18,37,41,47].



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Figure 2. Marine Species Richness with Latitude. (A) Calculated as the mean (\pm standard error) number of species ($n = 65\,000$) (i.e., alpha diversity) and the total number of records in 5° latitudinal bands with a three-point moving-average line. (B) Kernel density estimation plot for the same data.

Bimodality in Species Richness with Latitude

Despite the evidence of elevated peaks in species richness in both hemispheres and a dip near the equator, most studies had not considered it to have been bimodal. This may have been because the dip was not noticed and/or was considered part of sample variation. Alternatively, some authors attributed it to sampling bias [18]. Moreover, most regional-scale studies did not cross the equator (Figure S1) and some plotted data from 0° to 90° rather than across the equator. In other cases, the use of latitudinal bands $>5^\circ$, diversity indices, species ranges, or sample richness (alpha diversity) rather than total species richness (gamma diversity) for each latitudinal band may have concealed the gradient.

We found that marine gamma diversity peaked between latitudes $+10^\circ$ and $+35^\circ$. Powell *et al.* [6] also found higher marine species richness in the northern hemisphere than at the equator and that this was not due to sampling effort. Similarly, the latitudinal gradient of species richness for

sea anemones found gamma diversity a good fit to rarefaction predictions of species richness [4]. The contrasting peak we found between $+50^\circ$ and $+55^\circ$ for alpha diversity in the OBIS data was also where the error bars were widest. The area of 5° cells decreases with distance from the equator. Thus, species richness per cell (alpha diversity) should be higher near the equator, but it was not (Figure 2). Alpha diversity does not consider which species occur in each cell, while gamma diversity is the total number of species in each 5° latitudinal band. Thus, the relationship between alpha and gamma diversity may vary with latitude depending on how widespread species are (i.e., beta diversity). Thus, average alpha diversity may not be a true representation of diversity patterns at global scales. Considering the assessment of sample bias in previous studies [4,6], the effect of 5° -cell area, and that similar sampling effort occurred throughout the tropics, the bimodality and dip at the equator are unlikely to be due to biased sampling effort.

While attractive as null models, Rapoport's rule and the MDE no longer seem useful to describe latitudinal gradients of marine species because they do not match the patterns or clarify the causal mechanisms. The peak in richness is not symmetric as these models propose; rather, it is higher in the northern than the southern hemisphere for recent and fossil data, reflecting the available area of shallow shelf habitat. To redefine the domain boundaries on alternative environmental variables (e.g., temperature) [19,20] is a circular argument as it is effectively saying that species richness is highest where conditions have led to most species being present.

Role of Temperature

The bimodality of latitudinal gradients in species richness in most studies on marine taxa supports the hypothesis that species evolved through adaptation to temperature at the edges of the tropics [7]. Thus, the ranges of these new species and their tropical ancestors overlap in mid-latitudes. Tropical temperature would not necessarily exclude these mid-latitude species from the equator. Thus, other factors, such as physiological preferences, food, competition, and/or hybridization, may explain the dip in species richness near the equator. It is also possible that the mid-latitude species are less physiologically, immunologically, and/or ecologically fit at equatorial temperatures and/or may be moving away from the tropics due to climate warming [21]. The fossil record also indicated reduced species richness at the equator during warm interglacial periods [22]. Climate warming will affect all aspects of species' biology and consequently ecological interactions and biogeography [23]. Mass bleaching of coral reefs may be one of the more obvious symptoms of physiological stress near the equator [24]. It can thus be predicted that the dip in richness at the equator will get deeper and the mid-latitude peaks in richness will move further from the equator in response to climate warming. A more detailed assessment of the fossil record may find that the dip in richness at the equator did not occur during glacial periods, such that climate warming and cooling had a concertina effect on the latitudinal gradient.

Role of Depth and Productivity

The variation in the latitude of the peaks in species richness between taxa indicated that factors other than temperature were involved. Analysis on razor clams [8], which occur only in shallow-water continental shelves, suggested that while speciation at the edges of the tropics may be derived by temperature adaptation, the larger continental shelf (coastal zones) in the northern hemisphere provided more habitat availability for these species. The variation in latitudinal peaks may thus reflect the habitat preferences of taxa. Similarly, the shift in peak richness of fossil taxa northwards over time reflected continental drift [17,25]. This habitat effect may be due to productivity and shelf areas will have higher productivity due to plant production. Deep-sea ophiuroids had a bimodal latitudinal gradient that was coincident with areas of higher carbon input and being close to continental shelves [9].

Concluding Remarks

The taxa studied here were primarily coastal, as are most marine species [13]. When species richness is contrasted between terrestrial and marine and freshwater and marine environments it is evident that the long-term geographic distribution of habitat has strongly influenced species richness [26]. The effect of temperature on speciation on land (including freshwater) may be less clear than that in the oceans due to the island nature of land masses and other habitat effects such as water availability. Further insights on how habitat influences speciation may thus benefit from comparisons between these environments and within the ocean between shallow and deep-sea environments. The depth ranges of marine species increase with depth, so deeper assemblages of species are subsets of shallower communities. Analyses of global patterns of species richness over time should thus consider temperature, such as due to climate change, habitat availability, and productivity and recognize that, at least in the ocean, the latitudinal gradient is generally asymmetric and bimodal.

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Supplemental Information

Supplemental information associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.tree.2016.06.001>.

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Outstanding Questions

Why is there a dip in species richness near the equator?

Are the peaks in species richness moving further apart in response to climate warming?

Do fossil data show that species richness peaked at the equator during glaciations and then became bimodal during interglacials?

How do alpha, beta, and gamma diversity vary with latitude and depth and spatially in oceans?

Can temperature and area of productive habitat similarly correlate with species richness in terrestrial and freshwater environments?

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