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Global warming is causing a more pronounced dip in marine species richness around the equator [title on published version differs slightly from manuscript version]

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## **Main Manuscript for**

### **Global warming is causing a dip in marine species richness at the equator**

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## Author Contributions

Chhaya Chaudhary developed the research question and conducted the data analysis and led writing of the manuscript. All other authors contributed to the study design, methods, interpretation of results and writing of the paper.

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Main Text  
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## Abstract

The latitudinal gradient in species richness, with more species in the tropics and richness declining with latitude, is widely known and has been assumed to be stable over time. We analysed data from 49,785 marine animal species since 1955, accounting for sampling variation and spatial aggregation, to assess whether the global latitudinal gradient in species richness is being impacted by climate change. We confirm recent studies that show a slight dip in species richness at the equator. Moreover, richness was sensitive to temperature, reaching a plateau or declining above a mean annual sea surface temperature of 25°C in most taxa. In response, species richness has declined at the equator since the 1970s, increased in mid-latitudes, and shifted north in the northern hemisphere. Climate change is thus impacting the latitudinal gradient in marine biodiversity at a global scale. The intensification of the dip in species richness at the equator suggests that it is already too hot there for some species to survive.

## Significance Statement

We show that marine species richness levels off or declines above a mean annual sea surface temperature of 25°C. This results in a dip in species richness at the equator that has deepened over time as the climate has warmed. Previous studies have either only predicted such effects or provided data at regional scales and/or with limited numbers of taxa. Here, we use empirical evidence across 49,785 species to show that marine biodiversity (pelagic and benthic), has been responding to climate warming at a global scale.

## Main Text

### Introduction

The latitudinal gradient in species richness is a striking biogeographic pattern in both terrestrial and marine realms that is likely to reflect evolutionary history and current environmental conditions (1-4). It is strongly correlated with temperature (5-8) (**Table S1**) and may thus serve as a natural laboratory to study the impact of climate change (9). A unimodal latitudinal gradient in species richness peaking at the equator had been assumed to be the general pattern for most taxa (10-15). However, almost all global studies have been limited to a specific taxonomic group, and other multi-taxon studies have been restricted to certain parts of the world, making generalisations difficult. Recently, Chaudhary et al. (10, 16) found that the distribution of marine diversity was bimodal, with a dip at the equator, and that all marine taxa followed this pattern, with the possible exception of planktonic radiolarians (17), which are known to occur deeper in tropical waters (the so-called 'tropical submergence' (18)). Species distribution models forced by Earth System Models predict that species will move away from the equator in the future (e.g., 19), further depressing

equatorial richness. This begs the question: has climate change already altered the global latitudinal gradient in species richness? Here, we compare the latitudinal pattern in species richness relative to latitudinal temperature gradients since the 1950s for 49,785 marine species across ten major pelagic and benthic taxa.

## Results

### *Bimodality in species richness with latitude*

The latitudinal gradient in species richness was bimodal for all individual taxonomic groups, as well as when these groups were pooled by habitat (benthic and pelagic) or overall (All Species) (**Figure 1**). The bimodal pattern for All Species and All Benthos was approximately symmetrical (**Figure 1**), as were those for 6 of the 10 taxonomic groups (reef-associated fish, bathy-demersal fish, benthic-pelagic fish, bathypelagic fish, bivalves, and pelagic chordates). However, the equatorial dip was less pronounced for demersal fish and benthic chordates (**Figure 1**). Benthic arthropods had asymmetric peaks in each hemisphere, with higher richness in the northern hemisphere, and gastropods exhibited a higher peak in the southern hemisphere (**Figure 1**). All groups showed sharp declines in richness towards the poles. Latitude alone explained >70% of the total variation in species richness (**Table S2**).

### *Temperature and other potential predictors of species richness*

Similar to latitude, mean annual sea surface temperature (SST) explained >70% of the variation in species richness in all groups, except bivalves, gastropods, and benthic arthropods (**Table S3**). Species richness declined in waters >25°C for All Species, All Benthos and All Pelagos (**Figure 2, Fig. S1**), as well as for 8 of the 10 taxonomic groups (**Figure 2**). As expected, taxa that exhibited a greater decline in species richness at temperatures >25°C showed the greatest dip in species richness near the equator (**Figure 1, Fig. S1 & S2**). Geographic variables known to influence species richness (ocean area, the proportion of shelf, and the proportion of slope) (**Table S1**) were significantly correlated with SST (**Fig. S3 & S4**), but their relationships with richness varied across taxonomic groups (see Methods).

### *Impact of ocean warming*

To investigate the effect of ocean warming on the latitudinal gradient of species richness, we examined three equal time periods: viz. 1955—1974, 1975—1994, and 1995—2015. Latitude explained >75% of the variation in overall species richness in each of the three time periods (**Table S4**). From 1955—1974, All Benthos had a broad equatorial peak in biodiversity (**Figure 3A**), and All Pelagos is weakly bimodal, with a minor dip at the equator and a relatively large peak in the northern hemisphere (**Figure 3B**). However, after 1975, the pattern changed. Both All Benthos and All Pelagos groups showed a more intense dip at the equator, consistent with species moving poleward as climate warms (**Fig. S5 & S6**). This was most pronounced for All Benthos, with distinct peaks appearing in the subtropics that did not previously exist (**Figure 3A**). A similar but distinct pattern was evident in All Pelagos (**Figure 3B**). Here, the equatorial dip intensified, widened, and shifted northward from 0° to 10°N. Most dramatic was a rapid poleward shift in the biodiversity peak in the northern hemisphere over time from 30°N in 1955—1974 to 45°N in 1995—2015.

## Discussion

Using the largest available dataset (20) on global biodiversity, we show for the first time that the dip in the latitudinal pattern of marine species richness around the equator has deepened with global warming, as predicted (8, 19). Ocean warming is thus causing large-scale changes in the global latitudinal distribution of marine biodiversity.

We confirm bimodality is the latitudinal distribution pattern of marine species richness (7, 8, 10, 16, 21, 22). While it has been suggested that the cause of the equatorial dip in species richness was under sampling in the tropics (21), this is unlikely to be the case here because we

accounted for the number of samples in different areas and their spatial aggregation (see Methods). The greater sampling in the northern hemisphere did not produce uniformly higher richness peaks (5 taxa have greater peaks in the southern hemisphere and 5 taxa in the northern hemisphere). Furthermore, a global analysis using fish species ranges, which minimise the effect of sampling gaps, similarly found a bimodal pattern (23), as have other studies (8, 22, 23, 24). We found the equatorial dip in all taxa, pelagic and benthic chordates, and benthic invertebrates (bivalves, gastropods and arthropods), despite variations in their ecology, methods used to sample them and the amount of taxonomic attention they have received.

The strong non-linear relationship between richness and SST, with richness plateauing and declining above 25 °C for most taxa, is a clear explanation for the deepening of the equatorial dip over time as the ocean has warmed. A similar pattern has been found in other studies on benthic and pelagic data, although these had restricted taxonomic and/or geographic coverage (7, 8, 22-25). The greater northern-hemisphere latitudinal shift in the richness of pelagic species than benthic species post-1975 (consistent with the SST anomaly) suggests pelagic species respond more quickly to climate warming than benthic ones (26, 27). This may be because demersal and benthic species have thermal refugia in deeper water, as suggested by studies on demersal fish (28-31).

A similar equatorial dip and movement of the richness peaks toward the subtropics that we have observed here occurred in corals during the last inter-glacial (32). Similarly, a sudden loss in equatorial diversity occurred in late Quaternary (8) and early Triassic (33) in response to warming, indicating that the present equatorial biodiversity is particularly threatened by climate change. Indeed, a sudden loss of diversity at the tropics has been predicted in future under different climatic scenarios (34). The decreasing richness at the equator since 1975 suggests that the equator is already too hot for some species to survive and indicates that that further low latitude declines of species are likely with continued warming.

## Materials and Methods

### *Species data*

Distribution data comprising 12.5 million observation records for 49,785 animal species collected between 1920 and 2015 used for our analyses were previously used by Chaudhary et al. (16) downloaded from Ocean Biodiversity Information System (20). These data included species that (1) could be defined as benthic or pelagic based on a literature review, and (2) had sufficient occurrences for global analysis based on their global distribution. The taxa with most occurrence records were Chordata, Arthropoda, Cnidaria, Echinodermata, and Mollusca. Each of these five taxonomic groups had observations for >3,000 species and >150,000 occurrence records (**Table S5**). Species in these groups were defined as benthos if they were exclusively benthic or had any benthic life stage (except 74 species of jellyfish, which were considered pelagic); and species were defined as pelagos if they had no benthic life stage, according to FishBase (35), MolluscaBase (36), and the literature (37). The chordates comprised fish, tunicates, mammals, birds, and reptiles (Sauria, Squamata and Testudines).

Fish species were classified based on depth distribution and functional groups in accordance with FishBase (35), that is: (1) demersal (near or on seabed) and coral reef-associated fish occur between 0 m and 200 m depth; (2) bathy-demersal fish occur below 200 m depth; and (3) bathy-pelagic fish between 1000 m and 4000 m. There were insufficient records in other depth zones for separate analyses.

Benthic vertebrates comprised (1) demersal, (2) reef-associated, (3) bathy-demersal and (4) benthic-pelagic fish. Benthic chordates included (5) these vertebrates and benthic tunicates, mammals, birds, and reptiles (Sauria, Squamata, and Testudines). Pelagic chordates included (6) pelagic fish, tunicates, mammals, birds, cephalochordates and reptiles (Sauria, Squamata, and Testudines) and (7) Bathy-pelagic fish. Benthic invertebrates with sufficient geographic data for analysis were (8) arthropods, (9) bivalves, and (10) gastropods. Thus, there were five groups of fish, three groups of invertebrates, two groups of chordates (benthic and pelagic), and collectively, thirteen benthic and pelagic taxonomic groups including All Benthos, All Pelagos and All Species. The final quality-controlled data used for analysis in this study had 12,582,706 observation records for 49,785 species, out of which there were 44,297 benthic species, with 8,293,210 records, and 5,488 pelagic species, with 4,289,496 records. The data used are available on figshare (<https://doi.org/10.17608/k6.auckland.12672884.v1>).

Data for All Benthos and All Pelagos were subdivided into three time periods, 1955—1974, 1975—1994, and 1995—2015, to analyse the change in latitudinal pattern in species richness over time. These time periods were selected to ensure that there were sufficient data with global spatial coverage in each period (**Fig. S7**) and so that the strong warming signal in ocean temperature was captured. Since 1980s, global warming has accelerated (**Fig. S5 & S6**), with the greatest temperature increases in the North Atlantic (38). On the scale of our analysis, there is nearly 0.06°C warming from 1955—1974; nearly 0.10°C warming from 1975—1994; nearly 0.08°C from 1995-2015 (**Fig. S5**).

When we initially analysed data at the scale of hexagonal cells of size ~800,000 km<sup>2</sup>, we found that many regions were severely under-sampled, particularly when the data were divided into different taxonomic groups (**Fig. S8**). Moreover, these hexagons reveal geographic patterns of alpha (local) diversity. Also, they do not account for the overlap in species composition between adjacent hexagons within a region, while the total number of species per 5° latitudinal band does (2). Indeed, Chaudhary et al. (16) showed that alpha diversity does not accurately represent the latitudinal pattern in species richness because it is more biased by sampling than is gamma (regional) diversity. The influence of the bias is also visible in **Fig. S8**, where hexagons with higher species richness also have a greater number of samples, where each sample is the unique combination of date of collection and location of the record. To ensure a sufficient number of data points for robust statistical analysis amongst ten taxonomic groups, we aggregated the data into 5° latitudinal bands.

### *Temperature data*

Monthly sea surface temperature (SST) data in °C were downloaded from the Hadley Centre Global Sea Ice and Sea Surface Temperature (HadISST 1.1) database (39). The temporal range of the SST data analysed here was 1920-2015, and spatial scale was 1° latitude by 1° longitude cells. The monthly averaged SST over the 95 years was calculated for each sample location using the point extraction method in ArcGIS 10.3.3, and then averaged for each 5° latitudinal band, ~800,000 km<sup>2</sup> hexagons, and ~50,000 km<sup>2</sup> hexagons. To remain consistent within the study and with the literature, and also because of the long-term (from 1920 to 1950s) unavailability of sea bottom temperature time series to correlate with benthic species richness, we used SST. In addition to poor temporal and spatial availability of near-seabed temperatures, they seem to correlate less well with demersal fish responses to climate warming (40).

To assess the change in global SST within latitudes over time, we averaged the monthly SST in each of the 5° latitudinal bands for each decade starting from the 1920s and ending with a final five-year band, 2010-2015. The anomaly in each 5° latitudinal band for each period was calculated as the difference between the decadal mean SST and the long-term (over 95 years) mean SST.

### *Geographical data*

Higher coastal diversity has also been attributed to the presence of more biogenic habitats in the shallow waters of the continental shelves (41), although these are often also species in their own right. The presence of mangroves, seagrass, and coral reefs in tropical coastal regions creates greater habitat heterogeneity and higher productivity. In 7 of 29 studies reviewed here, food availability and productivity have been reported the next-most common explanations for the latitudinal gradient in species richness (**Table S1**). Thus, it is possible that latitudes with more continental shelf area would harbour more species than latitudes with less continental shelf area. Thus, we assessed the effect of ocean and shelf area on the latitudinal pattern in species richness. The ocean area per 5° latitudinal band was calculated in ArcGIS 10.3.3. We used the data for the continental shelf area and the continental slope area, based on Harris et al. (42) at a scale of 1:500,000. The proportion of oceanic shelf and the proportion of oceanic slope were then calculated as a ratio of the shelf area, and the slope area to the ocean area in each 5° latitudinal band, respectively.

### *Data analysis*

#### (a) Sampling bias

Sampling bias can be methodological, taxonomic, geographic and temporal. There can be methodological bias because different methods are used to sample species from different habitats and body sizes (43). Thus, analyses across as wide a range of taxa and habitats as possible will distinguish the generality of phenomena irrespective of biases associated with sampling method and taxon. Taxonomic bias may arise when studies do not identify all taxa to species level. To minimise this bias, we analysed only those records identified to species level. Coastal areas and surface waters have been sampled more frequently compared to the deep sea (43), and the frequency of sampling varies over time and location (44). Here, we have standardised the sampling effort by taking a unique combination of date of collection, latitude, and longitude as one sample. Thus, samples contained one or more species (16).

Another form of sampling bias is spatial aggregation of samples. For example, there may be more sampling near marine research stations or locations of particular interest. Samples collected closer together are likely to have more similar species composition than those collected further apart (45). Thus we accounted for spatial aggregation (measured as Clark Evans index) by using it as one of the predictors of species richness (Supplementary material).

(b) Generalised Additive Modelling

Generalised Additive Modelling (GAM) was used to understand the expected nonlinear relationship of the number of species with environmental and geographical variables using the package “mgcv” (46) in R. GAM sums a series of smoothed functions of individual covariates and can thus capture non-linearity (47). Latitude, mean SST, the proportion of oceanic shelf, and the proportion oceanic slope, ocean area, and Clark Evans index per 5° latitudinal band were used to explain the variation in the total number of species.

We fitted the model with Normal, Poisson and Negative binomial error structures and compared their residual plots,  $R^2$  (adjusted) and Akaike information criterion (AIC). Based on the best residual plot (in terms of the randomly distributed residuals), QQ plot, and histograms of the residuals and relatively lower AIC, we chose a normal error structure with identity link (**Table S6, Fig. S9**). The identity link function gives the relationship between the mean of the response and predictors, keeping the variance constant.

Natural logarithms (ln) of the number of samples per 5° latitudinal band were used as an offset variable rather than as a predictor. With the help of the offset, the number of species can be modelled given the total number of samples. Thus, the use of an offset compensates for the need to rarefy species richness and enables the use of the whole dataset.

In the GAM, we found an inconsistent relationship of species richness with the explanatory variables (the ocean area, the proportion of oceanic shelf and, the proportion of oceanic slope) in different taxonomic groups (i.e., All Benthos, All Pelagos, Benthic Arthropods, Bivalves, Bathy-demersal fish, Bathy-pelagic fish, Pelagic Chordates) (**Fig. S10**). The relationship between species richness and the proportion of oceanic shelf in each taxonomic group was not always positive as may be expected, especially for benthic species. Similarly, the ocean area was not always positively correlated with species richness for all the groups (**Fig. S10**).

Within 5° latitudinal bands, the correlation of SST with: (a) ocean area was positive ( $r = 0.85$ ,  $P < 0.001$ ), (b) the proportion of shelf was negative ( $r = -0.39$ ,  $P = 0.02$ ) (**Fig. S3**), and (c) the proportion of slope was not significant ( $r = -0.02$ ,  $P = 0.90$ ). Ocean area was negatively correlated with the proportion of ocean shelf ( $r = -0.69$ ,  $P < 0.001$ ) (**Fig. S4**). Because the ocean area and the proportion of shelf were significantly correlated with SST, when added to the GAM along with the proportion of slope, they neither significantly changed the variation explained in species richness nor the residual plots, also the AIC remained nearly consistent throughout (**Table S7, Fig. S11**). Therefore, to avoid the complexity of the relationships among the variables, only SST was chosen to be included in the model.

Two models were developed: a model of species richness as a function of latitude and a model of species richness as a function of SST (**Tables S2-S4, Fig. S12-S13**). The model for species richness as a function of latitude is:

$$\text{Number of species} = \text{offset}(\log(\text{Number of samples})) + s(\text{Latitude}, k = 9),$$

where,  $s$  is a spline smoother, latitude is the midpoint of 5° latitudinal bands, and  $k$  is the maximum effective degrees of freedom (related to the flexibility of the smooth);  $k = 9$  was chosen as it captured a smooth pattern without overfitting to the data. The model for species richness as a function of SST is:

$$\text{Number of species} = \text{offset}(\log(\text{Number of samples})) + s(\text{SST}, k = 5),$$

where,  $s$  is a spline smoother, SST is sea surface temperature (°C) in the 5° bands, and  $k$  is the maximum degrees of freedom (related to the flexibility of the smooth);  $k = 5$  was chosen as it captured a smooth pattern without overfitting to the data.



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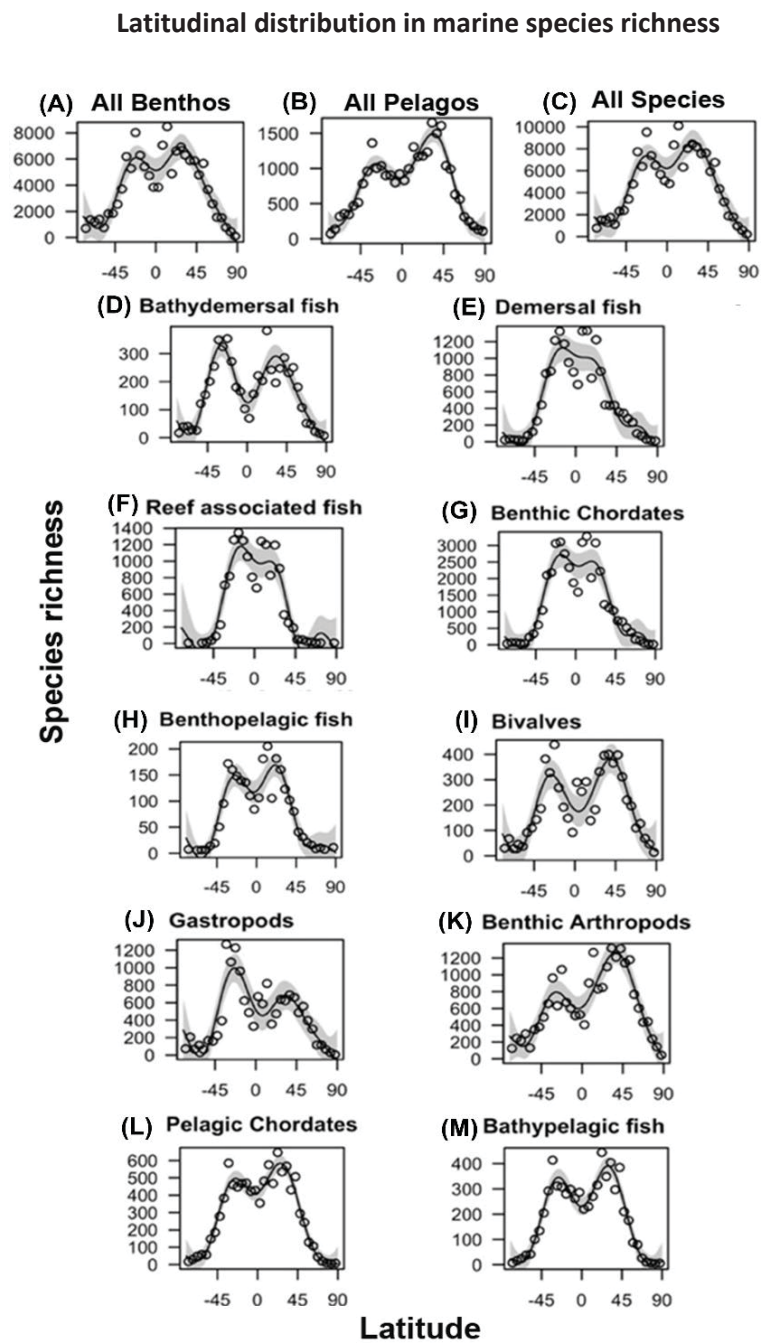
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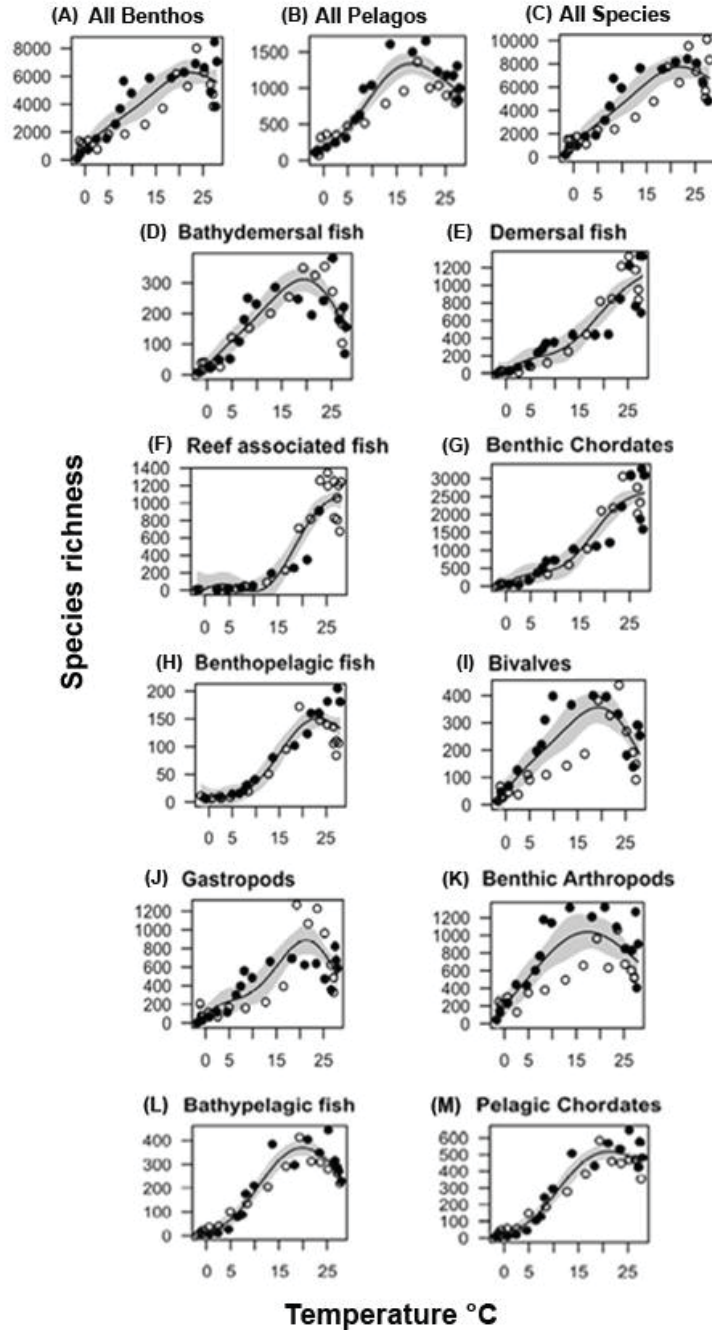
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Figures and Tables



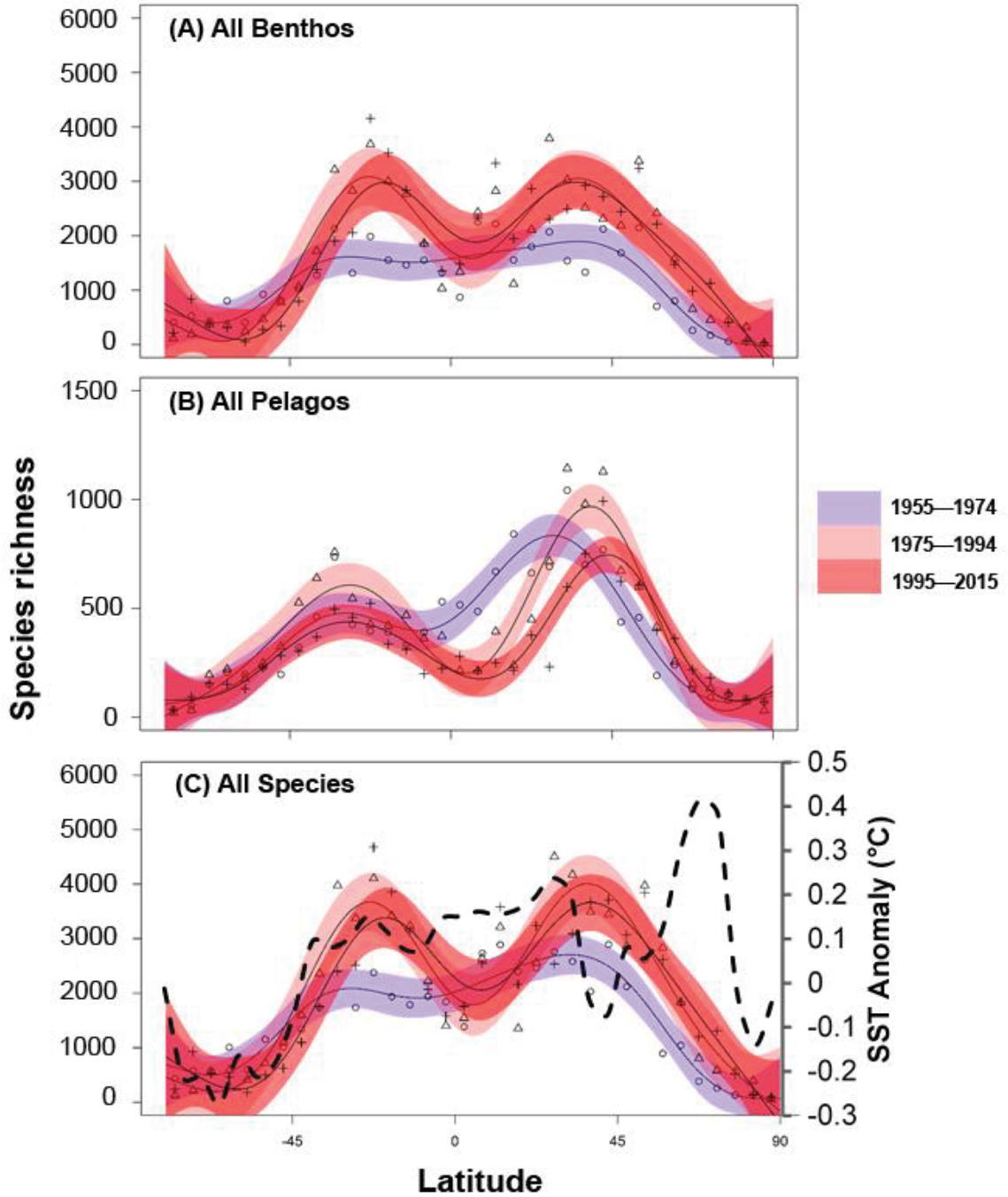
**Figure 1.** The latitudinal distribution of species richness in marine taxa at the scale of 5° latitudinal bands (using GAM, **Table S2, Fig. S12 A**). The first row encloses (A) all benthic species, (B) all pelagic species, and (C) all species. For the remaining columns (D-H), are fish living near the seabed, except (G) benthic chordates (fish and tunicates); (I-K) are benthic invertebrates; and bottom row (L-M) comprises pelagic taxa. The shaded region in each graph shows the  $\pm 95\%$  CL.

## SST distribution in marine species richness



**Figure 2.** SST gradient in species richness per 5° latitudinal band (using GAM, Table S3, Fig. S12 B). The first row encloses (A) all benthic species, (B) all pelagic species, and (C) all species. For the remaining columns (D-H), are fish living near the seabed, except (G) benthic chordates (fish and tunicates); (I-K) are benthic invertebrates; and bottom row (L-M) comprises pelagic taxa. The shaded region in each graph shows the  $\pm 95\%$  CL. White and black dots show the Southern and Northern hemisphere richness, respectively.

### Latitudinal distribution in species richness over time



**Figure 3:** Latitudinal distribution in species richness (using GAM, Table S4, Fig. S13) in (A) all Benthos, (B) all Pelagos, and (C) all Species in three time periods: 1955–1974 (circles), 1975–1994 (triangles), and 1995–2015 (crosses); dashed line is SST anomaly (before and after 1985). The shaded regions represent  $\pm 95\%$  confidence intervals for models fit to each of the periods, with shades (from blue to red) reflecting progression of time periods from older to more recent.