Marine species turnover but not richness, peaks at the Equator

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ABSTRACT

Turnover in species composition, also called beta diversity, can indicate natural habitat diversity and fragmentation of populations due to environmental stress, such as heatwaves. Latitudinal gradients in species diversity help synthesise local diversity into more general evolutionary and climatic patterns. Recently it has been shown that local (alpha) and regional (gamma) measures of marine species richness do not peak but dip at and peak on either side of the Equator, and decline in higher latitudes, creating a bimodal gradient. Here we show that for a dataset of 50,113 marine animal species, that species turnover peaked at the Equator. Thus, species richness declined where turnover was highest. This high turnover but dip in species richness at the Equator may indicate population fragmentation due to thermal stress. Such fragmentation could be the mechanism behind declining marine species richness in latitudes with an annual mean temperature > 25 °C.

One Sentence Summary: The latitudinal gradient in species turnover but not species richness is unimodal, with a peak at the Equator.

1. Introduction

With over 1,000 papers, the latitudinal gradient in species richness is the most discussed global biogeographic pattern in the literature (Hillebrand, 2004; Tittensor et al, 2010; Brown, 2014; Chaudhary et al., 2016). The two main types of gradients reported are unimodal (with the highest richness at the equator) and bimodal (with a richness dip at the equator). Recently, Chaudhary et al. (2017), showed that, overall, marine taxa exhibit bimodality when richness is measured as alpha (local) or gamma (regional) diversity and rarefied richness to account for sampling bias. Alpha and gamma diversity do not measure variations in species composition between samples in a geographic region or among geographic regions (Melo et al., 2009). Faunal differences within and among geographic regions are measured using beta diversity measurements, which estimates species turnover and nestedness (Vellend, 2001; Legendre et al., 2005; Baselga, 2010; Chiu et al., 2020). Dividing beta diversity into components is important to understand the processes behind latitudinal diversity gradients over long periods of time (Tomašových et al., 2016; Chiu et al., 2020). Two scenarios dominate changes in species composition among sites: (1) replacement of one species with another species along a spatial, temporal, or environmental gradient, also known as species turnover (Harrison et al., 1992) and (2) no replacement of species along the gradient but yet a loss or gain in species. This latter scenario results in sites poorer in species' number is a subset of, and "sink or nested within" the neighbouring site having more species known as "source" (Baselga, 2010; Baselga et al., 2012; Tomašových et al., 2016; Chiu et al., 2020). In both scenarios, the two sites would have different species composition. However, in scenario two, the difference in overall richness would cause dissimilarity among the sites (Simpson, 1943). The component of beta diversity that accounts for the proportion of dissimilarity due to the difference in species richness is defined as "Nestedness" (Baselga et al., 2012).

Spatial turnover in diversity can vary independently of alpha and gamma diversity because species composition may change even if the actual number of species can stay the same. Thus, the latitudinal gradient in species turnover can be used as a proxy of change in species composition, such as due to regional endemicity and/or habitat heterogeneity. A latitudinal peak in beta diversity may thus indicate the presence of regions contrasting in species composition due to geographic barriers, and low extinction and/or high speciation rates on evolutionary time scales. Low beta diversity may indicate a latitude with high connectivity and gene flow such that the same species occupy wide

ranges. Shifting species ranges may arise from climate change (Melo et al., 2009), and may be better detected by beta than alpha and gamma diversity.

The general latitudinal gradient in beta diversity has been reported as unimodal as had generally been the case for species richness (Rodríguez & Arita, 2004; Adler & Lauenroth, 2003; Blackburn & Gaston, 1996a,b; Soininen et al., 2018; Chiu et al., 2020). Some examples include (a) owls of North and South America (Koleff et al., 2003), (b) North American non-flying mammals (Rodríguez & Arita, 2004), vascular plants (Qian & Ricklefs, 2007), and mammalian fauna (Qian et al., 2009), (c) amphibians at a global scale (Baselga et al., 2012), and (d) and ostracods in Western North Atlantic (Chiu et al., 2020). However, such generalisations have been contradicted in some cases, such as for bats in North America (Rodríguez & Arita, 2004), birds in North and South America (Blackburn & Gaston, 1996b) and cacti in Argentina (Mourelle & Ezcurra, 1997). The differences have been attributed to the use of different spatial grid sizes, taxa, and measures of beta diversity (Blackburn & Gaston, 1996a).

In the marine environment, beta diversity has been reported to decline with increasing latitude and depth (Hatosy et al., 2013; Anderson et al., 2013). However, these studies were based primarily at regional scales and only for bacteria, demersal fish and coral reefs (Hatosy et al., 2013; Anderson et al., 2013; Harborne et al., 2006). On a global scale, only bacteria (Zinger et al., 2011) and biogeographic realms (Costello et al., 2017) have been mapped but did not clearly show how beta diversity changed with latitude. In this paper, we provide the most comprehensive and holistic assessment of the latitudinal gradient in marine beta diversity to date. We use a global dataset of over 50,113 fish, molluscs, crustaceans and other species.

At a local scale, Koleff and Gaston (2002) found a negative relationship between species richness and turnover for birds in south-east Scotland, whereas, Blackburn and Gaston (1996b) reported a positive linear relationship for birds in North and South America. Other studies stated that species richness is independent of turnover, and the relationship is scale-dependent (McCain & Beck, 2016; Tuomisto et al., 2017). We provide the first global-scale comparison of the relationship between marine species richness and turnover and whether they follow the same gradient with latitude.

On land, phenomena such as island isolation, precipitation, soil, and altitude complicate spatial patterns in beta diversity (Costello and Chaudhary, 2017; Costello et al., 2017). Analyses of beta diversity in the ocean may better illustrate how species have evolved in relation to latitude because there are fewer absolute barriers in the ocean than land (Costello et al., 2017). The most commonly discussed explanations of latitudinal gradients in species diversity are: area (Willig & Presley, 2018), temperature (Brayard et al., 2005), and habitat availability (Dunn et al., 2017; Paxton et al., 2017). Because the tropics have most ocean area and the warmest and most stable temperatures, we may expect them to have low beta diversity, and beta diversity to increase in more seasonal high latitudes. Here we explore the correlation of marine beta diversity with long-term averaged sea surface temperature (SST), and geographical variables indicating available habitat area (ocean area, land area and the proportion of oceanic shelf). We include both land and ocean areas because these are not the inverse of each other due to the curvature of the Earth, and we used the Clark-Evans index to test for spatial aggregation effects.

2. Methods

2.1. Species data

We used the same distribution data (50,113 species) that were selected for the calculations of ES50 in ~ 50,000 km² hexagons in Chaudhary et al. (2017). The species occurrences were binned in 50,000 km² hexagons. This scale was chosen based on preliminary analyses to ensure sufficient data within each spatial scale to reduce the effects of

sampling bias. The data used are available at https://doi.org/10.17608/k6.auckland.12672884.v1. As the species incidences were based on varying numbers of samples (Chaudhary et al., 2021), we resampled the species incidences per 1000 samples using rarefaction with the help of "Vegan" package (Oksanen et al., 2018) to provide an incidence matrix adjusted for sampling bias.

2.2. Temperature and geographic variables

Monthly sea surface temperature (SST) data in °C were downloaded from the Hadley Centre Global Sea Ice and Sea Surface Temperature database (Meteorological Office and Centre, 2006). To match the temporal range of species distribution data, the temporal range of the SST data was 1920–2015 at a scale of 1° x 1° latitude-longitude cells. To analyse the relationship between SST and beta diversity, the monthly averaged SST over the 95 years was calculated and extracted for each sample's location using the point extraction method in ArcGIS 10.3.3. These SSTs were then averaged for each 5° latitudinal band and ~ 800,000 km² hexagons.

For further analysis, we used ocean area and land area and the proportion of oceanic shelf as the geographic variables in each 5° latitudinal band. Ocean and land area were calculated for each 5° latitudinal band in ArcGIS 10.3.3. Data for the continental shelf were downloaded from Harris et al. (2014). The proportion of oceanic shelf was calculated as a ratio of shelf area to ocean area in each 5° latitudinal band and 800,000 km² hexagons.

2.3. Spatial aggregation index

Beta diversity patterns can also be influenced by spatial aggregation (clumping) of sampling stations, which may cause high compositional similarity for species where sites are close together (Tuomisto & Ruokolainen, 2006). Thus, it is important to consider the spatial distribution of samples while studying gradients in beta diversity (Tuomisto & Ruokolainen, 2006). The spatial aggregation of samples can be estimated using the nearest-neighbour distance analysis approach (Clark & Evans, 1954). In this method, the distance between the individual samples is measured, irrespective of direction, and the mean distance value is calculated. Also, a randomised mean value of the distance is measured. The ratio of observed mean to expected (random) mean distance then gives an estimate of a sample's deviation from a random distribution (Clark & Evans, 1954).

The spatial aggregation in samples was calculated using the Clark Evans index as a measure of clustering or dispersion of samples per 5° latitudinal band and 800,000 km² hexagon. It is defined as the ratio of the mean distance of the nearest neighbouring samples to the expected distance under complete randomness (Poisson process) (Clark & Evans, 1954). A value near zero indicates aggregation, and a value near one indicates randomness. The index, corrected for edge effect using Kaplan-Meier type edge correction, was measured in R using package "spatstat" (Baddeley et al., 2015) and packages "sp" (Pebesma & Bivand, 2005; Bivand et al., 2013), "rgdal" (Bivand et al., 2018), "maptools" (Bivand & Lewin-Koh, 2017), "rgeos" (Bivand & Rundel, 2018), and "reshape" (Wickham, 2007).

2.4. Beta diversity measures

The most commonly used direct measures of beta diversity are Jaccard's index and Sørensen's index (Baselga, 2010). However, species richness influences both of these measures (Qian and Ricklefs, 2007; Simpson, 1943). The Simpson's index of beta diversity is independent of species richness (Soininen et al., 2018; Baselga, 2010). Both the Sørensen's and Simpson's indices account for spatial turnover in species composition between sites. Because the Sørensen's index combines turnover (Simpson's) and Nestedness, the Nestedness index is calculated as a difference between the Sørensen's and Simpson's indices (Baselga,

2010).

Conventionally, beta diversity measures have been applied as similarity coefficients (e.g., Sørensen) between pairs of sites. The resulting resemblance matrix can be shown as a hierarchical dendrogram, with site clusters representing a community of species in a region. The similarity coefficients are typically averaged to calculate the beta diversity of the region; and this method is known as group-averaged pairwise dissimilarity (Soininen et al., 2018) and has been widely used in the literature (Soininen et al., 2018; Gaston et al., 2007; Leprieur et al., 2011). However, it has also been criticised because it does not recognise the patterns exhibited by the co-occurrence of species in more than two sites (Baselga, 2013). To overcome this, "multiple site comparisons" are used to compare more than two local sites within a region to estimate beta diversity of that region. Thus, the use of "multiple site comparisons" over "pairwise comparisons", while studying the heterogeneity within any region, has been recommended (Baselga, 2010, 2013).

Here, we calculated beta diversity, species turnover and nestedness, within regions, at two spatial scales (5° latitudinal band and *c.a.* 800,000 km² hexagon), using smaller hexagons (*c.a.* 50,000 km²) as local and multiple sites (Figure S1). To standardise the comparison of beta diversity among regions, we used a constant number of local sites. Fifteen local sites within each 5° latitudinal band and three sites within each 800,000 km² hexagon were chosen for the analysis. We chose these numbers because they were the minimum at each respective scale. The Sørensen's (beta diversity), Simpson's (species turnover) and Nestedness indices were calculated as an average based on 100 random comparisons among the local sites in their respective regions. All the calculations were carried out using the package "Betapart" in R (Baselga & Orme, 2012). The ~ 800,000 km² hexagons were used to map longitudinal variation in beta diversity.

2.5. Model selection (beta diversity-latitude relationship)

We first used linear regression modelling to assess the effect of latitude after accounting for the effect of the Clark Evans index on the beta diversity, species turnover and nestedness, in both 5° latitudinal bands and 800,000 km² hexagons. The multiple R^2 explained by the latitude and Clark Evans index was <0.07, which suggested that the models did not fit the data well. Thus, we tested for the change in slope in the linear regressions of the beta diversity, species turnover and nestedness indices against latitude using a P-score test. This tests the null hypothesis that the change in slope is zero (Muggeo, 2016). A significant change in slope was found at both the spatial scales in the three indices (P < 0.05). We then used piecewise regression modelling to fit the data with the highest variance best explained (multiple R^2) the three indices by latitude. A piecewise regression presumes that the co-variables have more than one linear relationship and can be depicted by two or more straight lines joined at a breakpoint, where the slope's linearity changes (Muggeo, 2008; Muggeo & Muggeo, 2017). For piecewise regression modelling, we used the package "segmented" (Muggeo & Muggeo, 2017). To simplify the analysis, we chose latitude (2.5°N) at which the slope linearity changed (and ± 95 % CL overlapped) in both the species turnover and nestedness, as a common breakpoint in both the scales. There was a significant increase in the R^2 in the models with piecewise compared to simple linear regression (Table S4).

2.6. Variation in species turnover and nestedness explained by SST and geographic variables

The species turnover and nestedness indices were correlated with the environmental and geographical variables, considering all the latitudes, and north and south of the breakpoint. We used the Pearson correlation coefficient, corrected for spatial autocorrelation with Dutilleul's correction (Dutilleul, 1993; Dutilleul et al., 1993), following Baselga et al. (2012), for both 5° latitudinal bands and 800,000 km² hexagons. This test was performed using the package SpatialPack" (Vallejos et al.,
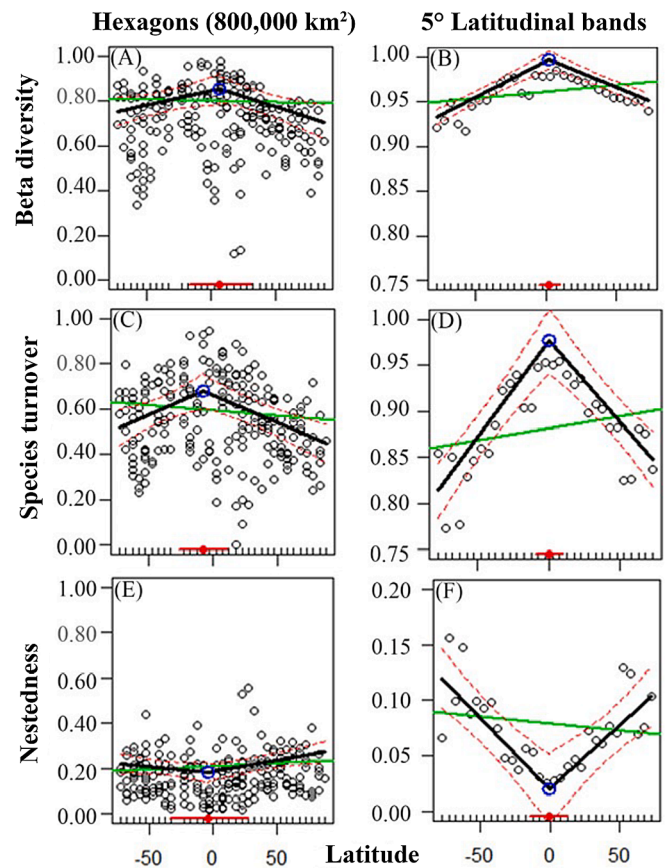

Fig. 1. Latitudinal gradient in beta diversity. The top row of figures is beta diversity; the middle row is species turnover, and the bottom row is nestedness based on multiple sites within hexagons (800,000 km²) and 5° latitudinal bands. Black lines represent the piecewise regression trend lines. Red dashed lines show ± 95 % CL. Red dots indicate the breakpoint in the slopes on latitude and the associated red lines are ± 95 % CL. The green line is the linear regression trend line for the whole model. Note the variation in scales. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2018).

To identify the combined and sole effect of these environmental and geographical variables on the species turnover and nestedness indices, we used linear regressions and partial regressions. For 5° latitudinal bands, the colinear variables, based on the Pearson correlation coefficient, were assessed in separate models.

For comparison of species turnover (within 5° latitudinal band) with gamma diversity, species richness was calculated as the predicted number of species per 5° latitudinal band after accounting for the number of samples in a Generalised Additive Model (GAM) (Chaudhary et al., 2021). We then modelled the species turnover (as a response variable) using species richness (as a predictor) per 5° latitudinal band with the help of a GAM with.

species turnover ~ s(Species richness, k = 5), family = gaussian(link = "log").

3. Results

Species turnover, as the Simpson's index and overall beta diversity, peaked at the Equator and declined in higher latitudes, resulting in a significant unimodal latitudinal gradient (Fig. 1 A-D; Table S1). This was the case for both the spatial scales of 5° latitudinal bands and ~ 800,000 km² hexagons. Additionally, we observed regions of low turnover at the tropics. In contrast, nestedness declined in the tropics and increased in
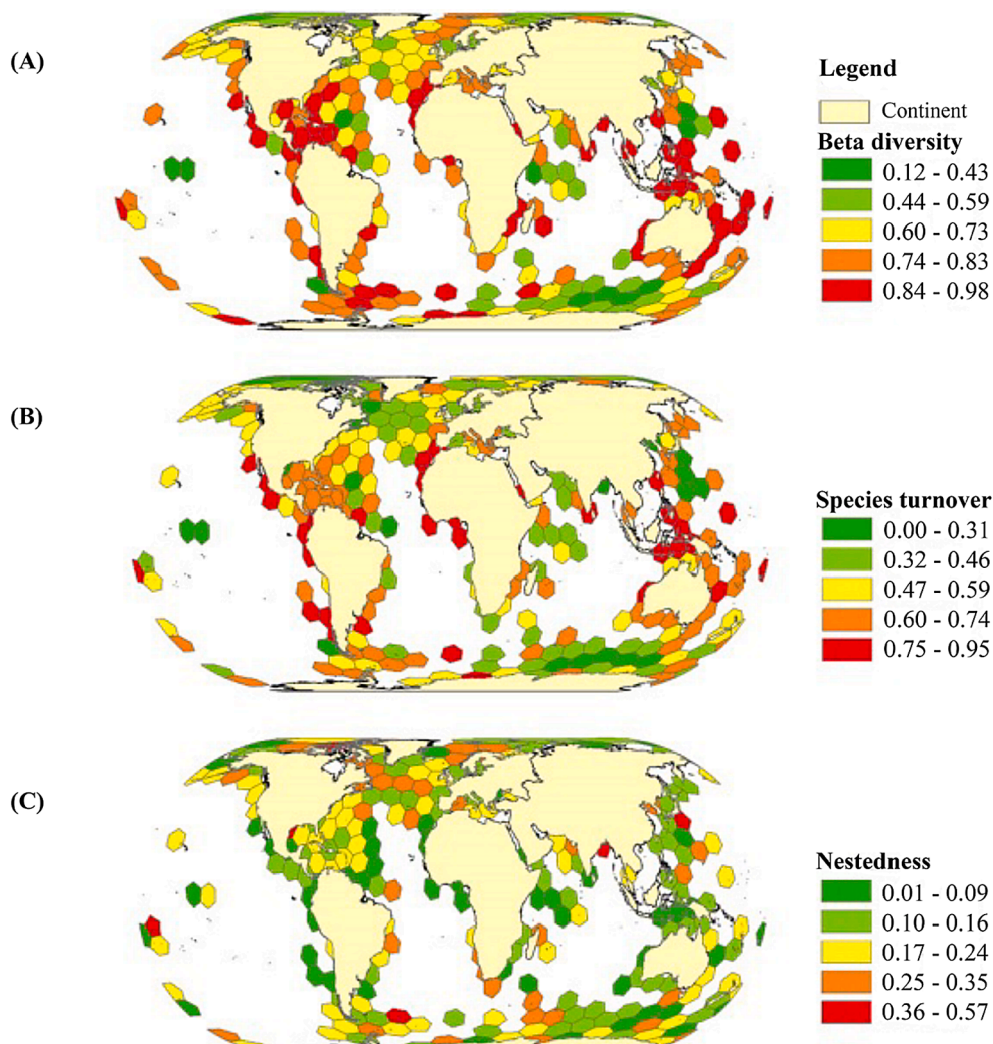
Fig. 2. Longitudinal variation in beta diversity. (A) beta diversity, and its components- (B) species turnover, and (C) nestednesss based on multiple sites (50,000 km^2) in each 800,000 km^2 hexagon. The values of the indices are colour coded from red (highest) to green (lowest). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the higher latitudes (Fig. 1 E-F).

Species turnover was highest in the coastal tropics and sub tropics, namely the Indo West Pacific, mid-west Atlantic Ocean, and the East Pacific Ocean (Fig. 2 A, B). In contrast, nestedness tended to be higher in polar seas (Fig. 2C).

SST and the geographical variables showed significant collinearity (Fig. 3). The correlation was positive with ocean area (R = 0.81, P < 0.001) and land area (R = 0.51, P < 0.001), and negative with the proportion of oceanic shelf (R = -0.45, P < 0.001). SST was positively correlated with species turnover (Tables 1 & 2) and explained 77 % and 28 % of the total variation in the turnover in both 5° latitudinal bands and 800,000 km^2 hexagons, respectively (Tables S2 & S3). The correlation was negative with the Nestedness index (Tables 1 & 2). Similarly, ocean area and land area were positively correlated to the species turnover and negatively to the nestedness (Table 1). In a separate model, ocean area, land area and the Clark Evans index, together explained 72 % and 57 % of the total variation in the turnover and nestedness, respectively (Table S2).

Species turnover increased with increasing SST and ocean area and reached a maximum at 28 °C in the tropics where ocean area is the largest (Fig. 3). Moreover, it increased with increasing land area, reached a maximum in the tropics and levelled off in the northern hemisphere (25°N-55°N) where the land area was greatest (Fig. 3). The

levelling off was reflected in the insignificant low percentage of total variation in the turnover explained by land area in the northern hemisphere (Table S2).

In contrast to species turnover, nestedness increased with decreasing SST and ocean area in the higher latitudes. The relationship with land area was only significant in the southern hemisphere, where nestedness increased with decreasing land area. It did not decrease with increasing land area in the northern hemisphere (Fig. 3). The proportion of oceanic shelf was not significantly correlated to either the species turnover and nestedness in the 5° latitudinal bands (Table 1). However, this correlation was significant for the 800,000 km^2 hexagons (Table 2, Table S3).

Species turnover increased with increasing species richness (Fig. 4 A) but levelled off where the temperature was highest at the Equator (Fig. 3). Species richness declined at 28 °C, where turnover peaked (Figs. 3 and 4 B).

4. Discussion

We found that the latitudinal gradient in marine species turnover across regions was unimodal, with a peak at the Equator, whereas nestedness showed the opposite gradient. We minimised the bias due to the number of samples and spatial aggregation (see Methods). However, methodological, sampling coverage and/or taxonomic bias may
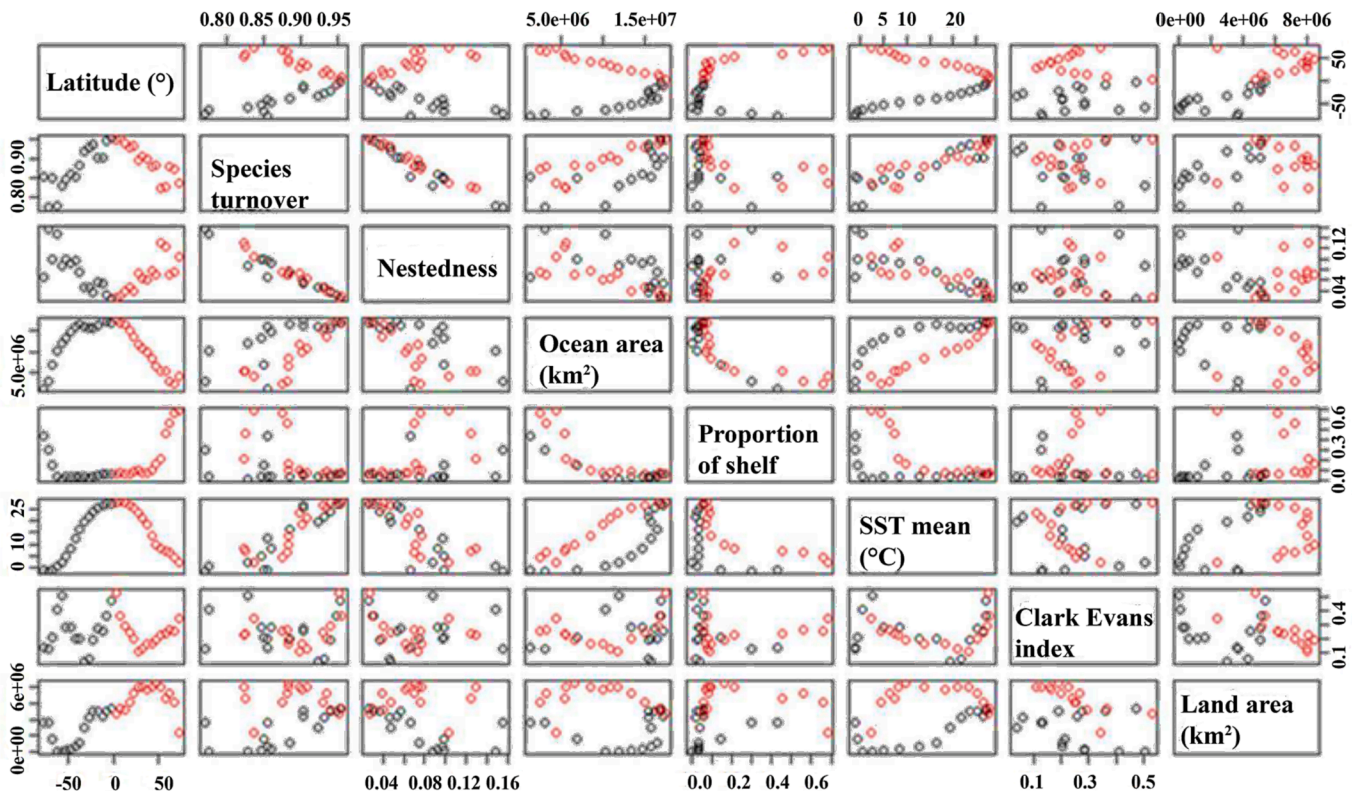
Fig. 3. Beta diversity indices versus temperature and geographical variables. Scatterplots showing the relationships between latitude (°), the species turnover and nestedness, ocean area, the proportion of oceanic shelf, SST mean (°C), Clark Evans index, and land area in each 5° latitudinal band (n = 34). The red colour represents the northern hemisphere, and black represents the southern hemisphere. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Correlation of the species turnover and nestedness with SST and geographical variables in 5° latitudinal bands (all latitudes, before and after the breakpoint) (Fig. 1). The Pearson correlation coefficient (R) was corrected for spatial autocorrelation with Dutilleul's correction. P-values are given in parentheses and bold numbers show significant correlations (significance level is P < 0.05 = *, < 0.01 = **, < 0.001 = ***). DF = degree of freedom.

Index	DF	SST (°C)	Ocean area (km²)	Land area (km²)	The proportion of oceanic shelf
Species turnover					
All latitudes	29	**0.89*****	**0.64***	**0.40***	−0.36
North of + 2.5° latitude	13	**0.89***	**0.86***	−0.09	−0.66
South of + 2.5° latitude	14	**0.89*****	**0.67****	**0.58****	−0.34
Nestedness					
All latitudes	29	**−0.81*****	**−0.60***	**−0.32****	0.31
North of + 2.5° latitude	13	−0.80	−0.76	0.14	−0.55
South of + 2.5° latitude	14	**−0.82*****	**−0.58*****	**−0.66***	0.24

Table 2

Correlation of the species turnover and nestedness with SST and geographical variables in 800,000 km² hexagons (all latitudes, before and after the breakpoint) (Fig. 2). The Pearson correlation coefficient (R) was corrected for spatial autocorrelation with Dutilleul's correction. P-values are given in parentheses and bold numbers show significant correlations (significance level is P < 0.05 = *, < 0.01 = **, < 0.001 = ***). DF = degree of freedom.

Index	DF	SST (°C)	The proportion of oceanic shelf
Species turnover			
All latitudes	184	**+0.32*****	**−0.25*****
North of + 2.5° latitude	104	**+0.41*****	**−0.27****
South of + 2.5° latitude	76	**+0.21***	−0.12
Nestedness			
All latitudes	184	**−0.14***	**0.15***
North of + 2.5° latitude	104	−0.08	**0.17***
South of + 2.5° latitude	76	**−0.24***	0.03

depth, as well as latitude and longitude.

Shallow depths, notably the continental shelves, contain all the ocean biomes, that is, areas of three-dimensional plant assemblages providing primary productivity and habitats for many other species, such as coral reefs, seagrass meadows, and mangrove and kelp forests (Costello et al., 2017; Jayathilake & Costello, 2018; Parker et al., 1983; Zhao et al., 2020). Coral reef ecosystems alone contain about one-third of all marine species (Costello, 2015). The variability in the distribution of biogenic shelf habitats combined with geographical and environmental barriers may cause these habitats to harbour different species assemblages, even if they share the same latitudes and temperature (Allen & Gillooly, 2006; Costello & Chaudhary, 2017; Gaylord & Gaines, 2000). For example, coral reefs, mangroves, and salt marshes cover 0.14–0.25 % of the ocean area between + 27° and −27° latitude but

nevertheless have influenced the data quality. Due to the lack of published data for the deep sea, our analysis was limited mostly to the coastal regions. We expect there to be reduced beta diversity with depth because species endemicity decreases with depth (Costello et al., 2017; Costello & Chaudhary, 2017; Zintzen et al., 2017). However, additional deep-sea data is necessary to allow comparisons of beta diversity with
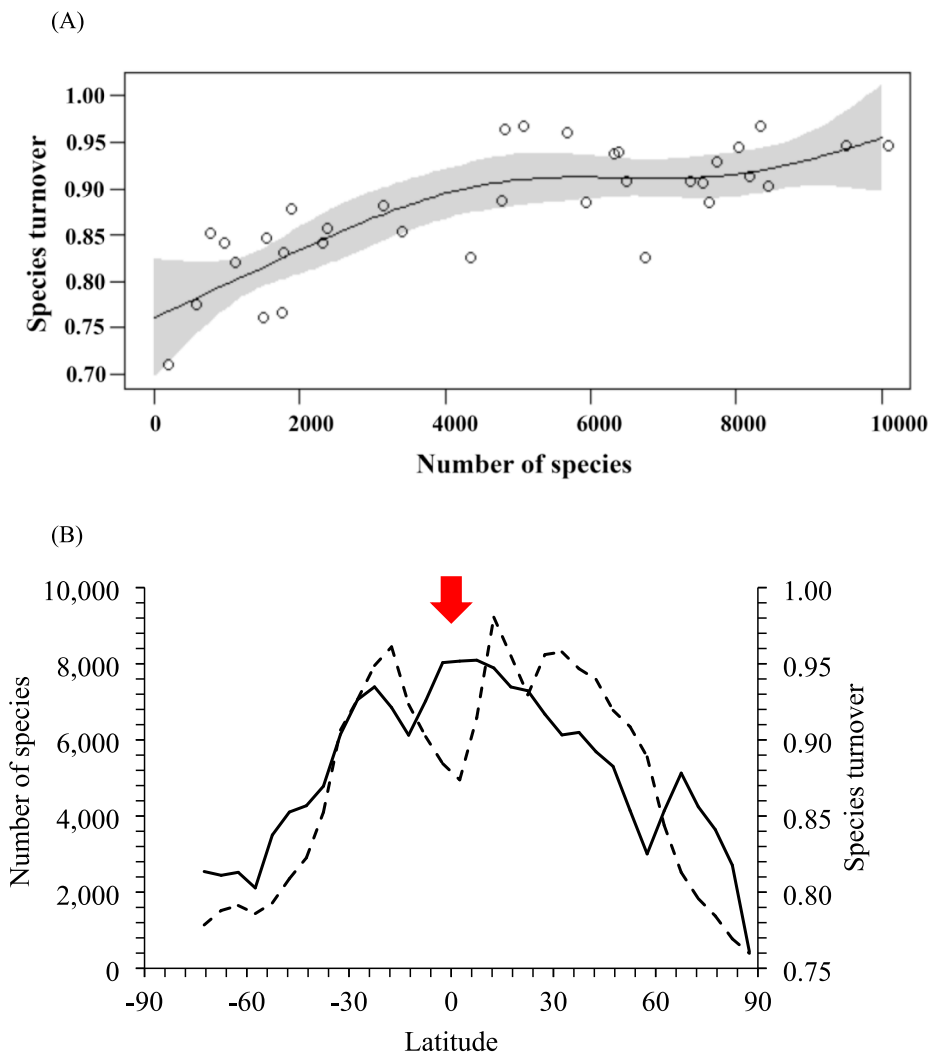
(A)

Fig. 4. Species richness versus turnover and their latitudinal gradient. (A) Relationship between species richness and the species turnover per 5° latitudinal band. The best-fit trend line is based on the GAM (Species turnover ~ s(Species richness, k = 5), family = gaussian(link = "log")) and the grey shaded area is the ± 95 % CL. (B) The latitudinal gradient (based on 5° bin) in the number of species (gamma diversity) (dashed line) and turnover (solid line) shown as a two-point moving average. Note the dip in species richness, but peak in turnover at the Equator (highlighted by a red arrow). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(B)

cover<0.15 % in higher latitudes. Similarly, because seagrass occupies more area in the tropics than in higher latitudes, its meadows further increase habitat heterogeneity (Jayathilake & Costello, 2018). High turnover in bryozoans in the lower latitudes of the North Atlantic (Clarke & Lidgard, 2000), and the variation in the tropical and temperate community structure of reef fish (Ebeling & Hixon, 1991) have also been attributed to habitat heterogeneity (Sanciangco et al., 2013). It is thus expected that more biogenic habitat heterogeneity along with geographical barriers would induce higher species turnover than in less heterogeneous habitats with fewer geographical and environmental barriers. That this has occurred on evolutionary timescales is apparent from there being greater species endemicity in coastal than mid-ocean regions (Costello et al., 2017; Cermeño et al., 2022; Song et al., 2020; Chiu et al., 2020). We attribute the greater nestedness at higher latitudes to larger ocean connectivity within and across latitudes.

In contrast to species richness which decreased at the Equator where the temperature was highest (Chaudhary et al., 2016, 2017, 2021), we found highest species turnover (Fig. 4B). We would have expected species richness to be highest where turnover was highest, as was generally the case (Fig. 4A). The equatorial dip in species richness appears due to excessive sea temperatures (Chaudhary et al., 2021; Yasuhara et al., 2020; Yasuhara & Deutsch, 2022; Mori et al., 2022), as also suggested by our data (Fig. 3). This equatorial peak in turnover could be because the tropics have high endemicity and habitat heterogeneity resulting in the highest number of biogeographic realms (Costello et al., 2017). This supports the hypothesis that the equator acts as a

cradle and museum of species evolution (Jablonski et al., 2017). However, under climate change, the tropics are too hot even for tropical warm water species, and they escape to higher latitudes (Yasuhara & Deutsch, 2022). Our results indicate that this is associated with higher turnover and lower nestedness.

Predictions that warming temperatures would cause species to shift their distribution (Brown et al., 2022; Colossi Brustolin et al., 2019; Burrows et al., 2019) have been confirmed by observations at a global scale (Chaudhary et al., 2021). As species decline in the parts of their range due to climate warming, their populations are likely to become disintegrated and decline because of local variation in their habitat suitability and climate change-driven habitat fragmentation. The low turnover hexagons observed here might be due to the remaining species being more widespread, resulting in assemblage homogenisation (Magurran et al., 2015; Ellingsen et al., 2020) within and between latitudes. However, whether the gradient and its steepness are changing over time, such as due to climate warming, remains unknown. Thus, the cause of the pattern observed here remains to be tested through analysis of time series data.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Acknowledgements

Author contributions

Chhaya Chaudhary developed the research question and conducted the data analysis and led writing of the manuscript.

Mark J Costello contributed in framing the research question and methodology, and writing the manuscript.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2022.102941.

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