

## **The effect of increasing sea surface temperatures (SSTs) on tropical and temperate fish biodiversity**

**Group 3:** Bulmer, Stuart (1202357); Dolanjski, Mya (1132674); Landon, Celeste (1354393); Nwafor, Ijeoma (1126294); Padiasek, Lukasz (1168988)

Rising sea surface temperatures (SSTs) are expected to have a significant impact on marine fish biodiversity. Ectothermic species, such as fish, are highly sensitive to temperature changes, which affect key biological processes such as reproduction, growth and metabolism [1]. The Climatic Variability Hypothesis (CVH) suggests that species' in high-seasonality regions, such as temperate, have broader and more adaptable thermal tolerances, while regions with lower climatic variability tend to have narrower tolerances [4, 11]. Tropical fish species have been found to have the narrowest thermal tolerances and are anticipated to experience the steepest rates of species redistribution and loss [1, 5]. Recent studies have suggested that rising SSTs will disrupt the latitudinal diversity gradient, threatening ecosystem function, undermining the delivery of essential ecosystem services and causing drastic socio-economic impacts [1,5,7]. Predicting biodiversity changes across ecosystems and clades is therefore essential in guiding conservation efforts and resource management decisions [5].

While temperature-related biodiversity changes have been studied, the relationship between these changes and species' thermal tolerance is underexplored. Data on thermal physiological traits is limited, with most studies focused on limited taxonomic groups and geographical areas [13]. Tropical regions, in particular, are underrepresented in research, raising concerns about our ability to address threats to these vulnerable areas [6]. Further analysis on experimentally derived species' thermal tolerance datasets is crucial for advancing our understanding as more taxa and geographic contexts are incorporated.

Our study investigated how rising SSTs in the northern hemisphere influence biodiversity rates of marine fish species in temperate and tropical regions. We hypothesize (H1) that rising SSTs will

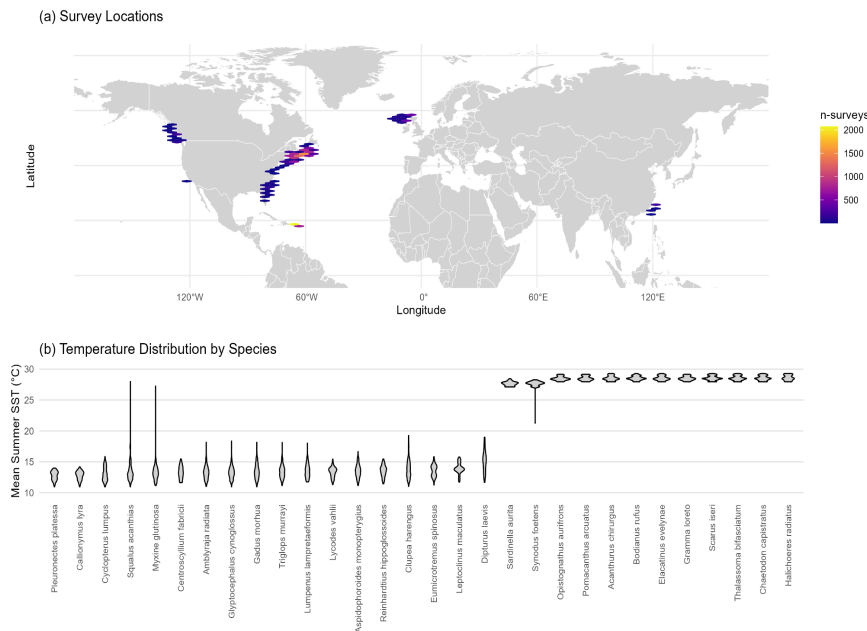
increase species richness in temperate regions and decrease species richness in tropical regions. To investigate this hypothesis we predicted that in temperate regions, differences in species composition will increase over time, resulting in a higher beta diversity measurement. While in tropical regions, differences in species composition will decrease over time, resulting in a lower beta diversity measurement. Additionally, we hypothesize (H2) that marine fish species with a broader thermal tolerance range are more resilient to long-term changes in temperatures than fish species with narrower thermal tolerance ranges. Therefore, we predict that rising SSTs will cause greater declines in abundance in tropical fish species, associated with narrow thermal tolerance ranges, while temperate fish species, associated with broader thermal tolerance ranges, will experience less of a decline in abundance.

## Methods

We analyzed these hypotheses using three open source datasets: BioTime, FishBase and the National Oceanic and Atmospheric Administration, NOAA. From BioTime, we selected fish data from the ‘Temperate shelf and seas ecoregion’ and ‘Tropical seas’ biomes, which resulted in 951,566 records from 39 studies spanning 1874-2016 and 4080 species [8]. Species names were standardized using a function that matched taxonomic ranks through the Global Biodiversity Information Facility (GBIF). From this data set we extracted species, spatial, and abundance data which left us 464,569 observations.

Since the dataset lacked thermal tolerance data, we combined it with data from Fishbase using the “rfishbase” R package [3, 9]. We combined Biotime’s abundance, temporal, latitude and longitude data with Fishbases’s minimum (Tmin) and maximum (Tmax) temperature data for each species, resulting in 155 species (144 temperate, 23 tropical) and 61,000 observations. We used a similar standardizing function provided from the package, which matched species names through FishBase’s occurrence data.

Finally, we used the NOAA temperature data from the COBE2 Sea Surface Temperatures (COBE2 SST) from the Japanese Meteorological Center (JMA), which collects long-term climate data in situ and from satellites (1850-present) in a  $0.5^\circ \times 0.5^\circ$  resolution [10]. We extracted SSTs from the temperate ( $23.5^\circ\text{N} - 66.5^\circ\text{N}$ ) and tropical ( $0^\circ\text{N} - 23.5^\circ\text{N}$ ) latitudes in the northern hemisphere, calculating the mean summer SST (July-August). We looked at mean summer temperatures as it is the warmest time of year and these temperatures were likely to be the drivers behind thermal intolerance. This dataframe was then merged with the combined BioTime and Fishbase data by year and location, resulting in a final dataset of 102 species (93 temperate, 17 tropical) across 15,000 observations.



**Figure 1. A: Locations and sampling intensity of species observations and B: Violin plots depicting the temperature distribution of the 30 most frequent species in our dataset.** Our final dataset consisted of a total of 15 059 observations in the northern hemisphere between the years 1963 and 2014. A total of 102 unique species were observed (93 in temperate regions and 17 in tropical regions). N-surveys represent the total number of observations in each location over the duration of the dataset. The violin plot represents the mean summer SST ( $^\circ\text{C}$ ) at the location and year of every observation of a given species.

## Analysis

We confirmed that summer SSTs were changing over time in each region using a linear model to analyze for significance. Temperature observations were not distributed continuously across all latitudes, rather they occurred in patches (Figure 1A). As a result, there is a gap in temperature distribution in the

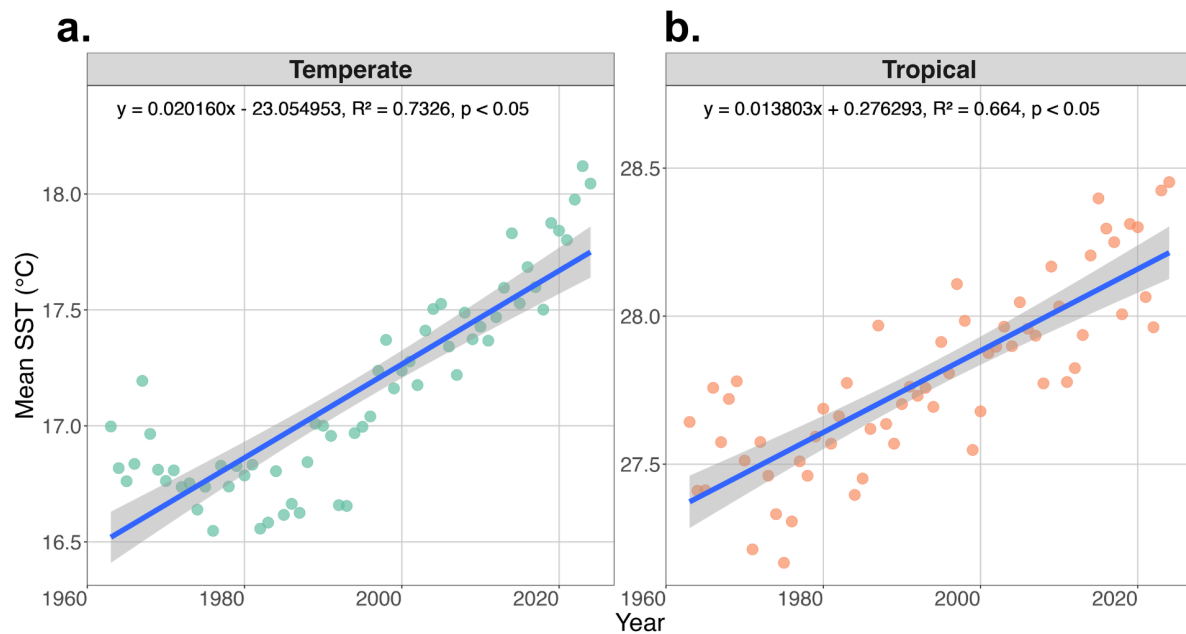
temperate region with no observations in the 20°C - 25°C range (Figure 1B). The same type of clumped distribution of observations occurred in tropical regions with no observations in the nearest latitudes to the equator.

For hypothesis 1, we calculated total abundance, species richness, Shannon diversity and beta diversity. Species richness and total abundance were calculated by grouping data by year, species and SST in their respective regions. This allowed for the most accurate matching of information and estimates. Beta diversity was assessed using Bray-curtis distance over time using a linear regression, to measure how species composition, measured by species richness, differs between temperate and tropical regions and years. Shannon diversity, which accounts for species number and relative abundance, was calculated using species abundance grouped by region and year, and then analyzed with a linear regression.

For hypothesis 2, we used the Tmin and Tmax data available in Fishbase to graph the thermal tolerance range (Tmax-Tmin) for each tropical and temperate species. We then calculated the average thermal tolerance range for both regions' species, to determine which had a broad or narrow thermal tolerance range. We analyzed abundance trends by using latitude and longitude coordinates associated with sampling locations where abundance observations were recorded for each species. Temperate and tropical regions were analyzed separately. For each unique location, we fit a linear regression model to quantify the slope of abundance and determine its trends over time. The slope values were then combined with the thermal tolerance range and Tmax to fit a second linear model. This model examined how variations in the slope of abundance over time could be explained by differences in the thermal tolerance range and Tmax across species and locations.

## Results

Our analysis of the mean summer SST from the years 1963 to 2024 found a significant increase ( $p < 0.05$ ) in the mean summer SST in both regions with an overall 0.2°C per decade increase in Temperate regions ( $R^2 = 0.7326$ ) (Figure 2A). Tropical regions were warming at half that rate with an increase of 0.1°C ( $R^2 = 0.644$ ) (Figure 2B).

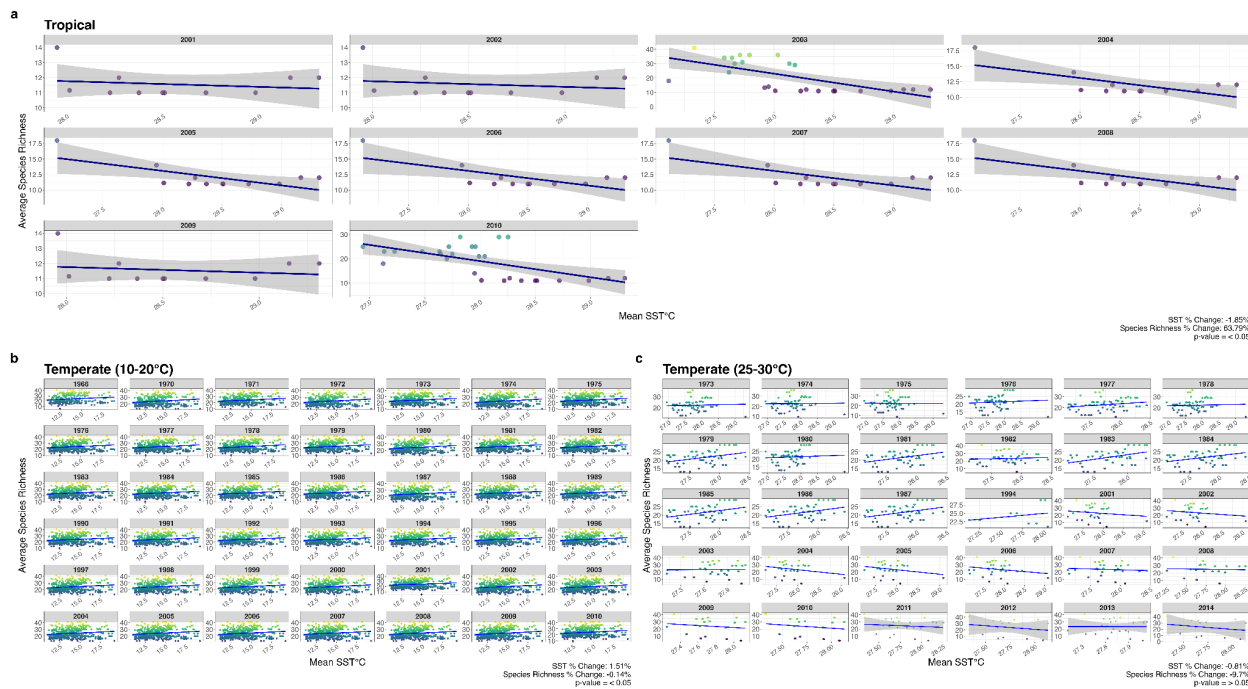


**Figure 2. Scatter plots of the mean summer SST (°C) in temperate (A) and tropical (B) regions between the years 1963 and 2024.** NOAA temperature data from the COBE2 Sea Surface Temperatures was used to calculate the mean SST across each region for the months of July to August (inclusive) in the northern hemisphere. Scatter plots depict the individual means for each year. A linear model found a significant ( $p < 0.05$ ) increase in mean summer SST for each region with tropical regions experiencing a 0.01°C ( $R^2 = 0.644$ ) increase per year and temperate regions experiencing a 0.02°C ( $R^2 = 0.7326$ ) increase per year.

### *Hypothesis 1*

In tropical regions, we observed a 1.85% decrease in mean SST and a 63.79% increase in species richness (Figure 3a). While this had a significant relationship ( $R^2 = 0.3051$ ,  $p < 0.05$ ) the variability in sampling data limited its accuracy. In temperate regions (0–20°C), SSTs increased by 1.51%, while

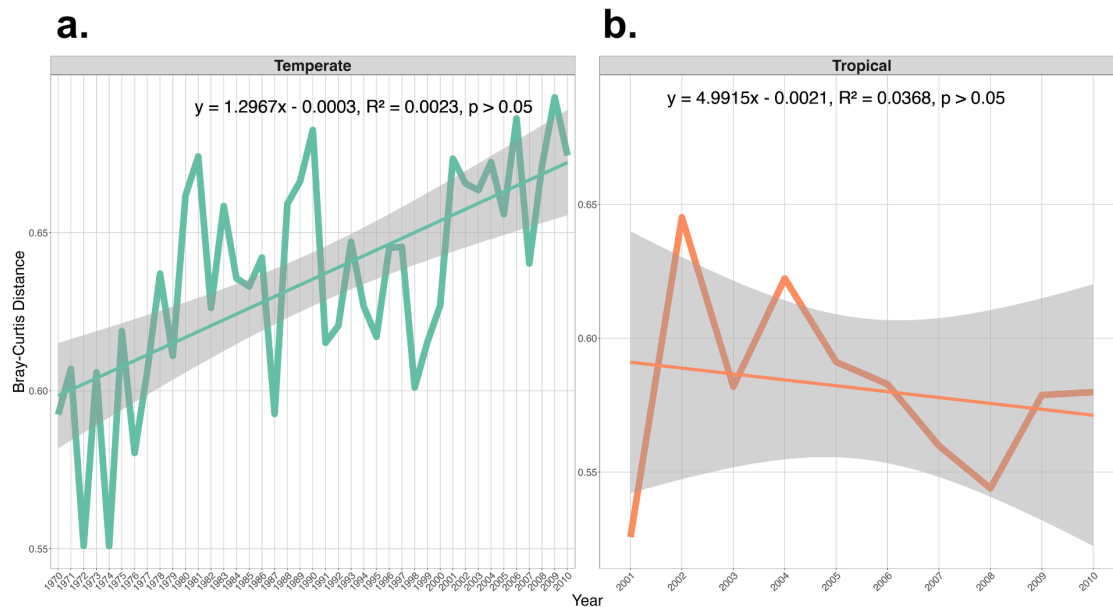
species richness declined by 0.14% (Figure 3b). This linear model yielded a significant relationship ( $R^2 = 0.02561$ ,  $p < 0.05$ ). At temperatures above 25°C, higher data variability due to limited species richness reduced reliability, yet we observed a 0.31% decrease in SST and a 9.7% decline in species richness ( $R^2 = 0.0019$ ,  $p > 0.05$ ) (Figure 3c).



**Figure 3.** Scatterplots of the average species richness and summer SST (°C) in the tropical region from 2001 to 2010 (a), in the temperate region from 10°C and 20°C from 1966 to 2010 (b) and between the temperatures of 25°C and 30°C from 1973 to 2014. Linear models were used to analyze the relationship between mean sea surface temperature and average species richness each year. For tropical regions there was no consistent trend for the relationship between species richness and temperature. However there was a significant ( $p < 0.05$ ) increase in species richness (63.79%) when comparing 2010 to 2001. In temperate regions between 10°C and 20°C, a significant relationship ( $p < 0.05$ ) between decrease in species richness (0.14%) and temp was detected when comparing 2010 to 1966. In temperate regions between 25°C and 30°C, there was no consistent trend for the relationship between species richness and temperature, however, there was a significant ( $p < 0.05$ ) decrease in species richness (9.7%) when comparing 2010 to 1966.

As predicted in our first hypothesis, there was an increase in beta diversity in temperate regions over the years (Figure 4a). Though this relationship was not statistically significant ( $R^2 = 0.0023$ ,  $p > 0.05$ ) due to the strange distribution of the data. The slope there has a small negative slope, but the trends show a

positive increase in the differences in species composition over years. In tropical regions, we calculated a gradual decrease in species richness over time, with a slope of -0.0021, suggesting a negative relationship between year and the Bray-Curtis distance (Figure 4b). This distribution was not statistically significant ( $R^2 = 0.0368$ ,  $p > 0.05$ ), though this model only explains 3.7% of the variance in Bray-Curtis difference in the tropical region, indicating a weak relationship between the variables.



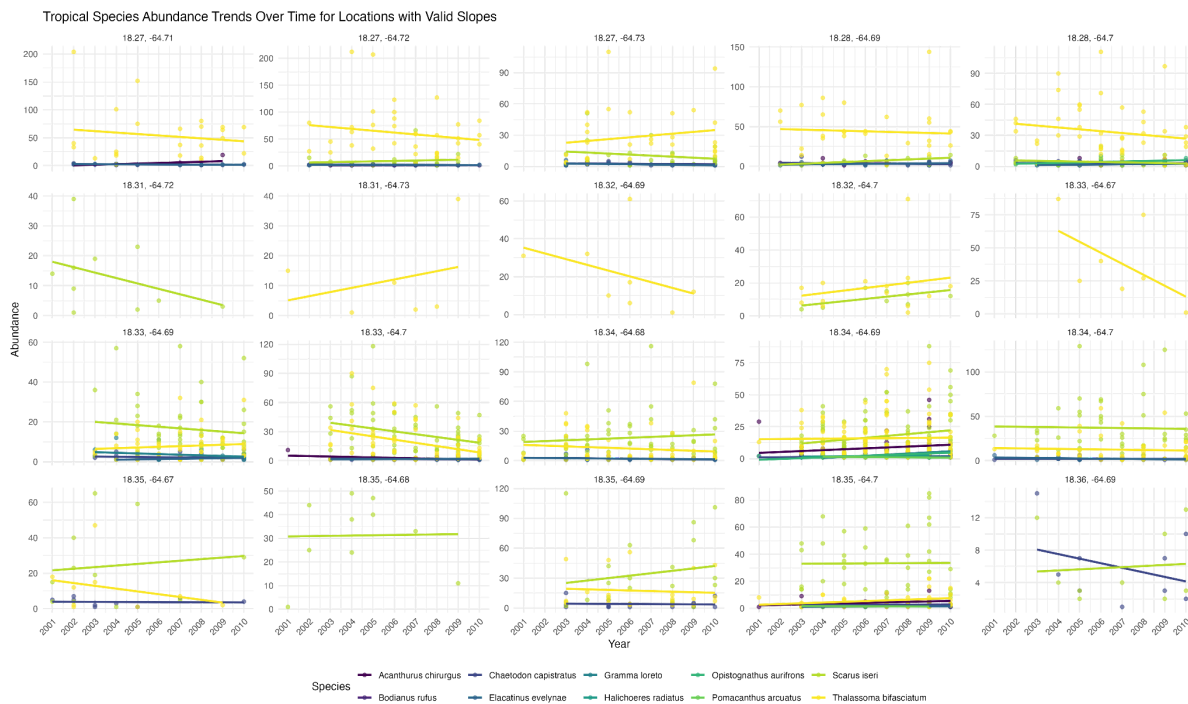
**Figure 4. Line graph of beta diversity (Bray-Curtis distance) calculated between years and regions.** This assessed the relationship between the change in species composition between each year of the two regions. In temperate regions (a), there was an increase in the Bray-Curtis distance from the first to last year, but this was not detected with a significant relationship ( $R^2 = 0.0023$ ,  $p > 0.05$ ). In tropical regions (b), we saw a decrease in the Bray-Curtis distance which also did not have a statistically significant relationship ( $R^2 = 0.0368$ ,  $p > 0.05$ ).

In temperate and tropical regions, we detected a positive increase in the Shannon diversity index ( $p < 0.05$ ) meaning that both regions are becoming more diverse over time (Figure 5). In temperate regions this linear model explains 39.4% of the variance in the Shannon diversity index ( $R^2 = 0.394$ ) (Figure 5a). While in tropical regions it represents 54.3% of the variance ( $R^2 = 0.543$ ), this denotes a strong relationship between the variables (Figure 5b).

## Hypothesis 2

In tropical regions, the average thermal tolerance range was 4.31°C while in temperate regions the average thermal tolerance range was 11.3°C demonstrating, as we predicted, that temperate fish species generally have a broader thermal tolerance range while tropical species generally have a more narrow thermal tolerance range (See Appendix I).

To evaluate whether species' with narrower thermal tolerance ranges were experiencing steeper declines in abundance over time, we fit multiple linear models separately for each latitudinal zone (Figure 6 and 7). This analysis indicated there was no significant relationship between changes in abundance over time (slope) and Tmax (Tropical:  $p = 0.424$ ; Temperate:  $p = 0.798$ ) or thermal tolerance range (Tropical:  $p = 0.280$ ; Temperate:  $p = 0.171$ ) in either tropical or temperate regions. Additionally, the overall model was not significant for tropical ( $p = 0.428$ ) or temperate regions ( $p = 0.358$ ). In tropical regions, the linear model explained only 2.4% of the variance in slopes, while in temperate regions it accounted for 11.9%. These results suggest that changes in abundance over time are not strongly influenced by these thermal traits, as indicated by the low  $R^2$  values across both latitudinal zones.





**Figure 5. Linear regression models showing abundance trends over time for each species and location in tropical regions from 2001 to 2010.** Abundance data was filtered to include models with locations that had a valid slope. The slopes from these models were then used to fit a linear model. The proportion of significant slopes ( $p < 0.05$ ) was 6 out of a total of 72 slopes.

As sampling for abundance was limited in both tropical and temperate datasets, with many locations lacking consistent sampling beyond 5 years, we grouped data by location and species, then calculated abundance slopes for groups with more than 5 unique years of sampling. Despite this approach, our models did not yield significant results for either region, and we were unable to support our hypothesis and predictions. However, we did a further investigation of the slope values and determined that on average, 55% of locations exhibited declining abundance trends, while 32% showed increasing trends in tropical regions. In temperate regions, on average, 34% of locations exhibited declining abundance trends, while 26% showed increasing trends.

## Discussion

Our findings show that differing rates of SST warming ( $0.1^{\circ}\text{C}$  per decade in tropical regions and  $0.2^{\circ}\text{C}$  per decade in temperate regions) affect biodiversity patterns. Our results support Hypothesis 1, providing strong evidence for increased biodiversity in temperate latitudes and moderate evidence for declines in tropical latitudes. Temperate regions exhibited increasing species richness and beta diversity, suggesting warming SSTs facilitate the influx of new species and greater species turnover. However, a linear model also detected a slight decline in species richness over time which may reflect short-term variability in available data or other environmental or physiological factors that were not assessed in this paper. These changes were accompanied by a significant positive trend in the Shannon-Weiner Diversity Index, reflecting a general increase in alpha diversity over time (Figure 9). In tropical regions, a significant increase in species richness of roughly 64% between 2001 and 2010 was observed, but inconsistent sampling and limited data hindered our ability to establish a reliable relationship between temperatures and species richness.

Limited long-term data and inconsistent sampling at the same locations significantly impacted the analysis of Hypothesis 2, making it difficult to evaluate a relationship between changes in abundance over time and species' thermal tolerance ranges. Although tropical species were found to have narrower thermal tolerance ranges, consistent with the CVH, our models did not find significant relationships between thermal traits and abundance changes, likely due to data limitations. Ultimately, the insignificant results from our models, which used thermal tolerance range and upper thermal maximum (Tmax) as predictors, may also suggest that thermal traits alone are insufficient predictors of abundance trends. Population variation, measured by abundance, can be influenced by competition, resource availability and evolutionary processes [7, 12]. Moreover, temperature-driven changes in biodiversity patterns can also be shaped by physiological factors like dispersal ability and abiotic factors such as water depth or light availability [12].

Our lack of significant results highlights the need for more comprehensive datasets, including long-term species abundance records across latitudes, to better evaluate the role of thermal traits in determining population trends. Our dataset included over 12,000 temperate observations but fewer than 3,000 from tropical ones. Missing data and biases towards commercially important species (Atlantic cod, Atlantic herring, and several flatfishes) reduced the representativeness of our sample and the confidence of our results.

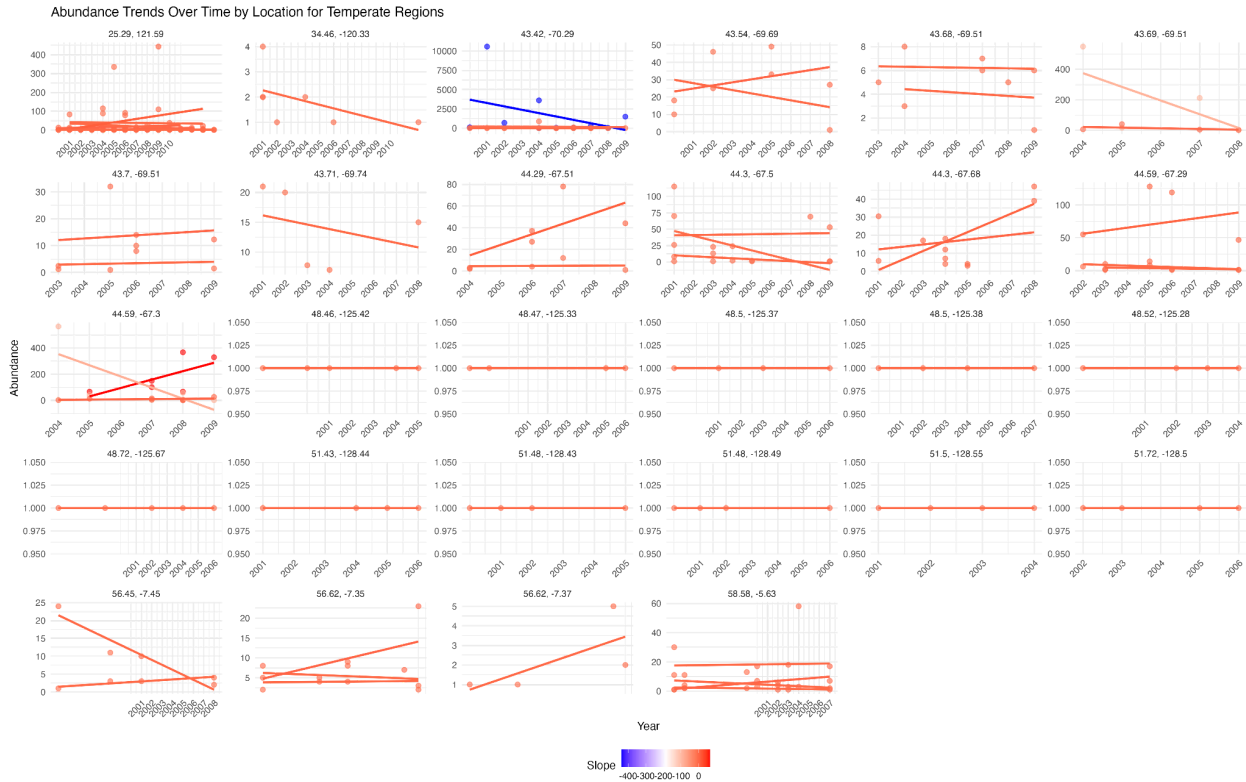
Our analysis has allowed us to amplify concerns relating to the fact that biodiversity in tropical latitudes remains understudied, despite greater declines and vulnerabilities observed in response to rising SSTs. The lack of research in tropical latitudes is concerning, given their vulnerability to biodiversity loss and associated socio-economic impacts. Increased research and targeted policies are essential to mitigate sampling bias and protect marine biodiversity in these regions.

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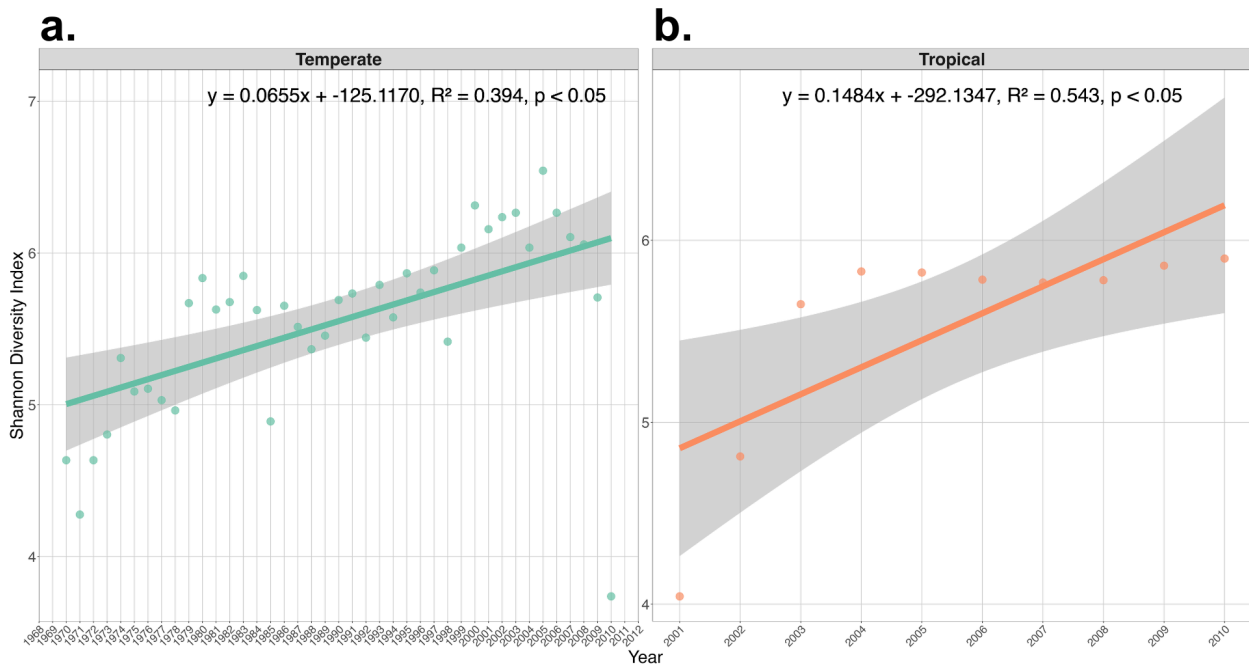
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**Figure 8. Linear regression models showing abundance trends over time for each species and location in temperate regions between 1989 to 2010.** Abundance data was filtered to include models with locations that had a valid slope. The slopes from these models were then used to fit a linear model. The proportion of significant slopes ( $p < 0.05$ ) was 2 out of a total of 60 slopes. Location and species groups with perfect fits were excluded.



**Figure 9. Line graph of Shannon Diversity Index between 1967 and 2010.** The temperate (a) plot saw a statistically significant increase ( $R^2 = 0.394$ ,  $p < 0.05$ ) in the Shannon Diversity Index which represented 39.4% of the variance in the Shannon diversity index variable. In tropical regions (b), there was a statistically significant increase ( $R^2 = 0.543$ ,  $p < 0.05$ ) in the Shannon Diversity Index over time, meaning that species are becoming more diverse in both regions.