Temporal dynamics of biotic homogenization and differentiation across marine fish communities

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Abstract

Humans have transformed ecosystems through habitat modification, harvesting, species introduction, and climate change. Changes in species distribution and composition are often thought to induce biotic homogenization, defined as a decline in spatial beta diversity through time. However, it is unclear whether homogenization is common in ocean ecosystems and if changes in beta diversity exhibit linear or more complex dynamics. Here, we assessed patterns of homogenization or its converse (differentiation) across more than 175,000 samples of 2,006 demersal fish species from 34 regions spanning six decades and 20% of the planet's continental shelf area. While ten regions (29%) recorded significant homogenization, eleven (32%) recorded significant differentiation. Non-monotonic temporal fluctuations in beta diversity occurred in 15 regions, highlighting complex dynamics missed by before-and-after snapshots that can drive spurious conclusions about trends in beta diversity. Fishing pressure and temperature helped explain variance in beta diversity across years and regions. However, the strength and direction of these effects differed by region. Here we showed that, despite intense anthropogenic impacts on the oceans, the majority of demersal marine fish communities do not follow the global homogenization paradigm common in other realms.

Introduction

As ecosystems face unprecedented changes driven by human activities, communities of organisms are reorganizing across space and time [1–4]. Many studies report that communities are experiencing a decline in spatial beta diversity through a process termed biotic homogenization, defined as a reduction in dissimilarity among species assemblages across space [5–7]. Dissimilarity decreases with an increase in the proportion of shared species among assemblages, thereby causing loss of uniqueness of individual communities [5,6]. A trend in spatial beta diversity towards either homogenization or its opposite, differentiation, can transform overall ecosystem function, but homogenization can also lead to instability due to heightened synchrony among communities [7,8]. Biotic homogenization is often considered to be a widespread phenomenon [9], but most research to date has focused on terrestrial and freshwater realms [6,10–19]. We currently lack understanding for whether biotic homogenization is common across a wide range of marine ecosystems [20].

In addition, homogenization has often been characterized by comparing only two sampling events [6,21,22], limiting our ability to understand temporal dynamics and possibly leading to spurious conclusions [23,24]. Marine continental shelf ecosystems have consistent, long-term, and spatially extensive scientific monitoring programs [25], and therefore provide a unique opportunity to reveal the temporal dynamics of homogenization. Research on marine ecosystems has found evidence of biotic homogenization in a handful of cases [26–32], most often in highly modified nearshore zones such as estuaries, wetlands, and coral reefs (but see Ellingsen *et al.* 2015, 2020 & Magurran *et al.* 2015). Because marine biomes exhibit faster rates of species redistribution than terrestrial and freshwater biomes [33], we may expect that homogenization is occurring more rapidly in the ocean despite the small number of documented cases.

The mechanisms leading to homogenization in the ocean may differ from those acting in terrestrial and freshwater systems. Biotic homogenization has often been linked to the spread of invasive species across space [34], but in marine communities, high impact invasions are uncommon by comparison (Arndt *et al.* 2018; Ricciardi & Macisaac 2010; but see Ballew *et al.* 2016; Campbell *et al.* 2022; D‘Amen *et al.* 2023; Galil 2007). In addition, habitat heterogeneity frequently shapes spatial beta diversity by providing niche opportunities and a variety of resources to support different species assemblages [41–43]. While temperature gradients are steeper in terrestrial environments, nutrient and light availability vary dramatically more in marine environments [44,45]. Landscape homogenization (e.g., conversion of natural landscapes to farmland or the loss of structured or biogenic habitat) can also lead to biotic homogenization [42,46–50], though human impact on many seascapes lags substantially behind the impact on terrestrial ecosystems [51].

In marine ecosystems, changes in species composition have been triggered by changes in temperature, fishing, and other factors [42,51–54]. Both press (i.e., warming or eutrophication) and pulse disturbances (i.e., a heat wave or oil spill) have led to biotic homogenization within marine communities [55–60]. Marine ectotherms are highly sensitive to water temperature due to metabolic constraints and their relative thermal specialization compared to terrestrial and freshwater species [61,62]. Declining spatial heterogeneity in temperature, therefore, may drive biotic homogenization as opportunities for niche differentiation and coexistence decline [28,63,64]. Alternatively, leading-edge range expansions that are faster than trailing-edge contractions in response to rising temperatures [65] could escalate species overlap and therefore homogenization. Homogenization may also result from fishing in regions where fisheries target endemic species with small range sizes [66,67]. In contrast, fishing may induce differentiation in regions where fisheries target mobile, large-bodied consumers due to the release of mesopredators that often exhibit less stable population dynamics [26,27,68].

Whether changes in temperature and fishing consistently impact spatial beta diversity in the ocean remains unclear.

Here, we used an extensive dataset of scientific bottom trawl surveys to assess the prevalence and dynamics of biotic homogenization across the coastal ocean of four continents (Tables S1-S2). Our primary hypotheses were that 1) marine bottom fish communities would show high prevalence of biotic homogenization because species range shifts are widespread and rapid, 2) time series of biotic homogenization would reveal complex and non-linear temporal dynamics not apparent from comparisons of two time points, 3) changes in biotic homogenization and differentiation in the ocean would be related to changes in spatial temperature heterogeneity because temperature strongly affects marine community structure, and 4) fishing would affect changes in biotic homogenization, though the effects would differ across regions because fisheries target species with different geographic range sizes and trophic levels in different regions (Fig. S1). An alternative Hypothesis #3 was that a metric of average or extreme annual temperature conditions, rather than spatial temperature heterogeneity, would be related to homogenization, since marine range shifts can drive homogenization. The surveys included observations of 2,006 marine fish species across 178,531 independent samples from 34 time-series in tropical, temperate, and subpolar regions in the Americas, Europe, Africa, and Oceania. Surveys had one to six decades of consistent sampling and spatial extents from 16,000 to 670,000 km^2. The sampling in total covered 20% of the area of shelf ecosystem habitat worldwide (Supporting Text). We tested for homogenization and differentiation by calculating annual spatial dissimilarity in each survey using beta diversity indices and estimated the effects of fishing and temperature on dissimilarity; lower beta diversity (lower dissimilarity) indicated a more homogenized community across space. We found that homogenization and differentiation were similarly common in bottom fish communities worldwide, but that most regions were not experiencing a directional change in spatial beta diversity.

Methods

Spatial beta diversity calculations

We used long-term scientific bottom trawl survey data for marine fishes recently compiled and integrated as FISHGLOB [25,69]. These are fisheries-independent surveys with standardized statistical designs. We omitted surveys that only reported metadata and those that had inconsistent sampling methods and locations through time. Surveys were only included if they had at least 10 years of sampling to facilitate detection of long term trends [70]. Seven regions were surveyed in multiple seasons and, to avoid pseudoreplication, we only included the season with the highest number of tows (Tables S1-S2). In total, 34 regions were included in this analysis (Fig. 1a & Table S1). All surveys were limited to the three most-sampled months–representative of a single season–except in the case of the West Coast United States survey for which we retained four months because of consistent sampling across those months.

Figure 1. Distribution of biotic homogenization and differentiation across surveyed continental shelf regions. (a) Map of temporal trends in spatial Jaccard dissimilarity by region. Changes in spatial community composition are represented in non-metric multidimensional scaling (NMDS) plots over the study period for example regions that experienced differentiation (b; West Coast South Island, New Zealand; first = 79 tow locations, last = 65 tow locations), homogenization (c; Southeast United States; first = 77 tow locations, last = 87 tow locations), and no trend (d; Iceland; first = 528 tow locations, last = 529 tow locations). Location of examples is marked by letter in subfigure (a). Each point in subfigures (b), (c), and (d) represents the community composition of an individual sampling event for the first survey year (white outline) or the last survey year (black outline). Each ellipse contains 95% of a multivariate t-distribution of the points of the first year of sampling (dotted line) or the last year (solid line).

Location in dimensional space was determined by species occurrences and Jaccard dissimilarity.

Each sample was a single tow, i.e., a drag of a bottom trawl net along the sea bottom. In the case where multiple samples occurred at the same latitude and longitude on the same day, we averaged abundance observations for all species and considered this to be a single sampling event. Additionally, we excluded low quality tows that did not match the standard area swept or duration for a given survey, which occasionally occur due to mechanical issues, oceanographic conditions, or other logistical constraints. We eliminated years, samples, and taxa unsuitable for temporal and spatial biodiversity analysis using author expertise and previous publications on survey data (see Supporting Text).

Because we were interested in temporal trends in dissimilarity, it was important to have a consistent spatial extent over time for each survey. To establish a standardized spatial extent in each region through time, we assigned each sample to a 7,774.2 km^2 hexagonal spatial cell, (except for the Norwegian survey of the Barents Sea for which we used a cell size of 23,322.2 km^2 due to low sampling density [25]). For each survey, we excluded years in which the survey sampled fewer than 70% of the hexagonal cells ever sampled by that survey (Fig. S2a-b, Table S3). Next, we excluded cells that were sampled in fewer than 70% of the remaining years (Fig. S2c, Table S3). Finally, we excluded regional surveys for which this standardization process excluded over 50% of the samples across the full time period (Table S3). This spatial extent standardization procedure resulted in 178,531 unique samples (tow events) across 34 regions between 1968 and 2021 (Table S2-3). We used tows as the basis for further spatial beta diversity analyses.

Each tow included species observations recorded as number of individuals or biomass, depending on the survey. We used both abundance and biomass to determine each species occurrence (presence or absence). A small number of tows (0.2%) did not include either abundance (count) or biomass (kilograms) values and were therefore removed. Cleaning and standardizing the data led some samples to have biomass or abundance values of zero for all observations. These tows were excluded from the analyses (0.03% of all tows) because dissimilarity calculations on communities with zeros across all observations are often meaningless [71].

All taxonomic names were standardized using WoRMS [72,73]. Only observations identified at the species-level were included in the analyses, leaving a total of 2,006 unique species. We performed two sensitivity tests to assess the impact of the inclusion of uncommon species and/or low abundance species on the results, as species identification quality can be lower for infrequently encountered species. First, we examined patterns in dissimilarity while excluding the bottom 15% species when ranked by abundance or biomass in each region (leaving 1,861 unique species). Second, we repeated analyses while excluding any species present in less than one-third of the years that a survey occurred (leaving 1,429 unique species).

We calculated beta diversity in each year of each region as the average pairwise dissimilarity between samples (tows) using Jaccard dissimilarity based on species occurrences (Fig. S1). Average pairwise dissimilarity is widely used for quantifying regional heterogeneity in community composition, has the intuitive interpretation as the expected dissimilarity of a randomly selected pair of samples, and is not sensitive to differences in sample size [74–83]. Average pairwise metrics, however, do not account for patterns of co-occurrence across more than two sites [84]. Additionally, this approach does not consider how community composition varies with the geographic distance between sites [85].

To also consider species dominance, we repeated analyses using abundance-based Jaccard dissimilarity based on species abundances for the 24 of 34 surveys with species count data available [86]. We also tested using relative species abundances to remove the influence of differences in total abundance across space. Jaccard dissimilarity is highly influenced by the degree to which species are shared across sites, and therefore to differences in both richness and species turnover [87]. Jaccard has been widely used to measure community dissimilarity in community ecology, and is robust to geographic and taxonomic undersampling [88,89]. We measured dissimilarity using the `vegdist` function from the *vegan* package in R [71].

Testing for directional temporal trends in beta diversity

To test for an average trend in dissimilarity over time across all surveys (Hypothesis #1), we fit a linear mixed effect model using the *lme4* package in R with a random slope and intercept for each survey to help account for differences in methodology across regions and repeated observations from each survey [90]. We also fit a linear model with a fixed effect interaction between survey and year to examine trends in dissimilarity for each individual survey (Hypothesis #1). Because surveys involved repeated sampling of regions through time, we compared a linear model with and without a temporal autocorrelation term for year (by survey), implemented using the *nlme* package in R [91].

We classified surveys with a significant negative coefficient ($p < 0.05$) for year as homogenizing (primary Hypothesis #1) and surveys with a significant positive coefficient as differentiating (alternative Hypothesis #1); surveys for which the coefficient +/- standard error crossed zero were classified as having no significant trend over time (null Hypothesis #1). To illustrate communities of bottom fish that underwent homogenization, differentiation, and no trend in dissimilarity, we constructed non-metric multidimensional scaling (NMDS) plots using the *vegan* package in R (Oksanen *et al.* 2022).

To assess the potential for detecting significant trends even if none existed, we compared results to a null model in which we reshuffled average annual dissimilarity values across years within surveys. This approach decoupled year from dissimilarity value and maintained correlations in abundance among species, but did not maintain temporal autocorrelations within species. We repeated this procedure 1000 times and, each time, classified surveys as homogenizing, differentiating, or not based on the same linear model approach used for the observed data. We tallied the number of homogenizing or differentiating surveys from each of the 1000 reshuffled datasets and calculated the 95th percentiles. Additionally, we compared the distribution of beta diversity trends from observed data versus the distribution from reshuffled values.

Testing for non-linear patterns in beta diversity

To illustrate non-monotonic fluctuations in dissimilarity through time in each region, we fit a generalized additive model (GAM) using the *mgcv* package in R with a smoother per survey [92]. We then tested for non-linear (non-monotonic) fluctuations in dissimilarity through time (Hypothesis #2) by comparing linear models with GAMs for each individual survey using Akaike Information Criteria (AIC_C; Akaike 1998; Burnham *et al.* 2011) (Fig. S1). We classified as non-linear those regions for which dissimilarity over the study period was better described by a GAM than by a linear model in support of primary Hypothesis #2 ($\Delta AIC_C > 2$). For those better described by a linear model ($\Delta AIC_C > 2$), we classified them as having linear trends (primary Hypothesis #2). Regions for which GAM and linear model approaches performed similarly ($|\Delta AIC_C| < 2$) were not classified as either (null Hypothesis #2).

Testing temperature and fishing as predictors of beta diversity

To test among potential drivers of annual dissimilarity, we built and compared a set of linear models including temperature (Hypothesis #3) and fishing (Hypothesis #4) (Fig. S1). The global model included temperature, fishing, and additional variables related to potential sources of heterogeneity among surveys that were not the main focus of this study. The additional variables included survey identity, primary season of sampling (adjusted for hemisphere), average latitude of the survey, the latitudinal range of the survey, the number of species sampled, the area surveyed, the average tow depth of a survey, the range of tow depths of a survey, and the average number of tows per year within a survey (Table S4). We also included interactions between temperature or fishing and survey so that the relationships could differ by survey (alternative Hypothesis #3, primary Hypothesis #4). Because of repeated sampling through time, we evaluated whether including a temporal autocorrelation term for year, implemented using the *nlme* package [91], was favored by AIC_C.

All covariates were calculated as annual values per survey, and we excluded years and surveys missing any covariates (we excluded the Southern Gulf of St. Lawrence and the Rockall Plateau surveys because they were missing depth and fishing data, respectively). In total, we fit these models to 32 surveys from 1982-2019. We calculated the annual survey area as a concave hull surrounding all tow locations using the *concaveman* package in R with a concavity of 1 and length threshold of 2 [95]. Covariates were calculated for the specified year of survey sampling, except for temperature (calculated for the 12 months prior to the first observation of a survey-year) and fisheries catch (calculated for the calendar year preceding each survey-year). All numeric covariates were scaled and centered across surveys to improve model convergence, except for fisheries catch, which was scaled within a survey and was therefore representative of relative catch within a region.

Our primary temperature Hypothesis (#3, Fig. S1) focused on the spatial heterogeneity of temperature [28]. However, alternative hypothesis #3 tested whether average, extreme, or the seasonal range of temperatures was a more effective predictor, since these metrics are closely linked to the species range shifts hypothesized to contribute to marine homogenization [28]. Demersal fishes respond to both extreme and average bottom temperature conditions, the range of temperatures experienced in a year, and the heterogeneity of temperature across space [96–99]. We used daily sea bottom temperature from the SODA 3.3.2 data product [100], which is a global historical reconstruction of sea temperature at multiple depths from 1980 to January of 2019 at a 1/4° resolution. As a metric of spatial heterogeneity in temperature within each survey and year (related to our primary Hypothesis #3, Fig. S1), we calculated the annual mean bottom temperature for each sample location and then calculated the standard deviation across sample locations within each survey and year. For the alternative temperature hypotheses, we calculated the mean, minimum, maximum, and seasonality (maximum - minimum) for each sample location for each year. Next, we took the average of these summary statistics for each survey and year. We restricted analyses to annual regional dissimilarities between 1982 (no usable tows in 1981) and 2019 because of the availability of high resolution temperature data.

We expected bottom fish to respond most directly to bottom temperature values, but we calculated the same metrics and repeated the same analyses using the NOAA 1/4° Daily Optimum Interpolation Sea Surface Temperature (OISST) [101]. The SODA and OISST temperature products effectively capture inter-annual and decadal climate regimes (Ren et al. 2023, Mauro Vargas-Hernandez et al. 2014, Giese and Ray 2011, Huang et al. 2016) that commonly impact regional fish population dynamics [102,103].

To explore the impact of resource extraction on mean annual dissimilarity (Hypothesis #4, Fig. S1), we used fisheries catch data as a proxy for fishing pressure. We extracted reconstructed annual fisheries catch in metric tons from Sea Around Us using the Large Marine

Ecosystem, Exclusive Economic Zone, or Marine Ecoregion that best overlapped with a survey's spatial extent [104] (Table S5). Catch values in Sea Around Us had been reconstructed using reported catch (primarily from the Food and Agriculture Organization of the United Nations) and estimates of unreported catch [104]. We only used catch of identified marine fish, and we restricted the catch type to landings only (i.e., excluding discards) to focus on records with high certainty. We used the total reconstructed catch (which included species that do not appear in the bottom trawl data sets) because fishing affects both target and non-target species through changes in biotic interactions [105,106].

We first compared a set of global models with AIC_C [93,94,107], each of which included one metric of annual temperature. From these, we selected a single temperature metric. We then used the dredge function in the *MuMIn* package in R to compare with AIC_C all possible nested models constructed with the selected temperature metric [94,107]. We estimated average covariate coefficients by averaging continuous parameters included in all models with $\Delta AIC_C < 4$.

Results

Prevalence of biotic homogenization and differentiation

Trends in spatial beta diversity differed substantially across 34 surveys of bottom fish in the coastal ocean (Figs. 1a & S3). Overall,10 surveys (29%) recorded significant regional homogenization (Fig. 1a,c), 11 surveys (32%) recorded significant differentiation (Fig. 1a,b), and the other 13 surveys (38%) did not record significant trends in regional dissimilarity (Fig. 1a,d). We did not find evidence of strong temporal autocorrelation (Δ AIC_C = 615). The null model suggested that two more regions were homogenizing than would otherwise be expected due to chance, and similarly, two more were differentiating than expected (Fig. S4a-b). Therefore, we did not find evidence of Hypothesis #1, that homogenization patterns would be pervasive.

Trends in beta diversity ranged from a 6% per decade loss of spatial dissimilarity (i.e., homogenization) in the Rockall Plateau (Northeast Atlantic), to a 4% per decade gain (i.e., differentiation) in Greenland (Northwest Atlantic) (Fig. 2b). The magnitude of trends in dissimilarity observed were also higher than predicted at the 95% level by the null model (Fig. S4c-d). Despite these large individual trends within surveys, we found no significant change in overall dissimilarity through time across all survey regions (slope = 0.008% +/- 0.03% SE per decade; *p* = 0.78; linear mixed effects model; Fig. 2a).

Figure 2. Trends in spatial beta diversity over time. (a) Annual Jaccard dissimilarity for each region (colored points, n = 705) with generalized additive model (GAM) smoothers for each region (colored lines) and 95% confidence intervals (colored ribbons). A decrease in dissimilarity represents homogenization (yellow); an increase represents differentiation (pink). A lack of significant trend is shown in blue. The average linear trend across surveys (black line with 95% confidence interval in gray) is also plotted from a linear mixed effect model with a random slope and intercept for survey. (b) Coefficients and associated standard error of dissimilarity versus time for each survey from a linear model (LM) with a fixed effect interaction between survey and time in ascending order by coefficient value. Point size represents the length of the survey period. Asterisks mark surveys for which dissimilarity through time was better described by a non-linear GAM than a LM.

Our finding that neither homogenization nor differentiation were widespread across regions was not sensitive to the metric of dissimilarity, although specific survey trends differed across metrics (Fig. S5). For raw abundance-based Jaccard dissimilarity, 8 regions (33%) differentiated and 8 (33%) homogenized out of the 24 regions. Seven regions (29%) exhibited a different trend as compared to the occurrence-based results. In the case of relative abundance-based Jaccard dissimilarity, eight regions (33%) differentiated, seven (29%) homogenized, and nine (38%) regions exhibited a different trend as compared to the occurrence-based results.

Sensitivity tests removing rare or low abundance species further supported the finding that instances of homogenization, differentiation, and a lack of a trend in dissimilarity were similarly common across bottom fish communities (Fig. S6). When the least abundant 15% of species were removed from each survey, there were no changes in trends. However, when species present in fewer than two-thirds of years of a survey were removed, 19 regions (56%) exhibited a different dissimilarity trend as compared to the full dataset; most often a shift from either homogenization or differentiation to no trend.

We tested whether changes in gamma diversity explained the observed trends in beta diversity, because dissimilarity increased with the number of species in a region (Fig. S7). However, we did not find evidence for such a relationship when Rockall Plateau (highly negative trend) was removed (p = 0.26, linear model; Fig. S8, R^2 = 0.04). Surveys differed in the first year (baseline) of sampling, the length of the survey period, the time of year of sampling, spatial extent, and sampling density (Table S2). However, we did not detect a relationship between the observed trend in beta diversity and the baseline year, the length of the survey period, the spatial extent, or sampling density (Fig. S9). Regions with surveys occurring in the later half of the year were more likely to exhibit homogenization, but there was no significant relationship between trend and season (Fig. S10). Surveys varied in sample (tow) density, but, in all regions other than the Southeast US, exhibited consistent density through time and no relationship between density and spatial beta diversity in a given year (Fig. S11).

Non-linearity in beta diversity through time

These long-term surveys revealed substantial multi-annual and decadal variability, such that they varied through time non-monotonically between more homogenized and more differentiated states (Figs. 2a & S3, & Table S6). For example, a decline in dissimilarity between the mid-1990s and mid-2000s off the coast of Namibia was followed by an increase continuing through the late 2010s. Additionally, the Eastern Bering Sea experienced increases in dissimilarity in the late 1980s and 2000s, followed by declines in the early 1990s and 2010s (Figs. 2a & S3). We found that non-linear GAMs performed better ($\Delta AIC_C > 2$) than linear models for 15 of 34 surveys (44%), partially supporting Hypothesis #2 that non-monotonic temporal dynamics would be common (Table S6, Fig. S3). Linear models outperformed GAMs for seven surveys (21%), and models for the remaining twelve surveys (35%) performed similarly.

Temperature and fishing as predictors of beta diversity

We then examined the extent to which temperature and fishing explained variation in annual dissimilarity (Fig. S1). Similar to dissimilarity, temporal trends in temperature and fishing differed across regions (Figs. S12-S13). The global model including minimum bottom temperature performed best ($\Delta AIC_C = 13$, Table S7), rejecting our primary Hypothesis #3 that spatial temperature heterogeneity would be most important. We carried minimum temperature forward in subsequent model comparisons.

The set of most parsimonious global models ($\Delta AIC_C < 2$) included minimum temperature, fisheries catch, and survey characteristics (Table S8 & Fig. 3). All of the high-performing models included an interaction between survey and both fishing and temperature, suggesting that the response of dissimilarity to temperature and fishing differed by region, supporting alternative Hypothesis #3 and primary Hypothesis #4 (Table S8, Fig. S14-15). The two best performing models explained 95% of the variance in annual spatial beta diversity (Table S8).

Figure 3. Average linear model coefficients predicting annual Jaccard dissimilarity for all regions (n = 32 surveys). Coefficients were allowed to vary by region for temperature (a) and relative fishing catch (b), but not for other characteristics (c). All variables were centered and scaled across all observations except for fishing catch, which was centered and scaled within each region. Coefficients for which the standard error did not cross zero are in black and others in gray.

Models including surface instead of bottom temperature performed similarly and led to similar conclusions, although maximum temperature out-performed other temperature metrics (ΔAIC_C = 5.3) and was therefore carried forward in subsequent analyses (Tables S9-S10 & Fig. S16). For all temperature metrics, models without a temporal AR term performed better than those with this term (Tables S7 & S9).

Discussion

While biotic homogenization is a common expectation and finding in terrestrial and freshwater ecosystems [11,16,108,109], we found that marine fish communities are not consistently homogenizing through time despite rapid and extensive species range shifts. Instead, we revealed complex multi-annual fluctuations in the heterogeneity of community composition through time. The high temporal resolution of scientific surveys on continental shelves around the world also allowed us to detect substantial and region-specific effects of both fishing and temperature on the biotic homogeneity of these communities.

Prevalence and temporal dynamics of homogenization

Demersal fish communities were more likely to exhibit no trend in spatial beta diversity than either homogenization or differentiation, reflective of other recent synthesis work [110].

While some regions, such as the Southeast United States and the Barents Sea have homogenized in the past two to four decades, others, such as Greenland and the Scotian Shelf have differentiated. Homogenization and differentiation of individual regions has been previously described (Ellingsen et al. 2020, Siwertsson et al. 2024, Ellingsen et al. 2015), but the relative prevalence of these patterns across continents has not previously been apparent. Marked regional differences in trends of spatial beta diversity over time—ranging from sharp declines to rapid increases in heterogeneity—highlight the critical role of context during periods of rapid environmental change [2,111,112]. The specific species composition, regional environmental conditions, and legacy of human impact shape both the types of disturbances a system encounters and how it responds. These findings illustrate the importance of comparing trends across diverse ecosystems to comprehensively assess global change, rather than focusing solely on those demonstrating dramatic change in community structure.

Despite widespread expectations that communities are consistently homogenizing [11,16,108,109], we found that change within marine fish communities is a highly dynamic process, regularly fluctuating between periods of higher and lower dissimilarity. Some regions exhibited distinct periods of more homogenized and more differentiated community composition, a phenomenon also observed in communities of freshwater diatoms [113], and plants across biomes [114–117]. For example, the Eastern Bering Sea and Sub-Antarctic New Zealand did not experience significant directional change in beta diversity, and yet these regions experienced swings of 10-12% in dissimilarity within just a decade. This variation across years is dramatic compared to what is known from other ecosystems. For example, the variation we observed across decades was two to three times greater than the homogenization observed among plants (3%) and birds (4%) across the centuries since human settlement, though we caution that differences in sampling, scale, and metrics also affect these comparisons [118,119].

The high temporal variability of spatial beta diversity also highlights the importance of the baseline effect in shaping observed trends, wherein the first observation has a strong influence on observed patterns (Navarrete et al. 2010, Edwards et al. 2010, Werner et al. 2020). The baseline effect is particularly strong when only two time points are available for assessing trends, which is how most homogenization trends have been detected to date [120,121]. Two time points are also unable to detect more complex dynamics. The relatively long time series (>10 years) with high temporal resolution (sampling every one to three years) examined here helps to minimize the impact of the starting year (Navarrete et al. 2010, Edwards et al. 2010). While we did not observe any obvious relationships between beta diversity trend and baseline year of sampling, the starting year may still have an impact on the trend we detect, especially in the case of shorter time series. For instance, the Aleutian Islands (North Pacific) exhibited no overall trend between 1983 and 2018. However, a time series beginning in 2000 would have suggested a strong pattern of homogenization supported by 19 years of observations. Understanding temporal variability of spatial beta diversity will be important for evaluating whether baseline effects may be biasing conclusions about homogenization trends in other ecosystems.

Predictors of spatial beta diversity

A large sample size and diverse regions allowed us to test mechanisms that may drive patterns of homogenization and differentiation [42]. Temperature and fishing are known to strongly influence marine species population dynamics, community composition, and geographic distributions [42,51–54], and here, we found that these factors also strongly influence the temporal dynamics of biotic homogenization and differentiation.

After testing a range of temperature metrics, we found that minimum annual temperature rather than temperature heterogeneity was the best predictor of annual dissimilarity. This finding matches recent work demonstrating that climate extremes shape species distributions more than average conditions [122]. Minimum temperature in a year can directly (i.e. thermal tolerance; Leriorato *et al.* 2021) or indirectly (i.e. predation; Morley *et al.* 2017) impact species range shifts. In the ocean, cold temperatures have long been known to act as a control on species distributions [125]. The lower bound of temperature extremes are currently increasing at a faster rate than the upper bounds [126], and we therefore anticipate a parallel change in the heterogeneity of bottom fish communities across space.

The influence of temperature on homogenization, however, was strongly context-dependent. For example, off of the west coast of the South Island of New Zealand, warmer years were more homogenized, while in South Georgia (South Atlantic), warmer years were more differentiated. One explanation may be that homogenization is more likely to occur at ecotones experiencing warming. Levels of homogenization are highest when species' establishments are common, regardless of whether or not they are paired with local extirpations of endemic species [127]. The introduction of warmer-water associated species with high dispersal capacity may initially lead to an increase of uniqueness across space as novel species accumulate poleward of the ecotone, then later drive a decline in uniqueness as those species spread more widely across the region. This ecotone-related phenomenon may explain homogenization in two northwest Atlantic regions–the Northeast and Southeast United States [128–130] These regions sit poleward of biogeographic breaks at Cape Hatteras and Cape Canaveral, respectively.

Similar to previous studies [131,132], we found that fishing also shaped fish community composition. As we hypothesized, this relationship between dissimilarity and fishing varied across region. In the Southeast United States and Newfoundland (North Atlantic), highly fished years were followed by differentiation, while highly fished years in Greenland and the North Sea were instead followed by homogenization. This regional variation suggests that the effect of fishing is more highly context dependent than previously appreciated, and possibly shaped by the distribution of fishing across space, food web structure, and the trophic level of species targeted in the system [52,133,134]. When fishing primarily targets dominant widespread predators, an increase in harvesting is often matched with an increase in beta diversity [26,27]. Differentiation can occur if population declines cause the range of top predators to contract [135], or cause a release of mesopredators that typically exhibit more heterogeneous distributions [27,68,136]. In contrast, homogenization may ensue if fishing in a region targets relatively rare species such as sharks and rays [137].

While long in the context of ecological research, the study periods included here only represent observations from the last ~60 years. Therefore, we could not detect if the current state of demersal fish communities are homogenized or differentiated in comparison to communities before the realized impacts of anthropogenic climate change and resource extraction in the ocean. It is important to note that marine resource extraction in some of these regions has occurred for thousands of years (Bess et al. 2001, Casteneda et al. 2020, Bolster et al. 2008). Future investigation into the mechanisms and pathways leading to changes in dissimilarity, including lagged and indirect responses, would improve our understanding of how communities respond to multiple stressors [138].

The drivers of homogenization and differentiation in ecosystems across realms have often been expressed as directional [28,34,108], but our results emphasize that they need not be so [27,139]. Instead, the degree of homogeneity may more commonly fluctuate through time and be related to environmental conditions (e.g., climatic oscillations and change) and direct human impacts (e.g., fishing). The variability in marine fish community composition across years further highlights the importance of long term observations at high temporal resolution that allow us to disentangle cyclic variability from long term directional trends (Hughes et al. 2017).

Considerations of metric and scale

Our main finding that homogenization and differentiation are relatively uncommon was robust to beta diversity metric. However, both the way in which communities are defined (species presence/absence vs. raw abundance vs. relative abundance), and the metric used to calculate dissimilarity led to differences in how some regions were classified. Including observations of species abundances in calculations can be more representative of the population dynamics underlying changes in community composition [127]. As one example, while occurrence observations led Northern Ireland to be classified as differentiating, abundance observations led the region to be classified as exhibiting no trend. This suggests that changes in community composition are muted in this region when species are weighed by abundance, and therefore, changes are stemming from relatively rare species. As another example, in the Bay of Biscay (North Atlantic), occurrence-based analyses classified the region as homogenizing, while abundance-based analyses classified the region as differentiating, suggesting that while changes in the distribution of uncommon species has led to homogenization across space, changes in the distribution of species making up a substantial portion of the overall community have led to differentiation. We also note that beta diversity trends are sensitive to spatial scale [127,140–142], and therefore our findings for regional communities may differ when assessed at a sub-regional or global scale. While we found that on average, community heterogeneity was higher for larger regions, we did not find a relationship between the size of a region and dissimilarity trend. We did not assess how distance-decay of community similarity varies across surveys, but acknowledge that this spatial pattern likely plays a role in homogenization dynamics and encourage future researchers to explore that intersection [85,143].

Trends in spatial beta diversity were also sensitive to survey-specific characteristics and sampling methodologies. While longer surveys are more likely to detect species gains and losses and therefore directional trends in dissimilarity [127], we did not detect a relationship between sampling period and likelihood of homogenization or differentiation. Surveys vary in their ability to detect and identify uncommon species. While removing species of low abundance did not change our results, removing species that were caught infrequently through time led many regions to exhibit no trend in dissimilarity and a few regions to exhibit trends different than those exhibited using the full dataset. As one example, while Chile exhibited no trend in dissimilarity using the full dataset, the region homogenized when infrequently caught species were removed from the analyses. Future work could explore the role of detectability and uncommon species in homogenization dynamics.

Additionally, we found that higher differentiation was paired with higher regional species richness, reflecting the widely recognized positive relationship between gamma and beta diversity [144]. Due to seasonal migrational patterns and variability in environmental conditions across the year, trends in beta diversity can vary depending on when communities are sampled [145]. We observed lower dissimilarity values and more regions homogenizing later in the year, although this likely reflects more surveys occurring later in the year because we found no significant differences in dissimilarity trends across season of sampling. While rare in ecological datasets, consistency in sampling methodology for long-time series is essential for detecting patterns through time and for performing time-series analysis [25,146,147]. We found no relationship between sampling density and dissimilarity trend, and for all but one region, sampling density was consistent through time. In the Southeast United States survey, an increase in sampling density over time coincided with a decrease in beta diversity. However, this interaction runs contrary to common assumptions that higher sampling density would lead to differentiation as more unique niches are represented.

Conclusion

The possibility of biotic homogenization across seascapes raises management and conservation concerns because it might erode the resilience of fish communities to future disturbances [148]. A decline in spatial beta diversity can precipitate a loss of ecosystem function and services as rare specialists are lost to widespread generalists [7,8,149]. Our finding of more heterogeneous patterns in marine ecosystems suggest that effective conservation planning will need to be adapted to regional trends and changes, rather than relying on global proxies [150]. Informing local strategies, in turn, relies on effective systems for monitoring these changes, which can include not only bottom trawl surveys, but also eDNA, sonar, and other technologies.

We found that multi-annual swings between more homogenous and more differentiated community composition have been common and that both temperature and fishing have been key drivers of these changes. Examining temporal dynamics in other marine ecosystems and in terrestrial and freshwater ecosystems will be important for understanding whether large fluctuations are also common in these realms. Future studies exploring the dynamics of functional and phylogenetic dissimilarity across time and space—in all systems, not only marine—will further deepen our knowledge on how structuring factors, such as climate and direct human impacts induce changes in species assembly [151–154].

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Supporting information

S1 File. Supporting figures, tables, and text. Contains Figures S1-S16, Tables S1-S10, and supporting text.

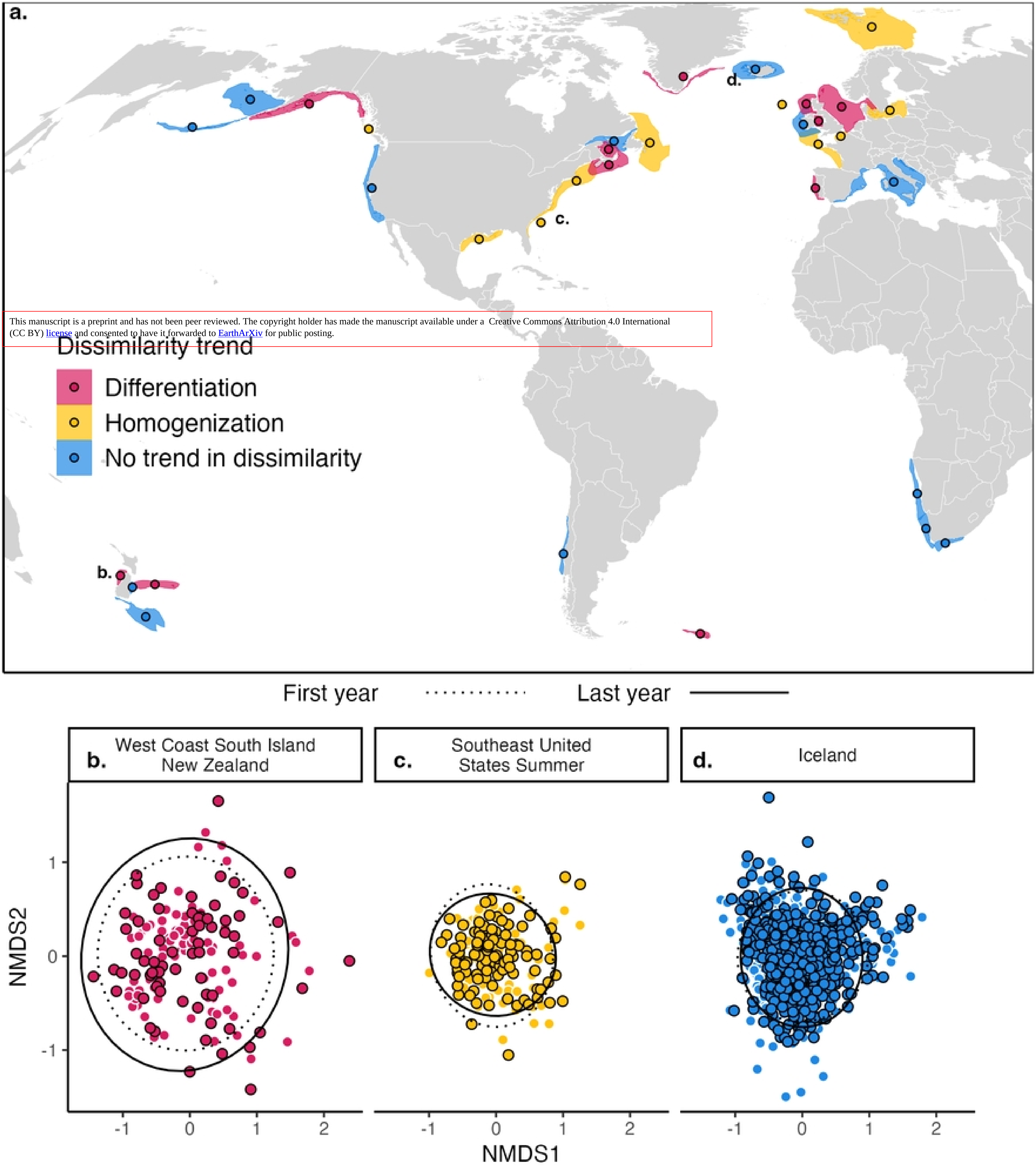
a.
Dissimilarity trend
Differentiation
Homogenization
No trend in dissimilarity
b.
c.
d.
First year
Last year
b. West Coast South Island New Zealand
c. Southeast United States Summer
d. Iceland
NMDS2
NMDS1
1
0
-1
-1
0
1
2

Figure 1

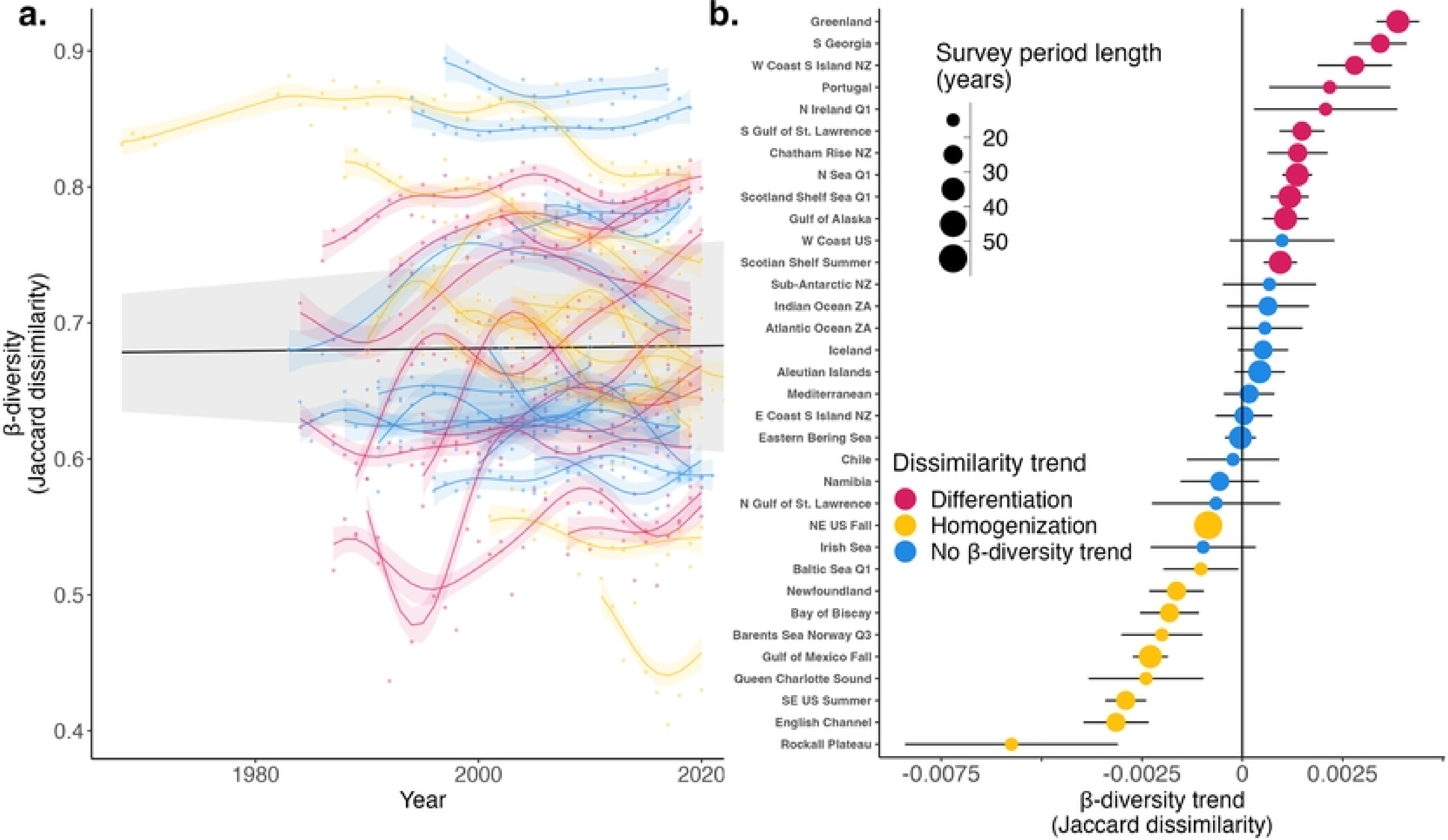
a.
b.
0.9
0.8
0.7
0.6
0.5
0.4
β-diversity
(Jaccard dissimilarity)
1980
2000
2020
Year
Greenland
S Georgia
W Coast S Island NZ
Portugal
N Ireland Q1
S Gulf of St. Lawrence
Chatham Rise NZ
N Sea Q1
Scotland Shelf Sea Q1
Gulf of Alaska
W Coast US
Scotian Shelf Summer
Sub-Antarctic NZ
Indian Ocean ZA
Atlantic Ocean ZA
Iceland
Aleutian Islands
Mediterranean
E Coast S Island NZ
Eastern Bering Sea
Chile
Namibia
N Gulf of St. Lawrence
NE US Fall
Irish Sea
Baltic Sea Q1
Newfoundland
Bay of Biscay
Barents Sea Norway Q3
Gulf of Mexico Fall
Queen Charlotte Sound
SE US Summer
English Channel
Rockall Plateau
Survey period length
(years)
20
30
40
50
Dissimilarity trend
Differentiation
Homogenization
No β-diversity trend
-0.0075
-0.0025
0
0.0025
β-diversity trend
(Jaccard dissimilarity)

Figure 2

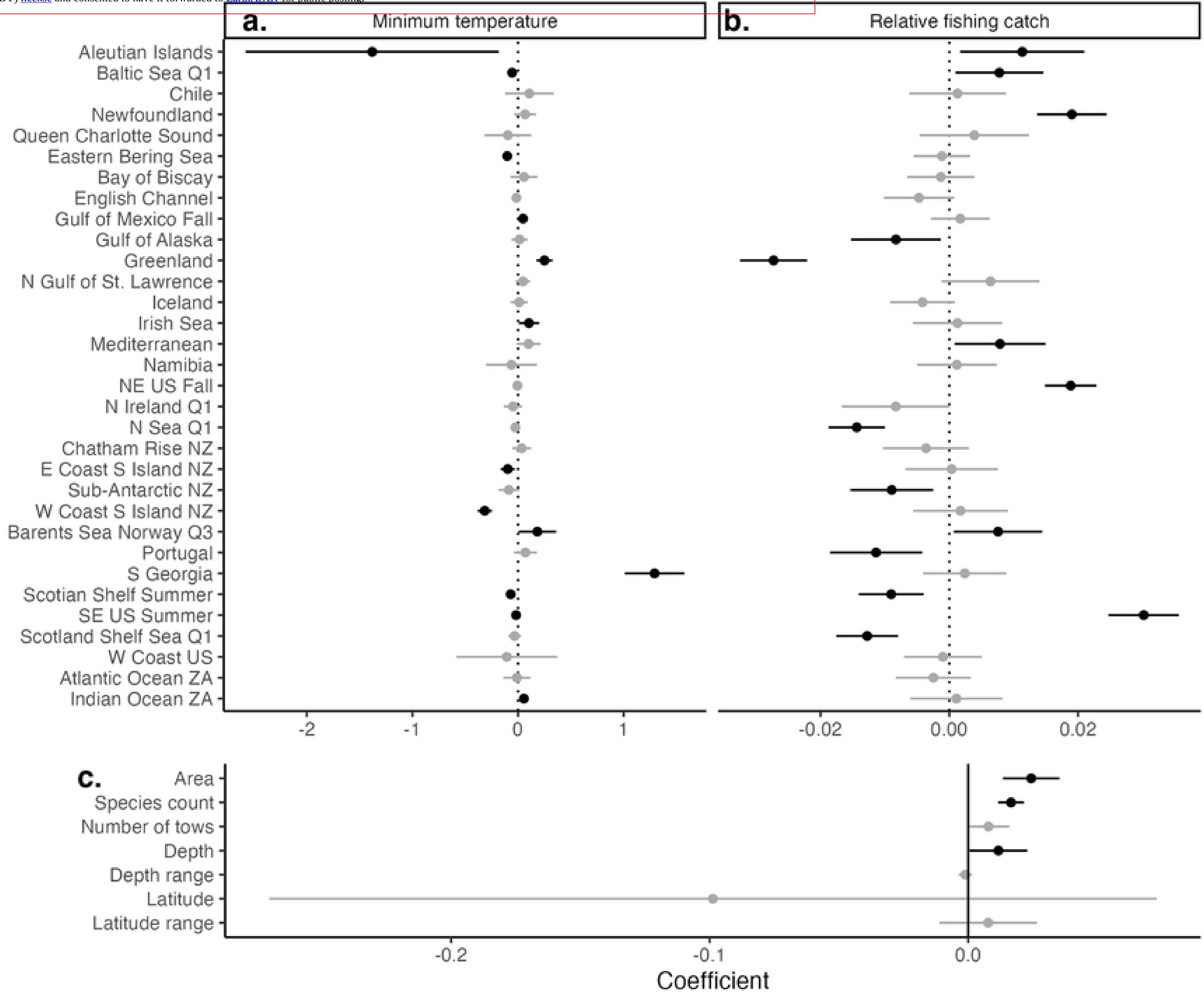
a.
Minimum temperature
b.
Relative fishing catch
Aleutian Islands
Baltic Sea Q1
Chile
Newfoundland
Queen Charlotte Sound
Eastern Bering Sea
Bay of Biscay
English Channel
Gulf of Mexico Fall
Gulf of Alaska
Greenland
N Gulf of St. Lawrence
Iceland
Irish Sea
Mediterranean
Namibia
NE US Fall
N Ireland Q1
N Sea Q1
Chatham Rise NZ
E Coast S Island NZ
Sub-Antarctic NZ
W Coast S Island NZ
Barents Sea Norway Q3
Portugal
S Georgia
Scotian Shelf Summer
SE US Summer
Scotland Shelf Sea Q1
W Coast US
Atlantic Ocean ZA
Indian Ocean ZA
-2
-1
0
1
-0.02
0.00
0.02
c.
Area
Species count
Number of tows
Depth
Depth range
Latitude
Latitude range
-0.2
-0.1
0.0
Coefficient

Figure 3