Disentangling tropicalization and deborealization in marine ecosystems under climate change

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Summary

As climate change accelerates, species are shifting poleward and subtropical and tropical species are appearing in temperate environments[1–3]. A popular approach for characterizing such responses is the community temperature index (CTI), which tracks the mean thermal affinity of a community. Studies in marine[4], freshwater[5], and terrestrial[6] ecosystems have documented increasing CTI under global warming. However, most studies have only linked increasing CTI to increases in warm-affinity species. Here, using long-term monitoring of marine fishes across the Northern Hemisphere, we decomposed CTI changes into four underlying processes – tropicalization (increasing warm-affinity), deborealization (decreasing cold-affinity), borealization (increasing cold-affinity), and detropicalization (decreasing warm-affinity) – for which we examined spatial variability and drivers. CTI closely tracked changes in sea surface temperature, increasing in 72% of locations. However, 31% of these increases were primarily attributable to decreases in cold-affinity species, i.e., deborealization. Thus, increases in warm-affinity species were prevalent, but not ubiquitous. Tropicalization was stronger in areas that were initially warmer, experienced greater warming, or were deeper, while deborealization was stronger in areas that were closer to human population centers or that had higher community thermal diversity. When CTI (and temperature) increased, species that decreased were more likely to be living closer to their upper thermal limits or to be commercially fished. Additionally, warm-affinity species that increased had smaller body sizes than those that decreased. Our results show that CTI changes arise from a variety of underlying community responses that are linked to environmental conditions, human impacts, community structure, and species characteristics.

Results and Discussion

Fish communities worldwide are responding to global warming through shifts in mean thermal affinity, which can be represented by the community temperature index (CTI)[4,7–9]. An increase in CTI necessarily implies an increase in the relative abundance of warm-affinity species. However, a key question is whether this is primarily due to increases in the total abundance of warm-affinity species or to decreases in the total abundance of cold-affinity species. To resolve this, we decomposed CTI changes into four underlying processes:

- 'tropicalization' (increasing abundance of warm-affinity species)
- 'deborealization' (decreasing abundance of cold-affinity species)
- 'borealization' (increasing abundance of cold-affinity species)
- 'detropicalization' (decreasing abundance of warm-affinity species)

Here, we define warm-affinity and cold-affinity species locally within each community: warm-affinity species are those whose thermal affinity is higher than the mean of the community and cold-affinity species are those whose thermal affinity is lower than the mean. Additionally, whereas past literature has used the term 'tropicalization' to describe increasing CTI[7] or poleward distribution shifts[3,10–12], we explicitly use this term to refer to an increase in warm-affinity species. We applied this approach to fish communities using scientific monitoring data from 558 grid cells covering 12 marine regions across the Northern Hemisphere that showed contrasting changes in sea surface temperatures (SST) over the period 1990 to 2015. We calculated the relative strength of each underlying processes in each grid cell and identified which process was strongest when CTI increased or decreased. Finally, we examined the potential influences of environmental conditions, human impacts, and community structure on differences in the strength of the underlying processes and examined differences between species contributing to opposite processes (e.g., borealization vs. deborealization).

Mean-annual SST increased in 72.4% (404) of grid cells between 1990 and 2015 with a mean of 0.23 ± 0.007°C decade^{-1} (mean ± standard error), while it decreased in 27.6% of cells (154) with a mean of -0.10 ± 0.008°C decade^{-1} (Figure 2A). CTI closely mirrored SST (Pearson's correlation: 0.47), increasing in 71.3% (398) of cells, with a mean of 0.28 ± 0.013°C decade^{-1} (Figure 2B), and decreasing in 28.7% (160), with a mean of -0.14 ± 0.014°C decade^{-1} (Figure 2B). Increases in CTI occurred primarily along the northeast coast of the United States, in the Scottish Seas, the North Sea, the Baltic Sea, the Barents Sea, and around the Aleutian Islands, while decreases were more prominent along the west and southeast coasts of the United States and in the Bering Sea (Figure 2B).

We next decomposed changes in CTI and quantified the strength of each underlying processes within each grid cell. Across all grid cells, tropicalization was the strongest process on average being dominant in 47% of cells, while detropicalization was the weakest, being dominant in only 7% of cells (Figure S1). Among the grid cells where CTI increased, tropicalization was stronger than deborealization in 68.6% (while deborealization was stronger in 31.4%) (Figure 2C). Hence, while past literature has focused extensively on increases in warm-affinity species and poleward distribution shifts[3,7,11,13], over one third of CTI increases were attributable to decreases in cold-affinity species. Among the grid cells where CTI decreased, borealization was stronger than detropicalization in 75% (Figure 2D). These patterns were clearly spatially structured, as tropicalization was stronger than deborealization along the east coast of the United States, in the Scottish Seas, the North Sea, the Baltic Sea, along the west coast of Norway, in the western Barents Sea, and around the Aleutian Islands. Deborealization was stronger in the Bering Sea, the Gulf of Mexico, and the eastern Barents Sea (Figure 2C). Borealization was stronger than detropicalization in nearly every region where CTI decreased, especially in the Bering Sea and along the west coast of the United States (Figure 2D).

To identify the biotic or abiotic conditions associated with each process, we next modelled the difference in the strength of (i) tropicalization vs. deborealization when CTI increased, and (ii) borealization vs. detropicalization when CTI decreased. Thus, the difference in the strength of the processes was the response variable (i.e., tropicalization minus deborealization; borealization minus deborealization). Explanatory variables were the rate of change in SST, initial (i.e., baseline) SST, mean-annual SST variation, depth, distance to the nearest human population center, mean maximum body size, community thermal diversity (CTDIV), and community thermal range (CTR) (see STAR methods and Table S2 for details). We used linear mixed effects models with Gaussian likelihood distributions where grid cells were the unit of observation and survey campaign was included as a random effect (i.e., varying intercept). When CTI increased, tropicalization was stronger than deborealization in cells that were initially warmer (effect size = 0.16 [0.07, 0.24; 95% CI]), experienced greater warming (effect size = 0.07 [0.02, 0.13]) or were deeper (effect size = 0.07 [0.02, 0.11]; Figure 3A). Deborealization was stronger than tropicalization in cells that were closer to human population centers (effect size = 0.07 [0.02, 0.11]) or that had greater community thermal diversity (effect size = -0.05 [-0.10,-0.01]; Figure 3A). When CTI decreased, borealization was stronger than detropicalization in cells that were initially warmer (effect size = 0.13 [0.01, 0.25]), had greater temperature increases (effect size = 0.07 [0.01, 0.12]) (or lower temperature decreases since CTI decreases are mostly associated with cooling), or were deeper (effect size = 0.06 [0.01, 0.11]; Figure 3B).

Theoretically, ignoring all factors other than temperature, when temperature and CTI are increasing, borealization and detropicalization should not occur, and when temperature and CTI are decreasing, tropicalization and deborealization should not occur. However, all four processes occurred to some extent in nearly every grid cell (Figure S1). We therefore hypothesized that there were mechanistic differences between species that explained this anomaly. For instance, when CTI is increasing, species that contribute to borealization likely differ in some key features from species that contribute to deborealization. We identified differences between species contributing to (i) borealization vs. deborealization, and (ii) tropicalization vs. detropicalization, using linear mixed effects models with binomial likelihood distributions where species were the unit of observation and grid cell nested in survey campaign were included as random effects (see STAR methods and Table S3 for details). Thus, the binary response variable was whether a species was contributing to i) deborealization (0) or borealization (1), or to ii) detropicalization (0) or tropicalization (1). In grid cells where CTI increased, explanatory variables included maximum thermal limit, thermal range, maximum body size, and whether species are commercially fished. In grid cells where CTI decreased, the same explanatory variables were used except that minimum thermal limit was used in place of maximum thermal limit. When CTI increased, species contributing to borealization had higher maximum thermal limits (i.e., more tolerant of warming) (effect size = 0.72 [0.53, 0.91]) while species contributing to deborealization were more likely to be commercially fished (effect size = -0.34 [-0.49, -0.19]) and had wider thermal ranges (effect size = -0.16 [-0.28, -0.04]; Figure 4A). Similarly, species contributing to tropicalization had higher maximum thermal limits (effect size = 0.57 [0.38, 0.76]) and smaller body sizes (effect size = -0.17 [-0.24, -0.10]) and species contributing to detropicalization had wider thermal ranges (effect size = -0.15 [-0.27, -0.03]; Figure 4A). When CTI decreased, species contributing to borealization had wider thermal ranges than those contributing to deborealization (effect size = 0.17 [0.04, 0.29]). Species contributing to detropicalization had higher minimum thermal limits (effect size = -0.35 [-0.52, -0.17]), were more likely to be commercially fished (effect size = -0.26 [-0.44, -0.08]), and had smaller body sizes (effect size = 0.09 [0.01, 0.18]; Figure 4B) than those contributing to tropicalization.

Previous studies have documented large-scale changes in CTI but have not identified the underlying processes of these community thermal shifts[3,4,6]. Unraveling these processes has clear implications for predicting future biodiversity responses under global warming, as well as potential impacts on community trait composition[14,15] and their consequences for ecosystem structure and functioning[16–18]. For example, communities increasing in CTI due to emigration or mortality of cold-affinity species (i.e., deborealization) could experience population crashes or local extinctions under future warming and could be considered conservation priorities[19–21]. In contrast, communities increasing in CTI due to immigration or population growth of warm-affinity species (i.e., tropicalization) may have increased abundance and productivity despite changing composition[8,22,23], and could be resilient to well-managed fishing pressure.

While increases in CTI have been frequently linked to immigration or poleward distribution shifts by warm-affinity species[3,10,13], we observed that over one third of CTI increases were primarily explained by decreases in cold-affinity species (i.e., deborealization). This result has major implications for understanding climate change impacts on community structure, particularly as tropicalization and deborealization were spatially non-random and associated with environmental variation and human impacts. Tropicalization was stronger than deborealization in areas with warmer initial temperatures and areas with greater overall warming. This is consistent with previous studies showing that community thermal shifts depend not only on the rate of warming, but also baseline climate. For instance, Antão et al.[24] showed that in marine communities exposed to warming, species gains outpaced species losses under warmer initial conditions, and Lenoir et al.[25] showed that marine species track isotherms more rapidly in initially warm waters. These results are consistent with faster colonization and range edge expansion and slower extirpation and range edge contraction[11,26]. These results may also be explained by more rapid dispersal and population growth in warmer environments. In marine organisms, the speed of metabolic and demographic processes increases with temperature[27], and both range expansion by new species and population growth of existing species should occur more rapidly under warmer conditions. Warm species gains may also dominate in warmer environments due to the latitudinal gradient in species richness, as greater numbers and proportions of warm-affinity species are expected in warm, species-rich areas[28].

Tropicalization was generally stronger than deborealization in deeper areas, likely owing to greater vertical temperature refuge for cold-affinity species[9]. For instance, tropicalization was particularly strong along the east coast of the United States, in the Scottish Seas, and in the western Barents Sea. These regions are situated along deep, open shelves, which could enable cold-affinity species to temporarily seek refuge in cooler, deeper waters during warming episodes, preventing their loss locally[29]. This is consistent with previous studies showing that relatively small shifts in depth may allow species to remain within their thermal niches[9,30] In the North Sea, a system primarily characterized by tropicalization, many species have shifted to cooler, deeper waters over the last few decades[30]. However, the North Sea is a relatively shallow, semi-enclosed ecosystem and Rutterford et al.[31] showed that North Sea fishes will eventually be constrained by depth limitations, compressing habitat suitability and potentially driving local extinction. Thus, the increase or immigration of warm-affinity species could be currently out-pacing the decline or emigration of cold-affinity species, but this trend could reverse in the future if cold-affinity species are unable to find thermal refuge.

Areas characterized by deborealization or detropicalization, i.e., decreasing abundance, had greater community thermal diversity than areas characterized by tropicalization or borealization. One hypothesis could be that communities with higher thermal diversity have fewer vacant niches (i.e., niche saturation) and therefore fewer opportunities for immigration and establishment by new species[32,33]. Communities with greater thermal diversity may also contain more species living closer to their thermal limits, and thus have greater potential for species losses or population declines due to temperature rises[9]. For instance, Burrows et al.[9]

showed that communities with greater thermal diversity may have higher sensitivity to temperature changes, as species near their thermal limits can be rapidly lost or gained[28].

Tropicalization and borealization were more common than deborealization or detropicalization. This suggests that habitat suitability is expanding for warm-affinity species faster than it is retracting for cold-affinity species[26]. Hence, many cold-affinity species may be tolerant of current warming, yet future warming could trigger major losses, potentially shifting the balance between tropicalization and deborealization. Even when CTI decreased, detropicalization was rarely dominant, as warm-affinity species rarely showed strong decreases. While some areas did experience cooling during the study period, the average rate of cooling was roughly half of the rate of warming, and all regions have experienced long-term temperature rises. Thus, warm-affinity species appear to be less impacted by periods of mild cooling, and detropicalization should become increasingly rare under future warming.

Interestingly, we found that when CTI increased, some cold-affinity species increased and some warm-affinity species decreased, counter to expectation. This was primarily explained by thermal limits and apparent fishing pressure. Cold-affinity species that increased had higher maximum thermal limits than those that decreased, and those that decreased were more likely to be commercially fished. Because species were compared within the same grid cells, species with lower thermal maxima were living closer to their upper limits. Species decreases can therefore be attributed to temperature rises surpassing thermal tolerances as well as potential overfishing. Hence, both thermal tolerance and fishing pressure are shaping long-term changes in marine fish communities, and future community responses will be driven by the cumulative impacts of climate change and human pressure[5,25,34]. The potential impacts of fishing were also highlighted by the finding that deborealization (i.e., decreasing abundance) was stronger in areas closer to human population centers.

When CTI increased, warm-affinity species that increased had smaller body sizes than those that decreased. Smaller-bodied species generally have faster growth rates, shorter generation times, and less parental investment, enabling populations to rapidly track environmental changes[14,35,36]. Thus, small-bodied species whose upper thermal limits were not surpassed by temperature rises could rapidly increase in abundance following warming, particularly as warming elevates metabolic and demographic rates. In contrast, large-bodied species have slower growth rates and reproduce later in life, leading to slower population turnover and environmental tracking[35,36]. Large-bodied species are also more susceptible to human impacts[37]. Hence, even large-bodied species that are favored by temperature rises might be decreasing in abundance faster than they can reproduce, leading to population declines despite warm-water affinities.

While limited to fish communities from 12 marine regions over a 26-year period, our approach is applicable to other ecosystems and taxa and may help unravel the underlying processes of community thermal shifts at a global scale[38]. Identifying how changes in species' distributions and abundances are impacting overall diversity and community dynamics will be key for planning future conservation and management efforts[39–42]. Areas with net losses of cold-affinity species may require careful fisheries regulation, whereas areas gaining warm-affinity species may have increased productivity and exploitation opportunities[8,23,43,44]. Overall, we found that over one third of CTI increases were more strongly explained by decreases in cold-affinity species than by increases in warm-affinity species, with significant roles of environmental conditions, human impacts, and community structure. Additionally, we found that species tendencies to increase or decrease in response to temperature changes were dictated by thermal limits and commercial fishing status. Future studies should link spatial patterns in the underlying processes of CTI to changes in seasonality, ocean currents, and other abiotic factors likely to be modified by climate change, as well as changes in fishing pressure and human impacts. While past studies have documented extensive shifts in CTI, ours is the first to decompose CTI into underlying processes at a multi-continental scale, which could help in anticipating future changes in biodiversity under climate change and implementing adapted management strategies.

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Author contributions

A.A., D.M. and M.M. designed the research, A.A.M., T.H., and M.M. collected and processed the data, M.M. analyzed the data, and all authors contributed to conceptual development and writing.

Declaration of interests

The authors declare no competing interests.

Figure legends

Figure 1. The four underlying processes contributing to changes in CTI. Increases in CTI occur when the combination of tropicalization (red) and deborealization (orange) is stronger than the combination of borealization (blue) and detropicalization (purple). CTI increases can therefore be attributed to either topicalization or deborealization, whichever process is stronger, and CTI decreases can be attributed to either borealization or detropicalization, whichever process is stronger.

Figure 2. Maps showing the rate of change in SST and CTI along with differences in the strength of the underlying processes. Rate of change in SST (A) and CTI (B) across the 558 spatial sampling grid cells for the period 1990 – 2015. Differences in the strength of tropicalization and deborealization in grid cells where CTI increased (C), and differences in the strength of borealization and detropicalization in grid cells where CTI decreased (D). See also Figure S1, which shows average relative strength of each underlying process, Figure S2, which shows the area covered by each monitoring survey, Table S1, which provides details on the monitoring surveys, Figure S3, which shows the method for calculating the strength of each underlying process, and Figure S4, which compares the rate of change in CTI vs. (topicalization + deborealization) – (borealization + detropicalization).

Figure 3. Results of linear mixed effects models of differences in the strength of tropicalization and deborealization in grid cells where CTI increased (A), and of differences in the strength of borealization and detropicalization in grid cells where CTI decreased (B). Grey circles represent standardized effect sizes and black horizontal bars represent 95% confidence intervals. In panel A, positive effects are associated with stronger tropicalization, and negative effects are associated with stronger deborealization. In panel B, positive effects area associated with stronger borealization, and negative effects are associated with stronger detropicalization. See also Table S2, which shows the output summary for each model.

Figure 4. Results of linear mixed effects models of i) the probability that a species contributed to borealization or deborealization, and ii) the probability that species contributed to topicalization or detropicalization when CTI increased (A) and when CTI decreased (B). Grey circles represent standardized effect sizes and black horizontal bars represent 95% confidence intervals. Positive effects are associated with species that contributed to borealization or tropicalization, and negative effects are associated with species that contributed to deborealization or detropicalization. See also Table S3, which shows the output

summary for each model, and Table S4, which compares model results using different subsets of species based on quantiles of abundance changes.

STAR METHODS

RESOURCE AVAILABILITY

Lead Contact

Further information and requests should be directed to and will be fulfilled by the lead contact, Matthew McLean (mcleamj@gmail.com).

Materials Availability

This study did not generate new unique reagents.

Data and Code Availability

This paper analyzes existing, publicly available data. Links for the datasets are provided in the key resources table. This paper does not report original code. Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

All fish monitoring data used in this study are freely available and open access; references and links are provided in the Key resources table and Supplemental information. No experimental models (animals, human subjects, plants, microbe strains, cell lines, primary cell cultures) were used in the study.

METHOD DETAILS

Fish community data

Thirteen bottom-trawl surveys from 12 marine regions across the northern hemisphere were used to examine changes in the community temperature index (CTI) in fish communities over a large geographic scale with substantial longitudinal, latitudinal, and depth gradients. All surveys used similar sampling protocols, where bottom trawls were towed for an average of 30 minutes and the species composition and abundances of all captured fishes were identified and recorded (see Table S1). Spatial coverage and resolution differed across surveys, and we therefore aggregated trawl surveys to 1° longitude × 1° latitude spatial grid cells. A 1° longitude × 1° latitude resolution was chosen to adequately capture both inter and intra-survey variation, to reveal gradients in community responses, to maximize data availability, and to match with the spatial resolution of the HadISST database (see 'Sea surface temperature' below). The length of time series also differed between surveys, and we therefore examined the period 1990 – 2015, which maximized temporal overlap between surveys. Following Burrows et al.[9], along the US West Coast, two surveys with overlapping spatial coverage but adjacent temporal periods were combined (see Figure S1 and Table S1). The combined data were inspected for discontinuities, and we verified that our main results and conclusions were robust to removing these data from the analyses. Because some surveys are conducted in multiple seasons, for each grid cell, we only used data for the quarter with the greatest number of years surveyed. Lastly, because of spatial and temporal heterogeneity in sampling effort both between and within grid cells, we performed a bootstrap sampling procedure. We randomly selected four trawl surveys per grid cell, per year (four was the median number of trawls per cell, per year), recorded the resulting species' abundances, repeated this procedure 99 times, and calculated species' mean abundances across the 99 permutations. Only grid cells with with maximum sampling gaps of five years or less were considered (some surveys are only conducted every 3-5 years), resulting in a total of 558 cells. All survey abundance data were then $\log_{10}(x+1)$ transformed before analyses. While we recognize that aggregating bottom trawl data to a 1° longitude × 1° latitude scale creates species assemblages that are not true locally interacting biological communities, we use the term 'community' for consistency with existing literature on concepts such as the community temperature index and community thermal diversity.

Sea surface temperature (SST)

For each grid cell, we extracted mean-annual sea surface temperature (SST) and annual SST variation. Minimum and maximum SST were also initially considered, but later dropped because they were highly correlated with mean SST, but much less informative (i.e., never had discernable effects in statistical models). SST data for each grid cell were derived from the Hadley Centre for Climate Prediction and Research's freely available HadISST1 database[46]. The HadISST1 database provides global monthly SST on a 1° longitude × 1° latitude spatial grid and is available for all years since 1870. These data were used to examine temperature changes during the study period and to model the underlying processes of CTI.

Calculating community temperature index (CTI)

Community temperature index (CTI) is the abundance-weighted mean thermal affinity of a community or assemblage, which reflects the relative abundance of warm-affinity or cold-affinity species[50]. The inferred thermal affinity for each fish species in this study (1091 species total) was first calculated as the median temperature of each species' occurrences across its' global range of observations for which data were available (Figure S2). Rather than surface temperature or bottom temperature, we used mid-water-column temperature (i.e., from the surface to 200 meters depth) because the surveys included a mixture of demersal (bottom-living) and pelagic species. We used temperature climatologies from the global database WOD 2013 V2 (https://www.nodc.noaa.gov/cgi-bin/OC5/woa13/woa13.pl?parameter=t) with a spatial resolution of ¼°. These climatologies represent average decadal temperatures for 1955-1964, 1965-1974, 1975-1984, 1985-1994, 1995-2004 and 2005-2012 on 40 depth layers. These data were aggregated vertically by calculating average temperature of the first 200 m depth. Species' occurrences were extracted from several databases including OBIS (https://obis.org/), GBIF (https://www.gbif.org/), VertNet (http://vertnet.org/) and ecoengine (https://ecoengine.berkeley.edu/). After removing duplicate occurrence records, we made a spatiotemporal match-up between temperature climatologies and species occurrences, considering both the geographic coordinates of occurrences, as well as their corresponding decade (to control for climate trends over the past 58 years). We then took the median value of temperature from these records for each species. Although we included both demersal and pelagic species and used mid-water-column temperature to infer thermal affinities in our analyses, we tested the sensitivity of our results to these choices by recalculating thermal affinities using surface temperature and bottom temperature, both with and without pelagic species (see Supplementary Material). Separate data sources were used to calculate species' thermal affinities and to model the underlying processes of CTI because estimating species' thermal affinities required matching species' occurrences with mid-water column temperatures, whereas modelling the underlying processes required a standardized, continuous, temporally resolved database. Mid-water-column data were only available as decadal averages and did not cover the entire study period. Lastly, for each grid cell, we calculated the rate of change in SST and CTI as the slope of simple linear regressions of SST and CTI vs. time.

Comparison of thermal affinities with Cheung et al. 2013[4]

While a variety of past studies have quantified species' thermal affinities using species' distribution models[51] or the midpoint of species minimum and maximum temperature observations[28], here we inferred thermal affinities as the median temperature value across a species' range of observations. To determine the accuracy of this approach, we compared our data with those of Cheung et al. 2013[4] for 252 overlapping species. We found an 83% correlation between our data and those of Cheung et al. 2013[4], indicating high consistency between the two studies. This provides strong support for our approach because Cheung et al. 2013[4] is a landmark study investigating changes in the community temperature index in marine fishes.

QUANTIFICATION AND STATISTICAL ANALYSIS

All data handling and quantitative analyses were performed using R[45] version 4.0.0.

Decomposing CTI into the four underlying processes

CTI is a community weighted mean and therefore reflects changes in the relative abundances of warm-affinity and cold-affinity species. CTI will increase when species with thermal affinities greater than the mean of the community increase and when species with thermal affinities lower than the mean of the community decrease. Conversely, CTI will decrease when species with thermal affinities greater than the mean of the community decrease and when species with thermal affinities lower than the mean of the community increase. Hence, CTI changes can be decomposed into four underlying process – tropicalization (increasing warm-affinity species), deborealization (decreasing cold-affinity species), borealization (increasing cold-affinity species), and detropicalization (decreasing warm-affinity species). The overall change in CTI reflects the relative strength of these processes. For instance, CTI will increase when the strength of tropicalization + deborealization is greater than the strength of borealization + detropicalization. To determine the strength of each underlying process, species within each grid cell must first be classified as either warm-affinity or cold-affinity. Because CTI (the mean thermal affinity of the community) changes every year, species may be warm-affinity one year (i.e., having a thermal affinity higher than the community mean) and cold-affinity the next (i.e., having a thermal affinity lower than the community mean). Therefore, to classify species as either warm or cold affinity within each grid cell, we used the mean CTI value across all years in the time series (i.e., mean of CTI values for 1990 to 2015 for each grid cell). We then separated warm and cold-affinity species into those that increased in abundance and those that decreased (Figure 1). Because CTI will shift up or down based on the amount of increase or decrease in species abundances along the thermal affinity axis (i.e., Figure 1), the strength of each process can be thought of as the amount of "pull" that each process exhibits on the overall community mean. This is determined by the degree to which species contributing to each process influence the overall community mean. Species that have thermal affinities much greater or much lower than the community mean will exhibit more influence than those with thermal affinities very similar to the mean. Additionally, species with large abundance changes will exhibit more influence than those with small abundance changes. Hence, each species contribution to the change in CTI is a combination of the difference between its individual thermal affinity (STI) and that of the community (CTI) and its change in abundance. We therefore calculated the strength of each processes by (i) calculating the difference between each species' thermal affinity and the mean of the community, (ii) multiplying this value by each species' change in abundance, and (iii) taking the sum of the resulting values for all species within each process (Figure S3). We assessed the accuracy of this approach by comparing the value of (tropicalization + deborealization) – (borealization + detropicalization) to the rate of change in CTI for each grid cell. Note, these two values will never be a perfect match because, as mentioned above, some species fluctuate between warm and cold-affinity over time, especially in grid cells where CTI is highly variable across years. However, we found a correlation of 0.85 between the two values, indicating that our metric for estimating the strength of the underlying processes accurately captured changes in CTI (Figure S4).

Conditions associated with the underlying processes

To identify the biotic and abiotic conditions associated with each underlying process, we modelled the difference in the strength of tropicalization vs. deborealization (i.e., tropicalization minus deborealization) when CTI increased, and the difference in the strength of borealization vs. detropicalization (i.e., borealization minus detropicalization) when CTI decreased. We used linear mixed effects models with Gaussian likelihood distributions and included survey campaign as a random effect (i.e., varying intercept). Explanatory variables were the rate of change in SST, initial (i.e., baseline) SST, mean-annual SST variation, depth, distance to the nearest human population center, mean maximum body size, community thermal diversity (CTDIV), and community thermal range (CTR). Initial SST was defined as the mean-annual SST for each grid cell for the period 1980-1989, the ten years prior to the study period. Depth was recorded during each trawl survey, and we calculated mean depth per grid cell. Distance to the nearest human population center came from Yeager at al.[47], which is calculated as the straight-line distance to the nearest provincial capital as defined by the ESRI World Cities data set. Body size data came from the open-access trait database of Beukhof et al.[48]. CTDIV was defined as the variation in thermal affinities in the community and was calculated as the abundance-weighted standard deviation of species' thermal affinities[9]. CTR describes whether species in the community have narrow or wide thermal ranges and was calculated as the abundance-weighted mean of species' thermal ranges[9]. Thermal ranges were defined as the difference between the 90th and 10th percentiles of species thermal affinity observations. For CTDIV, CTR, and mean body size, we took the mean across the first 10 years of the study period for each grid cell to define baseline conditions in community structure that may have shaped community responses to warming. All metrics were calculated for the entire community sampled in each grid cell. Hence, identical predictors were used for both models, rather than sub-setting predictors to only species contributing to tropicalization and deborealization or to borealization and detropicalization.

Species contributing to opposite processes

To identify differences between species contributing to borealization vs. deborealization, and between species contributing to tropicalization vs. detropicalization, we used linear mixed effects models with binomial likelihood distributions and grid cell nested in survey campaign as random effects (i.e., varying intercepts). In grid cells where CTI increased, explanatory variables included maximum thermal limit, thermal range, maximum body size, and whether species are commercially fished. In grid cells where CTI decreased, the same explanatory variables were used except that minimum thermal limit was used in place of maximum thermal limit. Maximum and minimum thermal limits were defined as the 90th and 10th percentiles of species thermal affinity observations, respectively, and species thermal ranges were defined as the difference between the 90th and 10th percentiles. Body size again came from Beukhof et al.[48]. We defined whether a species was commercially fished according to categories of commercial importance available from FishBase[49]. Species listed as 'highly commercial', 'commercial', or 'minor commercial', were considered commercially fished, and species listed as 'of no interest', 'of potential interest', 'subsistence fisheries', or 'unknown' were considered not commercially fished. All models were performed using the R package lme4[52]. Model quality and assumptions were verified using the R packages performance[53] and MuMin[54] (see Supplementary Material). Initial model inspection revealed low predictive accuracy and explained variation for the binomial models. This was likely because all species were initially included in this analysis whether they showed very slight or very large changes in abundance, i.e., any cold-affinity species whose change in abundance was greater than 0 was classified as contributing to borealization. All species populations fluctuate naturally, and so small increases or decreases in abundance are expected that may be independent of thermal affinity. Hence, including all species in this analysis could potentially blur patterns. We therefore reran models using i) all species, ii) species whose abundance changes were in the top 75%, iii) species whose abundance changes were in the top 50%, and iv) species whose abundance changes were in the top 25%. All approaches yielded very similar results, but with predictive accuracy and explained variation increasing with stricter species subsets. We therefore selected the model using species whose abundance changes were in the top 50% as a compromise between data deletion and model quality (at least 2000 observations per model and predictive accuracy over 70%), however, all model results are reported in Table S4.

Model performance

We assessed the performance of all models using the R package performance. For the two Gaussian models, we assessed linearity (i.e., residuals vs fitted values), homogeneity of variance, collinearity, the potential influence of high leverage observations, normality of residuals, and normality of random effects. This was accomplished with the function check_model. We also assessed predictive accuracy via the correlation between fitted values and observed values and via k-fold cross validation using the function performance_accuracy. Because cross validation results vary between iterations, we ran the performancy_accuracy function 99 times and recorded the average score. Both models satisfied all assumptions, including no high leverage observations and Variance Inflation Factors under 2.5 for all variables. For the model of differences between the strength of tropicalization and deborealization, the correlation between fitted values and observed values was 62% and the average cross validation accuracy was 57%. For the model of differences between the strength of borealization and deborealization, the correlation between fitted values and observed values was 79% and the average cross validation accuracy was 71%.

For the four binomial models, we assessed binned residuals and predictive accuracy using the functions binned_residuals and performance_accuracy. Binned residuals are assessed by first ordering predicted probabilities from smallest to largest and calculating raw residuals. Data are then split into bins of equal numbers of observations and the average residual is plotted against the average predicted probability for each bin. The quality of the model is then evaluated based on the percentage of binned residuals that lie within confidence limits/error bounds. Predictive accuracy was assessed as the area under the receiver operating characteristic curve (AUC – ROC), which evaluates how accurately a binomial model predicts group classification. AUC – ROC is bounded between 0 and 1, with 0 indicating 0% accuracy and 1 indicating 100% accuracy. For sites where CTI increased, the model of differences between species contributing to borealization and deborealization had 85% of residuals within error bounds and a predictive accuracy of 73%, while the model of differences between species contributing to tropicalization and detropicalization had 84% of residuals within error bounds and a predictive accuracy of 73%. For sites where CTI decreased, the model of differences between species contributing to borealization and deborealization had 83% of residuals within error bounds and a predictive accuracy of 71%, while the model of differences between species contributing to tropicalization and detropicalization had 86% of residuals within error bounds and a predictive accuracy of 70%.

Altogether, these results show that our models did not violate assumptions, but that predictive accuracy was less than desirable. This likely indicates that other drivers that we were unable to assess are important in explaining variation in the strength of processes and in differences between species contributing to opposite processes. Further exploration showed that poor predictive accuracy may have also resulted from inconsistent relationships between surveys (i.e., regions). For example, including a random slope term for survey in the binomial models showed that, in sites where CTI decreased, upper thermal maximum was a strong predictor of whether species underwent borealization or derealization for all surveys except the Gulf of Alaska, Gulf of Mexico, and Baltic Sea. Additionally, commercially fished status was a strong predictor of whether species underwent borealization or deborealization in regions that were closer to human population centers, but not those that were further from population centers. However, models that included random slope terms did not have greater predictive accuracy, indicating that improving model accuracy ultimately hangs on uncovering other important drivers of process strength and species differences.

Sensitivity to pelagic species and temperature zone

To determine how including or excluding pelagic species influenced our results, we recalculated i) the rate of change in CTI, ii) the difference in the strength of tropicalization and deborealization, and ii) the difference in the strength of borealization and detropicalization after removing pelagic species. Additionally, to examine the impact of calculating thermal affinities with different water column zones (i.e., bottom temperature, mid-water-column temperature, and sea surface temperature) we recalculated the above three metrics using all three temperature zones. We did this for all possible scenarios, hence for all species using bottom, mid-water-column, and surface temperature, and for demersal species only using bottom, mid-water-column, and surface temperature. We then examined the correlation in metrics across all six scenarios. Across the six scenarios, correlation values for the rate of change in CTI ranged from 0.666 to 0.996 with a mean of 0.83, correlation values for the difference in the strength of tropicalization and deborealization ranged from 0.776 to 0.997 with a mean of 0.873, and correlation values for the difference in the strength of borealization and detropicalization ranged from 0.816 to 0.997 with a mean of 0.894, altogether indicating that results were robust to including or excluding pelagic species and to potential choices in thermal affinity calculation.

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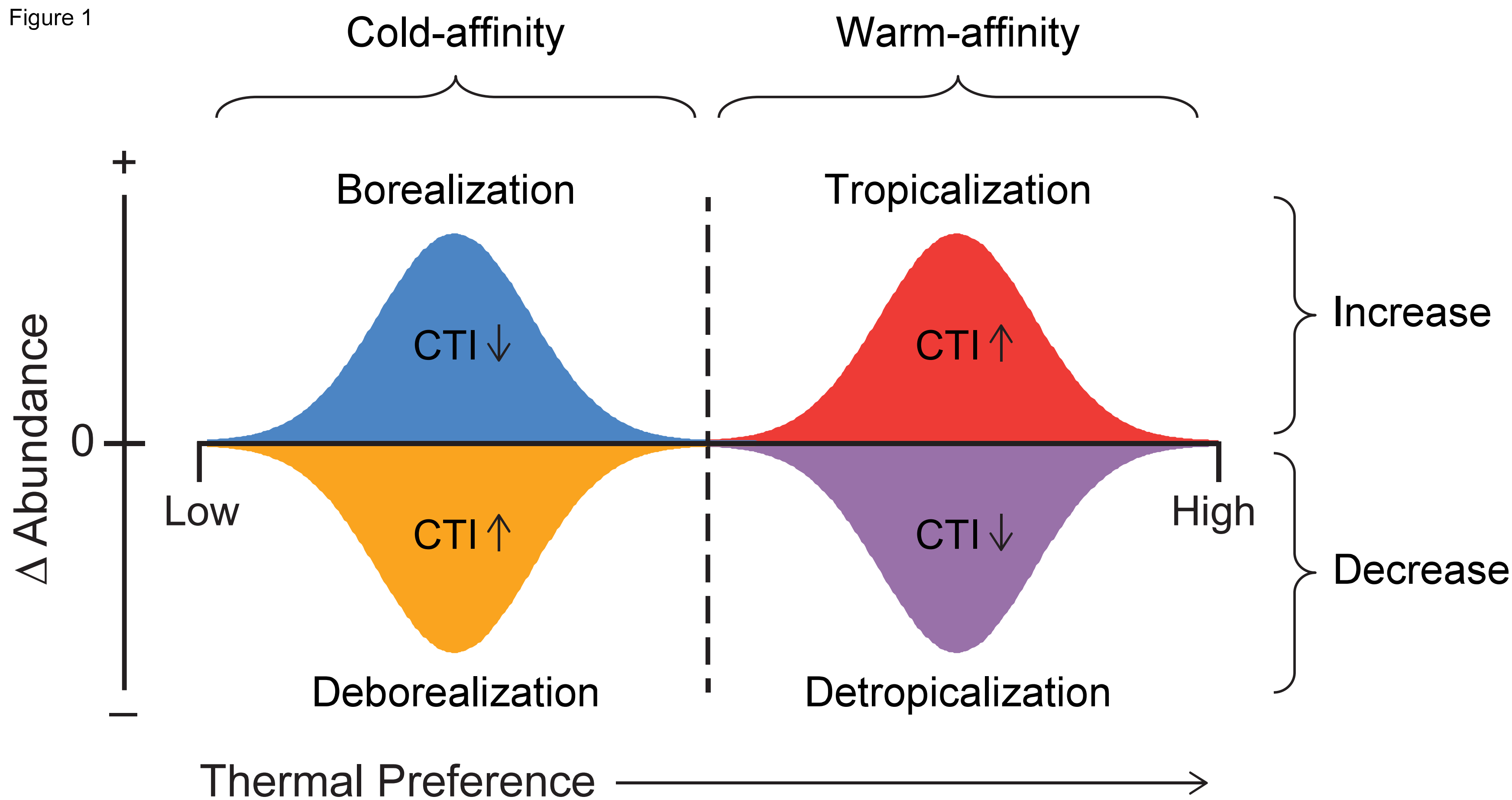
KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and algorithms		
R 4.0.0	The R Project for Statistical Computing[45]	https://cran.r-project.org/
Deposited Data		
Fish monitoring data	OceanAdapt NOAA[2]	https://oceanadapt.rutgers.edu/
Fish monitoring data	DATRAS ICES	https://datras.ices.dk/Data_products/Download/Download_Data_public.aspx
Fish monitoring data	IMR	https://www.hi.no/en/hi/forskning/research-data-1
Sea surface temperature data	Hadley Centre for Climate Prediction and Research[46]	https://www.metoffice.gov.uk/hadobs/hadisst/
Species occurrence data	OBIS	https://obis.org
Species occurrence data	GBIF	https://www.gbif.org
Species occurrence data	VertNet	http://vertnet.org
Species occurrence data	ecoengine	https://ecoengine.berkeley.edu
Mid-water-column temperature data	NOAA WOA 2013 V2 Database	https://www.nodc.noaa.gov/cgi-bin/OC5/woa13/woa13.pl?parameter=t
Distance to human population center data	[47]	https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecy.1884#support-information-section
Body size data	[48]	https://doi.pangaea.de/10.1594/PANGAEA.900866
Commercial fishing status data	FishBase[49]	http://www.fishbase.org

Figure 1



Cold-affinity
Warm-affinity
Borealization
Tropicalization
CTI ↓
CTI ↑
CTI ↑
CTI ↓
Deborealization
Detropicalization
Increase
Decrease
+
0
–
Δ Abundance
Low
High
Thermal Preference

Figure 2

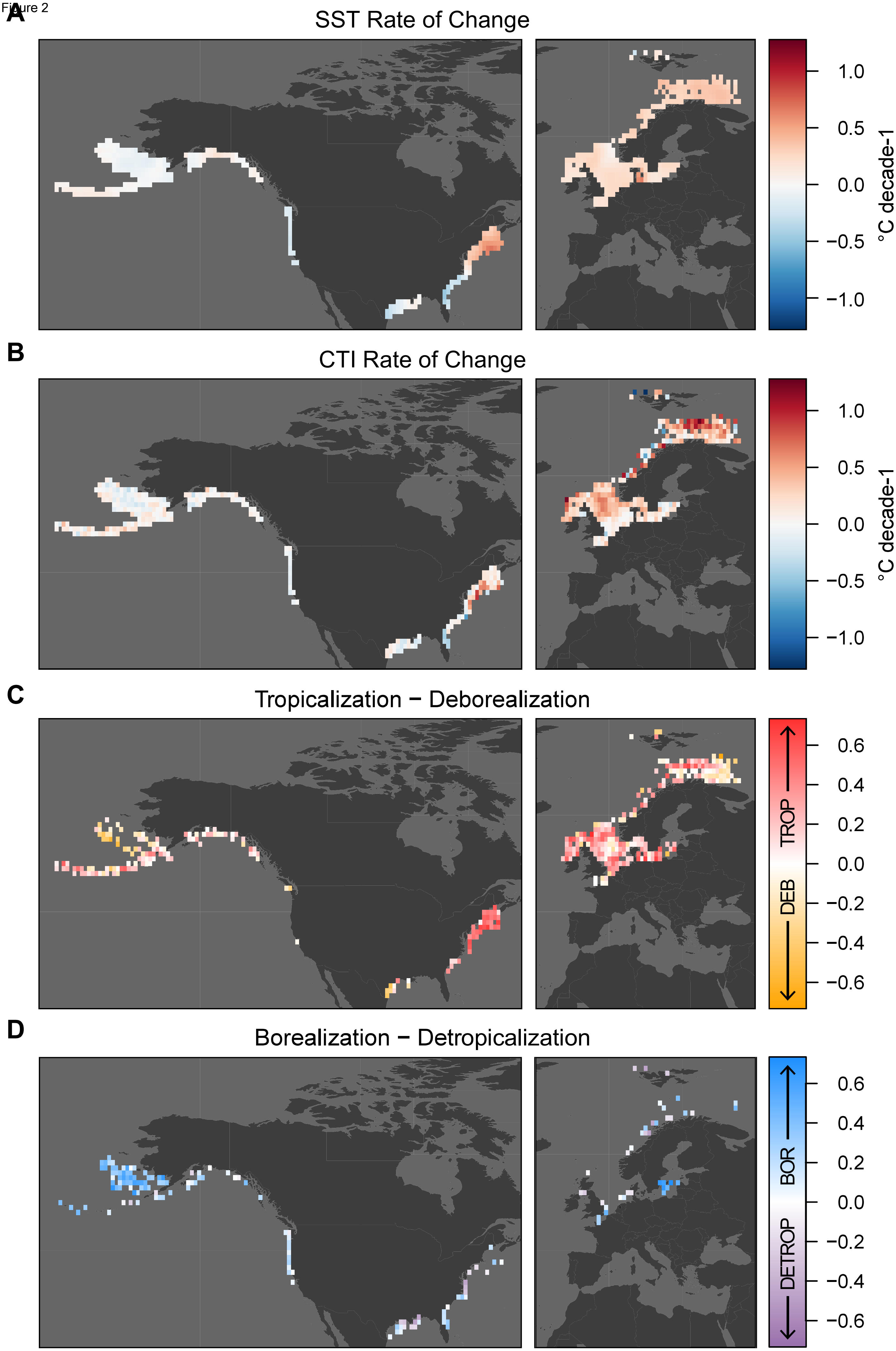
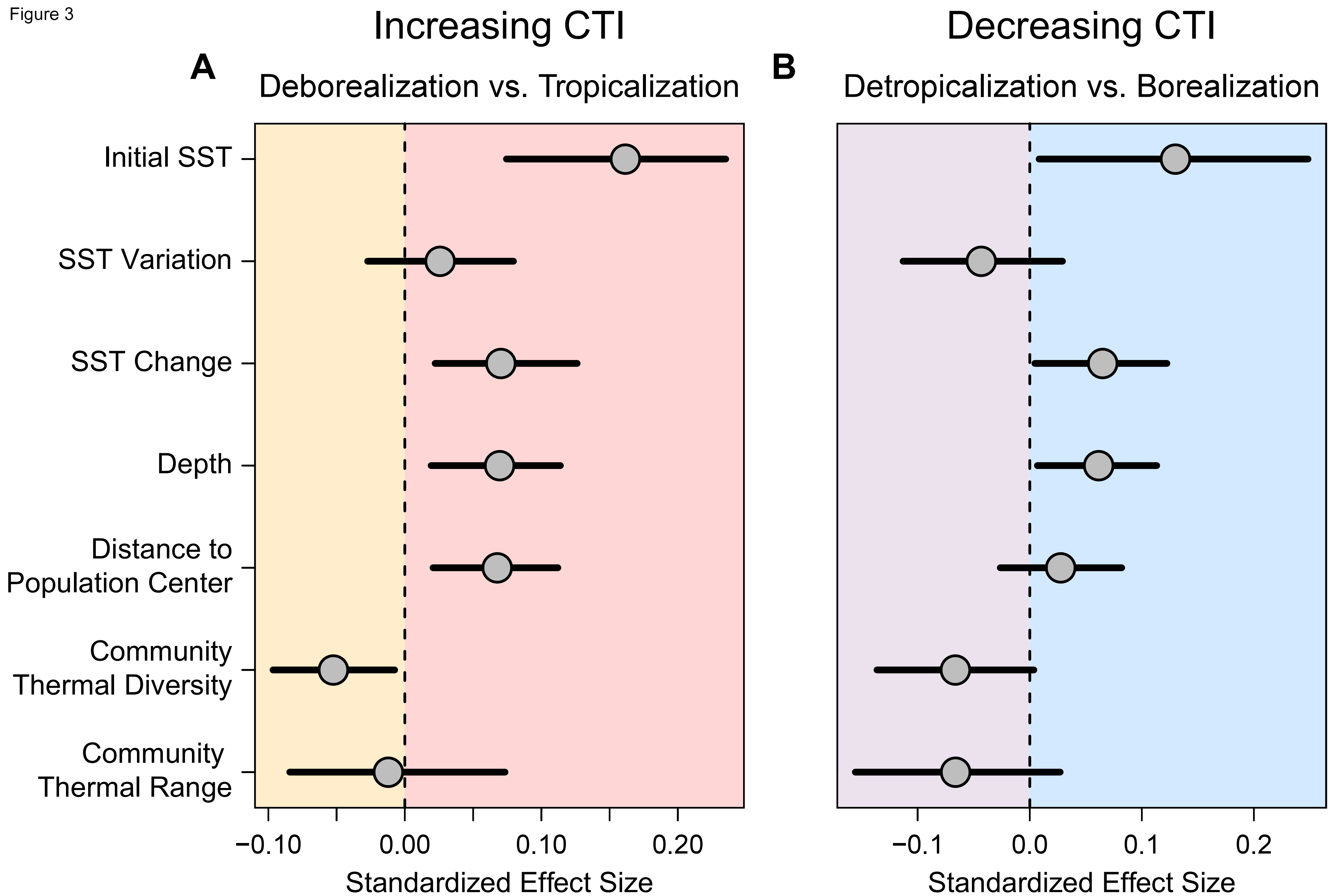
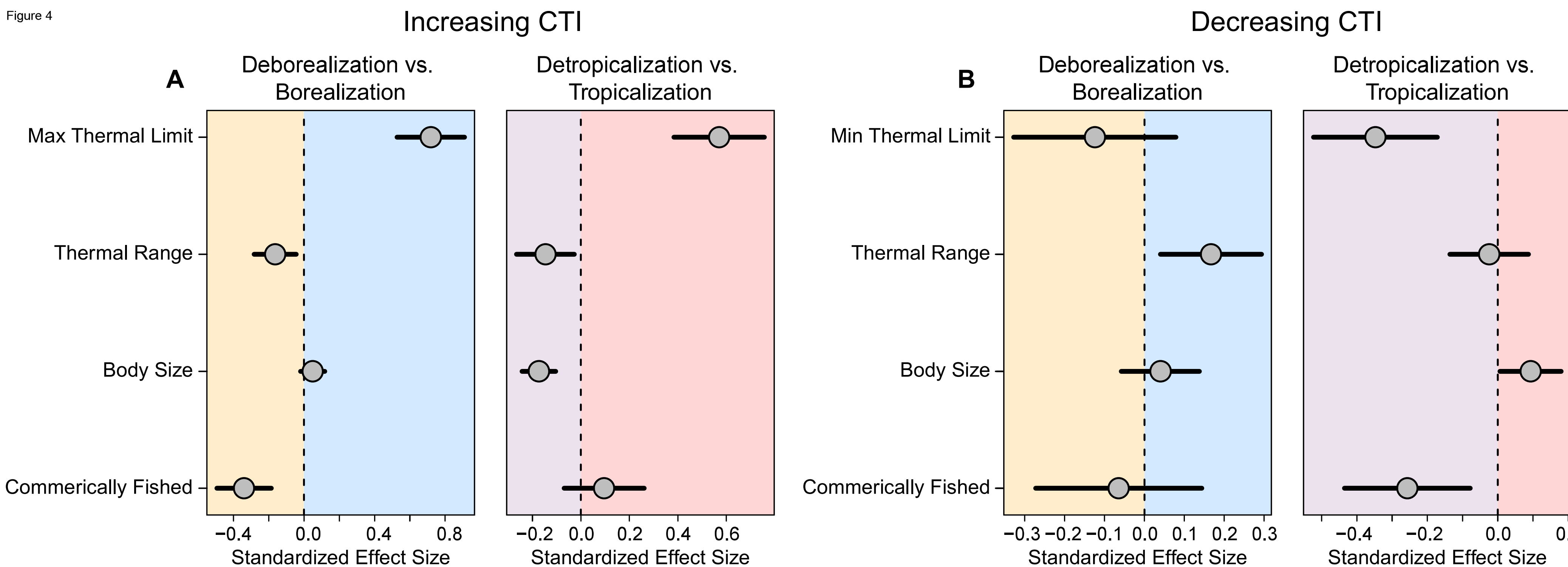

A
SST Rate of Change
1.0
0.5
0.0
−0.5
−1.0
°C decade-1
B
CTI Rate of Change
1.0
0.5
0.0
−0.5
−1.0
°C decade-1
C
Tropicalization − Deborealization
0.6
0.4
0.2
0.0
−0.2
−0.4
−0.6
TROP
DEB
D
Borealization − Detropicalization
0.6
0.4
0.2
0.0
−0.2
−0.4
−0.6
BOR
DETROP

Figure 3



A
Increasing CTI
Deborealization vs. Tropicalization
Initial SST
SST Variation
SST Change
Depth
Distance to
Population Center
Community
Thermal Diversity
Community
Thermal Range
−0.10
0.00
0.10
0.20
Standardized Effect Size
B
Decreasing CTI
Detropicalization vs. Borealization
−0.1
0.0
0.1
0.2
Standardized Effect Size

Figure 4



Increasing CTI
Decreasing CTI
A
B
Deborealization vs. Borealization
Detropicalization vs. Tropicalization
Deborealization vs. Borealization
Detropicalization vs. Tropicalization
Max Thermal Limit
Min Thermal Limit
Thermal Range
Body Size
Commerically Fished
Standardized Effect Size

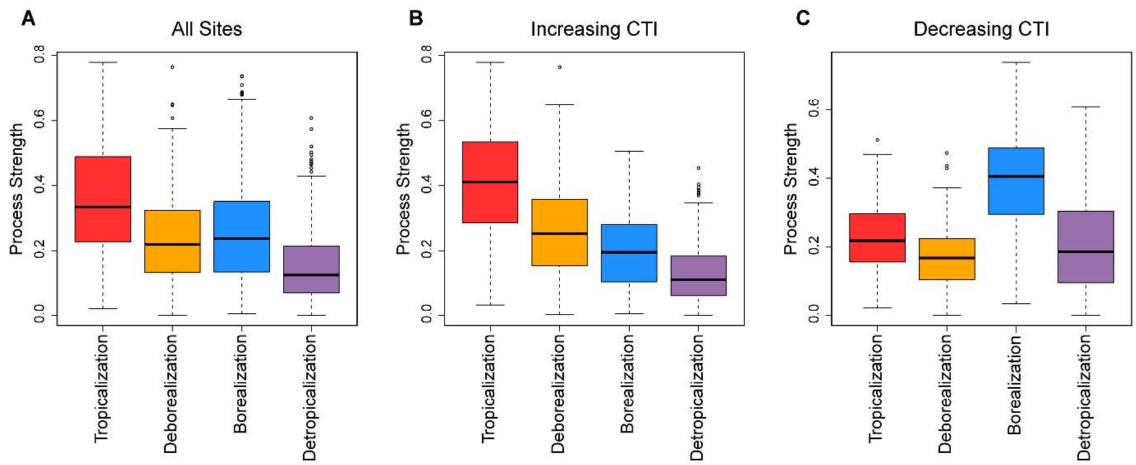


Figure S1. Boxplots of the strength of each of the underlying processes of CTI changes for all sites pooled (A), only sites where CTI increased over time (B), and only sites where CTI decreased over time (C), Related to Figure 2.

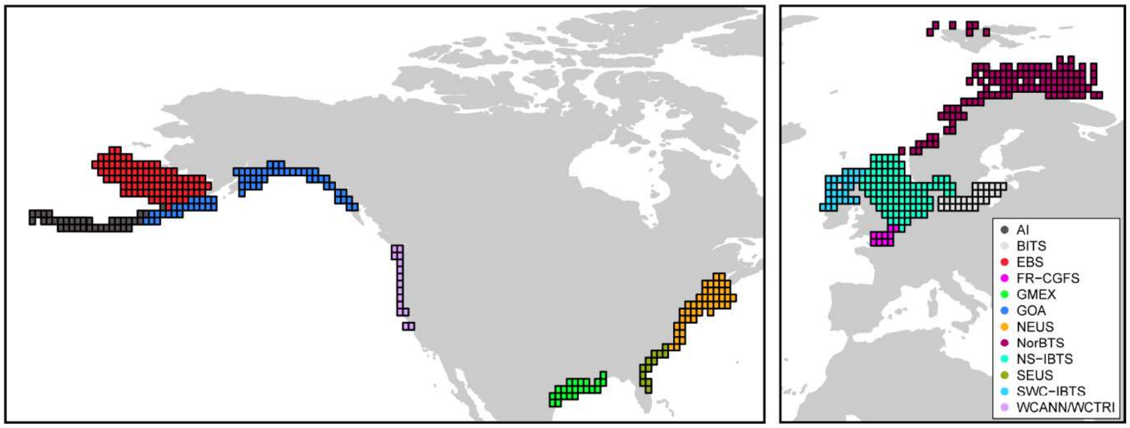


Figure S2. Map showing the spatial locations of the bottom trawl surveys used in the study, Related to Figure 2. Acronyms are defined in Table S1.

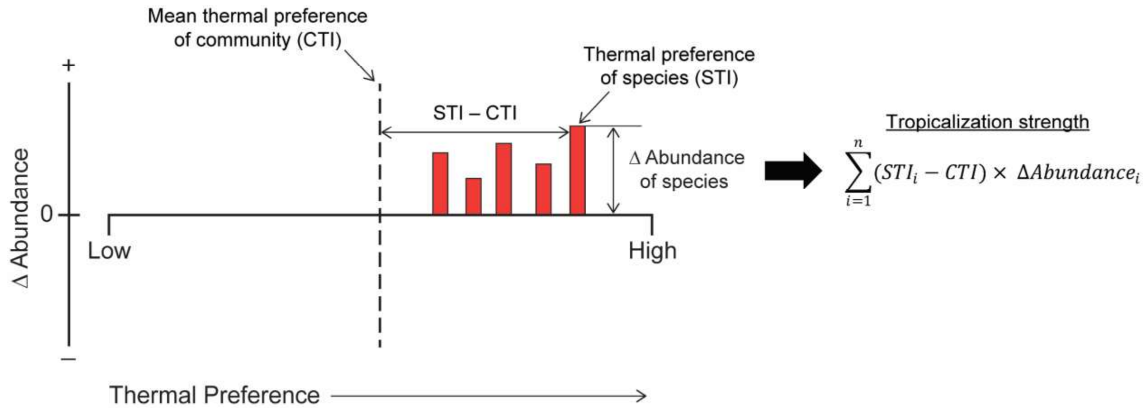


Figure S3. Method for calculating the strength of the underlying processes (tropicalization shown here), Related to Figure 2. First, the difference between each species individual thermal affinity (STI) and the mean thermal affinity of the community (mean CTI of all years for each site) is calculated (i.e., STI – CTI). Secondly, the resulting value is multiplied by species' individual changes in abundance (i.e., rate of change in abundance over time). Third, the sum of all resulting values is taken across all species.

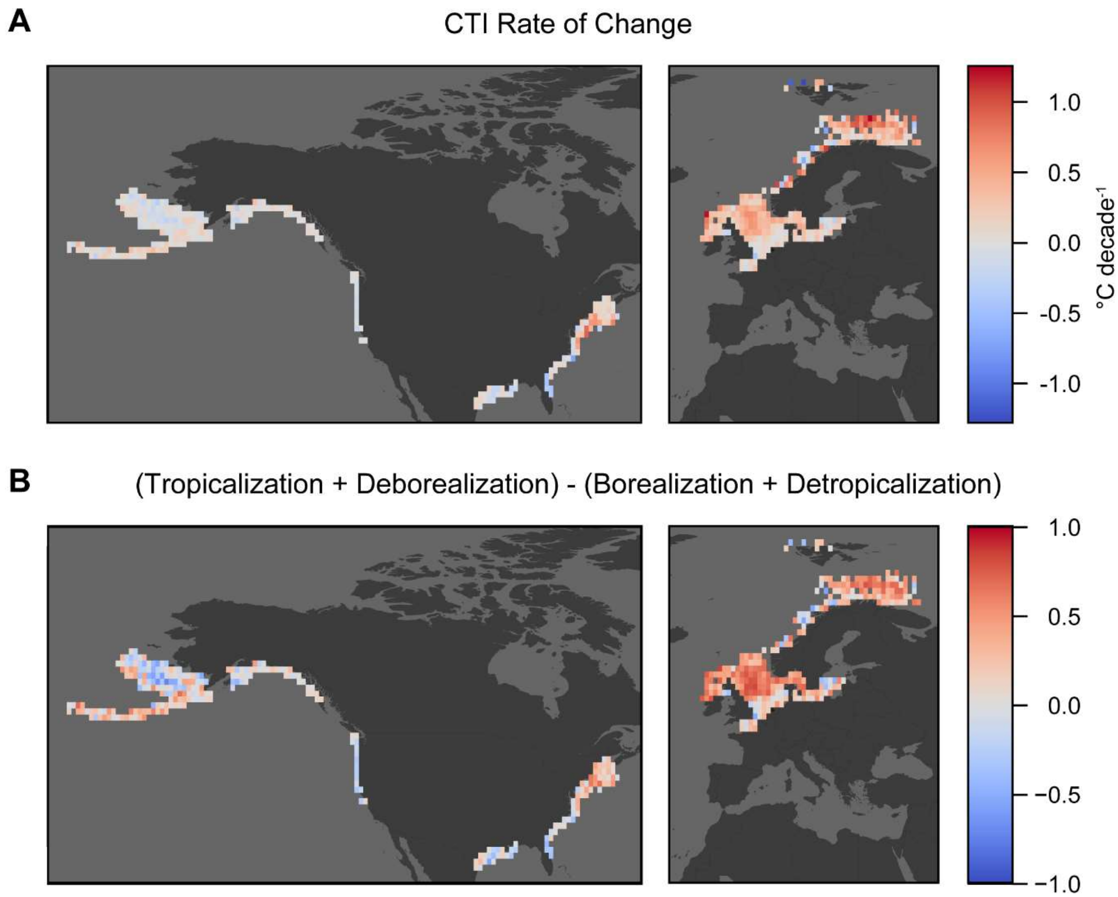


Figure S4. Maps of the rate of change in CTI (A) and the value of warm processes – cold processes, i.e., (topicalization + deborealization) – (borealization + detropicalization) (B), Related to Figure 2. The rate of change in CTI (A) and the value of warm processes – cold processes (B) had a correlation coefficient of 0.85.

Survey	Area	Years	Months	Source Reference
AI	Aleutian Islands	1991-2014	May – Sep	OceanAdapt NOAA[S1]
BITS	Baltic Sea	1991-2015	Jan. – Dec	DATRAS ICES[S2]
EBS	East Bering Sea Shelf	1990-2015	May – Aug	OceanAdapt NOAA[S1]
FR-CGFS	East English Channel	1990-2015	Sep – Dec	DATRAS ICES[S2]
GMEX	Gulf of Mexico	1990-2015	May – Oct	OceanAdapt NOAA[S1]
GOA	Gulf of Alaska	1990-2015	May – Sep	OceanAdapt NOAA[S1]
NEUS	Northeast US	1990-2015	Feb – Dec	OceanAdapt NOAA[S1]
NorBTS	Norwegian Sea, Barents Sea	1990-2015	Jan – Dec	IMR[S3]
NS-IBTS	North Sea	1990-2015	Jan – Dec	DATRAS ICES[S2]
SEUS	Southeast US shelf	1990-2015	Apr – Nov	OceanAdapt NOAA[S1]
SWC-IBTS	Scotland Shelf Sea	1990-2015	Feb – Dec	DATRAS ICES[S2]
WCANN	West US Coast annual	2003-2015	May – Oct	OceanAdapt NOAA[S1]
WCTRI	West US Coast Tri-annual	1992-2004	May – Oct	OceanAdapt NOAA[S1]

Table S1. Metadata and sources for the thirteen bottom trawl survey campaigns used in this study, Related to Figure 2.

	trop_minus_deb			bor_minus_detrop		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Intercept	0.08	-0.06 – 0.22	0.271	0.14	-0.04 – 0.32	0.121
SST Variation	0.03	-0.03 – 0.08	0.351	-0.04	-0.12 – 0.03	0.238
SST Initial	0.16	0.09 – 0.23	**<0.001**	0.13	0.01 – 0.25	**0.035**
SST Change	0.07	0.02 – 0.12	**0.005**	0.07	0.01 – 0.12	**0.031**
Depth	0.07	0.02 – 0.12	**0.003**	0.06	0.01 – 0.11	**0.024**
Distance to Market	0.07	0.02 – 0.11	**0.004**	0.03	-0.03 – 0.08	0.326
CTDIV	-0.05	-0.10 – -0.01	**0.022**	-0.07	-0.14 – 0.01	0.069
CTR	-0.01	-0.09 – 0.06	0.749	-0.07	-0.16 – 0.03	0.159
Random Effects						
σ^2	0.05			0.03		
τ_{00}	0.05 $_{survey}$			0.09 $_{survey}$		
ICC	0.51			0.72		
N	12 $_{survey}$			12 $_{survey}$		
Observations	398			160		
Marginal R^2 / Conditional R^2	0.100 / 0.559			0.135 / 0.761		

Table S2. Summary tables for models of differences in the strength of the underlying processes, Related to Figure 3.

	deb_vs_bor_warming			trop_vs_detrop_warming			deb_vs_bor_cooling			trop_vs_detrop_cooling		
Predictors	*Log-Odds*	*CI*	*p*	*Log-Odds*	*CI*	*p*	*Log-Odds*	*CI*	*p*	*Log-Odds*	*CI*	*p*
Intercept	0.02	-0.44 – 0.48	0.934	0.72	0.12 – 1.33	**0.019**	0.66	0.38 – 0.94	**<0.001**	0.29	0.05 – 0.52	**0.016**
Commerically Fished	-0.34	-0.49 – -0.19	**<0.001**	0.10	-0.07 – 0.26	0.256	-0.06	-0.27 – 0.14	0.543	-0.26	-0.44 – -0.08	**0.005**
Body Size	0.05	-0.02 – 0.12	0.164	-0.17	-0.24 – -0.10	**<0.001**	0.04	-0.06 – 0.14	0.422	0.09	0.01 – 0.18	**0.035**
Thermal Range	-0.16	-0.28 – -0.04	**0.007**	-0.15	-0.27 – -0.03	**0.016**	0.17	0.04 – 0.29	**0.010**	-0.02	-0.14 – 0.09	0.670
Max Thermal Limit	0.72	0.53 – 0.91	**<0.001**	0.57	0.38 – 0.76	**<0.001**						
Min Thermal Limit							-0.12	-0.33 – 0.08	0.231	-0.35	-0.52 – -0.17	**<0.001**
Random Effects												
σ^2	3.29			3.29			3.29			3.29		
τ_{00}	0.19 $_{site:survey}$			0.18 $_{site:survey}$			0.27 $_{site:survey}$			0.23 $_{site:survey}$		
	0.58 $_{survey}$			1.05 $_{survey}$			0.10 $_{survey}$			0.03 $_{survey}$		
ICC	0.19			0.27			0.10			0.07		
N	398 $_{site}$			398 $_{site}$			160 $_{site}$			160 $_{site}$		
	12 $_{survey}$			12 $_{survey}$			12 $_{survey}$			12 $_{survey}$		
Observations	4583			4670			2181			2615		
Marginal R^2 / Conditional R^2	0.084 / 0.258			0.063 / 0.317			0.011 / 0.109			0.038 / 0.107		

Table S3. Summary tables for models of differences between species contributing to opposite processes, Related to Figure 4.

Increasing CTI: Deborealization vs. Borealization								
Species subset	**Max Thermal limit**	**Thermal range**	**Body size**	**Fished**	**Marginal R^2 / Conditional R^2**	**Binned residuals**	**Predictive accuracy**	**Observations**
All species	0.52 [0.40, 0.65]	-0.13 [-0.21, -0.05]	0.07 [0.02, 0.12]	-0.39 [-0.50, -0.29]	0.054/0.156	86%	66.5%	8691
Top 75%	0.66 [0.51, 0.82]	-0.16 [-0.26, -0.07]	0.05 [-0.01, 0.10]	-0.33 [-0.45, -0.20]	0.076/0.215	84%	68.7%	6639
Top 50%	0.72 [0.53, 0.91]	-0.16 [-0.28, -0.04]	0.05 [-0.02, 0.12]	-0.34 [-0.49, -0.19]	0.084/0.258	85%	72.6%	4583
Top 25%	0.99 [0.69, 1.28]	-0.30 [-0.49, -0.11]	0.04 [-0.06, 0.14]	-0.48 [-0.72, -0.25]	0.114/0.406	75%	79.8%	2351
Increasing CTI: Detropicalization vs. Tropicalization								
Species subset	**Max Thermal limit**	**Thermal range**	**Body size**	**Fished**	**Marginal R^2 / Conditional R^2**	**Binned residuals**	**Predictive accuracy**	**Observations**
All species	0.21 [0.11, 0.32]	-0.07 [-0.15, -0.01]	-0.13 [-0.17, -0.09	-0.08 [-0.18, 0.01]	0.015/0.117	90%	65.6%	10406
Top 75%	0.26 [0.13, 0.39]	-0.06 [-0.15, 0.03]	-0.15 [-0.20, -0.10]	-0.09 [-0.21, 0.04]	0.021/0.186	85%	68.5%	7277
Top 50%	0.57 [0.38, 0.76]	-0.15 [-0.27, -0.03]	-0.17 [-0.24, -0.10]	0.09 [-0.07, 0.26]	0.063/0.317	84%	72.6%	4670
Top 25%	1.10 [0.76, 1.39]	-0.29 [-0.50, -0.09]	-0.09 [-0.20, 0.01]	0.17 [-0.10, 0.45]	0.118/0.565	72%	81.2%	2222
Decreasing CTI: Deborealization vs. Borealization								
Species subset	**Min Thermal limit**	**Thermal range**	**Body size**	**Fished**	**Marginal R^2 / Conditional R^2**	**Binned residuals**	**Predictive accuracy**	**Observations**
All species	-0.11 [-0.26, 0.04]	0.11 [0.02, 0.20]	0.06 [-0.01, 0.13]	-0.06 [-0.21, 0.09]	0.007/0.073	83%	66.8%	3970
Top 75%	-0.08 [-0.26, 0.10]	0.15 [0.04, 0.25]	0.05 [-0.03, 0.13]	-0.01 [-0.18, 0.16]	0.008/0.093	86%	68.6%	3188
Top 50%	-0.12 [-0.33, 0.08]	0.17 [0.04, 0.29]	0.04 [-0.06, 0.14]	-0.06 [-0.27, 0.14]	0.011/0.109	83%	71.0%	2181
Top 25%	-0.17 [-0.43, 0.10]	0.22 [0.04, 0.40]	0.15 [0.01, 0.30]	-0.14 [-0.44, 0.16]	0.025/0.141	79%	73.4%	1169
Decreasing CTI: Detropicalization vs. Tropicalization								
Species subset	**Min Thermal limit**	**Thermal range**	**Body size**	**Fished**	**Marginal R^2 / Conditional R^2**	**Binned residuals**	**Predictive accuracy**	**Observations**
All species	-0.23 [-0.35, -0.10]	-0.01 [-0.09, 0.06]	0.04 [-0.02, 0.10]	-0.18 [-0.30, -0.06]	0.017/0.066	86%	65.6%	5129
Top 75%	-0.22 [-0.38, -0.07]	0.01 [-0.07, 0.10]	0.04 [-0.03, 0.10]	-0.21 [-0.35, -0.07]	0.18/0.075	86%	67.1%	3959
Top 50%	-0.35 [-0.52, -0.17]	-0.02 [-0.14, 0.09]	0.09 [0.01, 0.18]	-0.26 [-0.44, -0.08]	0.038/0.107	86%	70.2%	2615
Top 25%	-0.78 [-1.20, -0.36]	-0.10 [-0.31, 0.11]	0.08 [-0.04,0.21]	-0.43 [-0.70, -0.16]	0.130/0.315	75%	78.5%	1301

Table S4. Model coefficients and explained variation for i) all species, ii) species whose abundance changes were in the top 75%, iii) species whose abundance changes were in the top 50%, and iv) species whose abundances changes were in the top 25%, Related to Figure 4. Values shown for predictor variables are standardized effect sizes and 95% confidence intervals.

Supplemental References

S1. https://oceanadapt.rutgers.edu/S5.

S2. https://datras.ices.dk/Data_products/Download/Download_Data_public.aspx

S3. https://www.hi.no/en/hi/forskning/research-data-1