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# Contrasted spatio-temporal changes in the demersal fish assemblages and the dominance of the environment vs fishing pressure, in the Bay of Biscay and Celtic Sea

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## ABSTRACT

Climate change and resource exploitation represent strong selection pressure affecting the spatio-temporal dynamics of marine assemblages that ensure food provision for humans. However, such dynamics remain poorly documented, and their drivers unclear. Here, we investigate changes in fish assemblages of two key European fishing areas, the Bay of Biscay (BoB) and the Celtic Sea (CS), during the last two decades. We quantify the relative contribution of change in energy (i.e. temperature and trophic resources), habitat (depth, substrate, oxygen) and fishing pressure to explaining observed spatial and temporal variations in fish diversity. We used long-term scientific surveys to evaluate the spatio-temporal changes in species richness (SR), abundance and composition of demersal fish (Actinopterygii) assemblages at different spatial scales combined with a range of regression models and variance partitioning. Diversity patterns showed greater variability in space than in time: SR weakly changed over time, while compositional dissimilarity showed local patterns of taxonomic homogenization in the CS and differentiation in the southern BoB, where local assemblages were becoming more similar and dissimilar over time, respectively. Energy funnelled through small pelagic species as a potential trophic link affecting the dynamics of demersal assemblages was the most important driver, while habitat and fishing pressure had limited importance. Our study revealed contrasted dynamics of demersal fish assemblages at a regional scale that were best explained by the dynamics of small pelagic species. Direct effects of environmental forcing and fishing pressure were limited in both regions which have a long history of fishing and still remain relatively buffered from global warming effects. This research paved the way to combine methods inspired by biogeography with scientific monitoring surveys to detect spatio-temporal dynamics of fish assemblages and their drivers in marine ecosystems under multiple pressures.

## 1. Introduction

Understanding the spatio-temporal dynamics of species assemblages in the Anthropocene is essential to predict and mitigate ongoing and future changes (Blowes et al., 2019) to ensure the provision of ecosystem

services (Tilman et al., 2017). Marine communities are prone to larger spatio-temporal dynamics and re-organisation than terrestrial communities (Dornelas et al., 2014) due to their greater sensitivity to environmental changes and faster rates of colonisation favoured by higher habitat connectivity (Pinsky et al., 2019). The pace of change of marine

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communities is not uniform across oceans and maximal in temperate regions, including the northeast Atlantic Ocean and European shelf seas (Antão et al., 2020). Long-term fishing pressure and (over-)exploitation of fish stocks represent additional drivers (Pauly et al., 2005). The exploitation of the northeast Atlantic and European shelf seas during the 19th and 20th centuries has negatively affected the abundance of many fish populations (Thurstan et al., 2010). Anthropogenic drivers are not acting independently, climate change interacting with fishing activities affects the recovery of depleted fish stocks (Planque et al., 2010) and these interactions are expected to intensify in the coming decades (Britten et al., 2017). Table 1.

Decadal variations in the spatio-temporal dynamics of communities are ultimately driven by the presence of individuals of different species that depends on 1) stochastic variation in abundance, 2) tolerance of individuals in regards to the selective pressure of local environmental conditions, and 3) arrival or departure of individuals via dispersal (Vellend, 2010). Environmental forcings of the Anthropocene increase the selective pressure on populations and depending on a species' dispersal capacities, its distribution range can shift, shrink or extend (Dornelas et al., 2019). Key variables related to environmental forcing are associated with energy either directly through changes of ambient energy (i.e. kinetic energy, or solar energy) or indirectly through variations of productive energy (i.e. chemical energy, Evans et al., 2005; Koenigstein et al., 2016). Ambient energy corresponds to the amount of solar radiation received in the system which is often approximated by temperature (i.e. global warming), while productive energy corresponds to the conversion of solar energy into organic matter by photosynthetic organisms (i.e. plants, cyanobacteria, phytoplankton) which becomes available as trophic resources for heterotrophic organisms (see Evans et al., 2005 for a review). Productive energy in marine systems is often approximated by net primary productivity (Tittensor et al., 2010; Woolley et al., 2016). Ambient and productive energy represent two key factors of species niche through physiological tolerance and trophic requirements known to play a crucial role for metabolism, and geographic distribution (Brown et al., 2004; Evans et al., 2005; Valentine and Jablonski, 2015; Tittensor & Worms, 2016). The species-energy hypothesis holds a central position to explain large biodiversity

gradients through a wide range of mechanisms (Wright 1983; Evans et al., 2005; Clarke & Gaston, 2006). Species-energy relationships are mostly either positive or hump-shaped (Bonn et al., 2004; Cusens et al., 2012). As such it implies that the number of individuals and species increase with energy up to a certain point before possibly decreasing (Cusens et al., 2012). Fishing pressure represents an additional selective force affecting species abundance in space and time (e.g. Lotze & Worm, 2009). Fishing might not be simply decreasing the abundance of caught species, but it can indirectly increase the abundance of non targeted species due to predation release or an increase in trophic resources (Moulllec et al., 2017).

Environmental forcings and fishing can increase the spatio-temporal variability of fish assemblages, whose diversity dimensions can be differentially affected. Within communities, measures of  $\alpha$  diversity (i.e. the mean species richness at local scale; Whittaker, 1972), including species richness (SR, i.e. the number of species) can increase, decrease or remain stable over time under environmental changes (e.g. Blowes et al., 2019; Antão et al., 2020). Variations of biodiversity over time can be scale-dependent, and differ in space, across taxa and ecosystems (Albouy et al., 2012; Dornelas et al., 2014; Magurran et al., 2019). Complementing  $\alpha$  diversity, measures of  $\beta$  diversity (Anderson et al., 2011) can be used to quantify how the difference in species composition among spatial communities (dissimilarity) changes over time (Olden, 2006). The arrival of generalist species and the loss of locally endemic species may not change species richness (Dornelas et al., 2019) but leads communities to become more similar spatially, a phenomenon identified as taxonomic homogenization (as opposed to taxonomic differentiation, McKinney & Lockwood, 1999).  $\beta$  diversity can also quantify the variability in species composition within a community over time, the so-called temporal  $\beta$  diversity (e.g. Albouy et al., 2012; Magurran et al., 2019). These incidence-based indices can be less sensitive to environmental variations than abundance-based biodiversity indices (Santini et al., 2017). For example, exploitation of fish stocks (i.e. populations) can strongly affect abundance (Hutchings et al., 2010), while incidence-based indices will be affected only by local extinction (Burgess et al., 2013). Investigating the spatio-temporal dynamics of species assemblages and their potential drivers requires a holistic approach documenting simultaneously changes in  $\alpha$  and  $\beta$  diversity within and among communities over time at different spatial scales (McGill et al., 2015) with both presence/absence and abundance-based biodiversity indices (Antão et al., 2020).

Increase in sea surface temperature is hypothesised to be the main driver of the distribution shift observed for major Northeast Atlantic commercial marine species (Baudron et al., 2020), the taxonomic homogenization of groundfish communities on the west coast of Scotland (Magurran et al., 2015), and the taxonomic differentiation of North Sea fish communities (McLean et al., 2019). In the Northeast Atlantic, the Bay of Biscay and the Celtic Sea are highly productive shelf seas (Moulllec et al., 2017) with a long fishing history (Gascuel et al., 2016) and harbouring benthic communities and habitats heavily degraded by bottom trawl fishing activities (Hily et al., 2008). Moreover, the combination of diversification of fish stock exploitation and the over-exploitation of several stocks has not yet led to a clear recovery in community biomass (Gascuel et al., 2016). Despite the effects of global warming being smaller in the Bay of Biscay and Celtic Sea in comparison to other regions (Chust et al., 2011), a forty-year time-series revealed an increase in temperature of the upper sea layer (200 m) of the Bay of Biscay (Michel et al., 2009), which correlates with a northward shift of boreal species (Poulard & Blanchard, 2005) and an increase in the abundance of lusitanian species (e.g. Hermant et al., 2010) that is expected to further increase in the coming decades (Le Marchand et al., 2020). Global warming effects on biodiversity dynamics are not necessarily monotonic (Pech et al., 2017) and subtle environmental forcings may have already triggered important community re-organisation (e.g. for species located at the limits of their distribution range) as suggested by several examples in the Bay of Biscay and the Celtic Sea (Poulard &

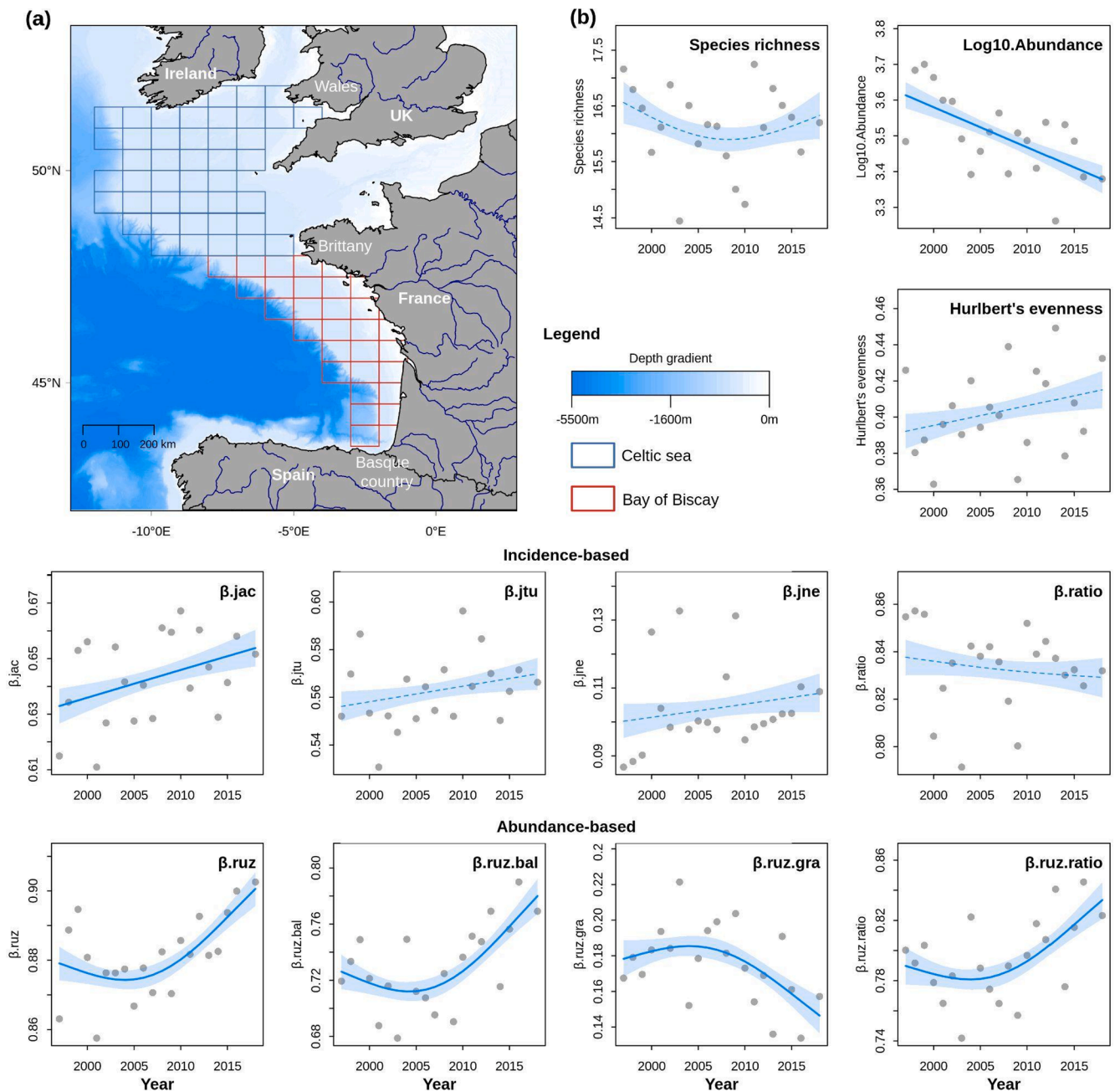
**Table 1**  
Definition of acronyms.

Acronym	Definition
SR	Species richness
$\beta_{jac}$	Beta diversity estimated by the Jaccard index (accounting for presence/absence)
$\beta_{jtu}$	Beta diversity estimated by the Jaccard's turnover component
$\beta_{jne}$	Beta diversity estimated by the Jaccard's nestedness-resultant component
$\beta_{ruz}$	Beta diversity estimated by the Ruzicka index (accounting for abundance)
$\beta_{ruz.bal}$	Beta diversity estimated by the balanced variation in abundance component of the Ruzicka index
$\beta_{ruz.gra}$	Beta diversity estimated by the gradient in abundance component of the Ruzicka index
LBD	Local beta diversity
LBD <sub>jac</sub>	Local beta diversity of the Jaccard index
LBD <sub>jtu</sub>	Local beta diversity of the Jaccard's turnover component
LBD <sub>jne</sub>	Local beta diversity of the Jaccard's nestedness-resultant component
LBD <sub>ruz</sub>	Local beta diversity of the Ruzicka index
LBD <sub>ruz.bal</sub>	Local beta diversity of the Ruzicka's balanced variation in abundance component
LBD <sub>ruz.gra</sub>	Local beta diversity of the Ruzicka's gradient in abundance component
TBI	Temporal beta diversity indices; suffix specifies which index (Jaccard, or Ruzicka) and which component (jtu, jne, bal, gra) is used.
GLM	Generalised linear model
LMM	Linear mixed model
GAM	Generalised additive model
GAMM	Generalised additive mixed model
MEM	Moran Eigenvector Map
BIC	Bayesian Information Criteria

Blanchard, 2005; Hermant et al., 2010; Iglésias and Lorange, 2016; Mérillet et al., 2020). So far, scientific bottom trawl surveys in the Bay of Biscay and Celtic Sea have contributed *inter alia* to the annual assessment of commercial species (e.g. ICES, 2017), to study their habitat preferences (Persson et al., 2009) and the dynamics of functional groups (Hosack & Trenkel, 2019). Studies were restricted to smaller areas or species pools (Poulard & Blanchard, 2005; Mérillet et al., 2020), or included disparate taxa groups (i.e. belonging to different phyla or subphyla) with variable taxonomic resolution (Poulard & Trenkel, 2007). However, these studies offered mixed results, and a holistic view of the spatio-temporal patterns of the demersal fish communities and

their potential drivers is currently lacking despite the importance of the ecosystem services provided by the Bay of Biscay and Celtic Sea ecosystems.

In this study, we investigated the spatio-temporal changes of demersal marine ray-finned fishes in the Bay of Biscay and the Celtic Sea during the last two decades, and assessed the relative contribution of energy, habitat and fishing pressure as drivers of spatial and temporal biodiversity patterns. We used data from a standardised scientific survey carried out in the Bay of Biscay and the Celtic Sea from 1997 to 2018 to derive biodiversity indices to document changes in  $\alpha$  and  $\beta$  diversity within and among communities over-time, considering incidence and



**Fig. 1.** (a) Map depicting the ICES rectangles of the Celtic Sea and the Bay of Biscay covered by the EVHOE bottom trawl survey from 1997 to 2018 sampling demersal fish assemblages ( $n = 171$  sp.). (b) Temporal trend average by ICES rectangle per year for species richness (SR), abundance ( $\log_{10}(\text{abundance})$ ), Hurlbert's evenness, and for all pairwise ICES rectangle comparisons for the Jaccard index ( $\beta.jac$ ), its species turnover ( $\beta.jtu$ ) and nestedness ( $\beta.jne$ ) components, the ratio of species turnover over the Jaccard index ( $\beta.ratio$ ), and abundance-based dissimilarity indices, including the Ruzicka index ( $\beta.ruz$ ) and its balanced variation in abundance ( $\beta.ruz.bal$ ), and abundance gradient ( $\beta.ruz.gra$ ) components as well as the ratio  $\beta.ruz.bal/\beta.ruz$  ( $\beta.ruz.ratio$ ). The continuous curves represent the fits of generalised additive models (GAM), with solid lines indicating a significant relationship, while dotted lines indicate a non-significant time trend ( $p.\text{value} > 0.1$ ), and the light blue area indicates the standard error around the fitted models.



abundance-based indices at regional and local scales. We hypothesised that the spatio-temporal dynamics of communities would be more evident using abundance-based indices than presence/absence indices because the effects of climate change in the study area remain currently more subtle than further north (Dye et al., 2013). Then, we selected a large set of environmental variables related to ambient (e.g. temperature) and productive energy (e.g. trophic resources), habitat, and fishing. We performed a variable selection procedure and used the best set of variables to assess the relative contribution of energy, habitat and fishing to spatio-temporal variability in biodiversity using a range of regression models. We hypothesised that fishing pressure should have a higher contribution than energy because the diversification of fish stock exploitation following fishing regulations attributed to several over-exploited stocks (Gascuel et al., 2016) may have a greater impact on spatio-temporal dynamics of fish communities rather than climate change effects.

## 2. Materials and methods

### 2.1. Data acquisition and study area

The biological data sets came from the French international bottom trawl survey (EVHOE) carried out annually during autumn to evaluate demersal fish resources in the Bay of Biscay (BoB) since 1987 and the Celtic Sea (CS) since 1997 (Fig. 1a). The BoB, which stretches from Spain to Armorica, is an intracontinental sea that is largely open to the Atlantic Ocean. The French part of the BoB continental shelf (80 000 km<sup>2</sup>) is narrow in the south and becomes broader in the north mainly influenced by the warm water of the Gulf Stream (Palter, 2015; Fig. 1A). The epicontinental CS is open to the Atlantic Ocean, stretching between Ireland, Wales, British Cornwall and Armorican Brittany. We compiled the presence/absence and abundance data for the period 1997–2018, the most homogenous time series in terms of research vessel, taxonomic identification and gear (GOV 36/47, the opening is 20 m horizontally at the wings and 4 m vertically). The time series is continuous, except for 2017 due to a technical problem, and the number of sampling stations varied between 119 and 158 per year ( $n = 2957$  in total). Our data set included 180 fish (Actinopterygii) species or genera after grouping taxa that could not be unambiguously identified at the species level for the whole time series. For example, *Trachurus mediterraneus* and *Trachurus trachurus* were merged into *Trachurus sp.* We analysed taxonomic diversity for 171 benthic and demersal species/genera. We excluded from diversity calculations, nine of the most abundant small and medium-sized pelagic species (*Alosa alosa*, *Alosa fallax*, *Atherina presbyter*, *Engraulis encrasicolus*, *Sardina pilchardus*, *Scomber japonicus*, *Scomber scombrus*, *Sprattus sprattus*, *Trachurus sp.*) because the bottom trawl used in EVHOE has a 4 m vertical opening, which leads to low catchability and thus unreliable spatial patterns (Laffargue et al., 2021, but see Supplementary material S.2 Fig. S6, Fig. S7, Fig. S8, Fig. S9, for biodiversity patterns including these 9 species). However, we found that the overall temporal abundance trends estimated with the EVHOE data set for most of these pelagic species (see Supplementary Material S2. Fig. S13) were in good agreement with temporal biomass trends estimated by the dedicated PELGAS acoustic survey (Doray et al. 2018). Therefore, we used pelagic species richness and total pelagic abundance from EVHOE as explanatory variables (see “Environmental variables and fishing pressure”). We used the ICES statistical rectangle resolution (1° longitude × 0.5° latitude, ICES, 2019) to analyse spatial patterns (74 rectangles) and the full data set included 1242 ICES rectangles sampled from 1997 to 2018. ICES rectangles corresponded to the highest spatial resolution available for fishing data. We controlled for the temporal imbalance in sampling effort (1 to 10 stations per rectangle per year) and the increasing number of stations over the years (i.e. increasing sampling effort over time,  $r_{\text{Spearman}} = 0.55$ ,  $p = 0.01$ ), which biases the temporal trends of biodiversity indices (e.g. creates an artificial increase in species richness). We used a sample-based rarefaction approach consisting of

randomly sampling 1 station per ICES rectangle for each year and repeating this process 100 times to calculate average biodiversity indices. This approach is commonly undertaken in biodiversity studies to account for heterogeneous sampling efforts for both presence/absence and abundance data in an  $\alpha$  and  $\beta$  diversity context (Dornelas et al., 2014; Magurran et al., 2015; Blowes et al., 2019; Antão et al., 2020).

### 2.2. Biodiversity indices

We first computed species richness (SR), abundance and evenness (i.e. the uniformity in abundance among species within a sample). Abundance was log10 transformed to decrease the overdispersion caused by the most abundant species (Zuur et al., 2007). We used Hurlbert's evenness index (Hurlbert, 1971) ranging from 0 (uneven community dominated by one species) to 1 (even abundance among species). Using presence/absence community data matrices, we decomposed the overall  $\beta$  diversity between communities measured by the Jaccard index ( $\beta_{\text{jac}}$ , Jaccard, 1912) into its two additive components, turnover ( $\beta_{\text{jt}}$ ) and nestedness-resultant -hereafter called nestedness - ( $\beta_{\text{jne}}$ ), that represent distinct mechanisms (Baselga, 2012).  $\beta_{\text{jt}}$  measures the differences in composition caused by species replacement independently of the differences in species richness between sampling sites, while  $\beta_{\text{jne}}$  measures the differences in species composition caused by species loss or gain. We also used the  $\beta_{\text{ratio}}$ , defined as  $\beta_{\text{jt}}/\beta_{\text{jac}}$ , to assess the relative importance of turnover vs nestedness. Overall,  $\beta$  diversity is dominated by turnover or nestedness for a  $\beta_{\text{ratio}} > 0.5$  and  $< 0.5$ , respectively. We also partitioned the abundance-based Ruzicka  $\beta$  diversity index ( $\beta_{\text{ruz}}$ , Ruzicka, 1958) into its two additive antithetic components, the balanced variation in abundance ( $\beta_{\text{ruz.bal}}$ ) and abundance gradients ( $\beta_{\text{ruz.gra}}$ , Baselga, 2017). The balanced variation in abundance corresponds to the replacement of individuals of some species in one site (or at time  $t-1$ ) by the same number of individuals by different species in another site (or at time  $t$ ). The abundance gradient describes the loss/gain of individuals from one site to another (or between two time periods). We used the  $\beta_{\text{ruz.ratio}}$  ( $\beta_{\text{ruz.bal}}/\beta_{\text{ruz}}$ ) to estimate the relative importance of the balanced variation in abundance compared to the abundance gradient. We then assessed how local  $\beta$  diversity (LBD) was structured in space, which was defined as the average  $\beta$  diversity between a focal ICES rectangle and neighbouring rectangles within a certain distance. High LBD values then indicate singular community composition in the focal rectangle in comparison to its neighbours. We tested 16 distance thresholds, 150–300 km in 10 km steps (Fig. S4), and retained the threshold that presented the largest number of rectangles with a significant temporal trend for the  $\beta$  diversity indices to test at which spatial scale communities were susceptible to express taxonomic differentiation/homogenisation over time. Ten kilometre increments allowed a constant increase in the number of neighbours between 150 and 300 km because distances among rectangle centroids were not evenly spaced. We explored LBD variations through time. A temporal decrease (increase) of LBD indicates that the neighbouring communities are getting more similar (dissimilar). Therefore, the temporal variation of LBD was used as a proxy of taxonomic spatial homogenization (differentiation).

### 2.3. Environmental variables and fishing pressure

For each year (1997–2018) and the 74 ICES rectangles, we selected 19 variables to test the relative influence of three main drivers on SR, abundance, evenness and the LBDs indices.

- Energy

To investigate the influence of ambient energy, we considered sea-floor temperature (°C) and a variable that integrated temperature (°C) across the water column. For these two variables, we considered annual

averages, monthly minima and as a surrogate for seasonality the standard deviation of monthly averages. To document the influence of productive energy, we considered the annual average of net primary productivity (NPP). We did not retain the seasonality of NPP as its standard deviation was highly correlated with the annual average ( $r_{\text{Pearson}} = 0.97$ ). In addition, we considered species richness and the abundance ( $\log_{10}$ ) of nine pelagic species as they represent potential key links in the food web (Cury et al., 2000).

- Habitat

We retained eight variables to document the contribution of habitats: rectangle surface area ( $\text{km}^2$ ), distance to the nearest coast (km), average depth (m), diversity of seabed habitats based on substrate, minimum and average of mixed layer depth (m, MLD) as a surrogate for water column stratification intensity, minimum and standard deviation of monthly oxygen concentrations ( $\text{O}_2\text{I}^{-1}$ ). The later variables allowed us to assess the prevalence of oxygen minimum zones (OMZs) and the effect of oxygen seasonality. Additional details about environmental variables are provided in *Supplementary material S1.1*.

- Fishing pressure

Fishing pressure (in hours fished) was extracted from the STECF Fisheries Dependent Information Database (STECF, 2018) using the spatial effort information from 2000 to 2016. Due to inconsistencies in the French effort time series, effort estimates were extracted from Ifremer's database (Demanèche et al., 2013) using the STECF methodology. We calculated annual fishing effort summing across all gear types and estimated fishing diversity using the Shannon index (Shannon, 1948) based on the proportion of fishing hours for the 11 main types of fishing gears. This fishing diversity index enabled us to assess the degree of heterogeneity in the fishing effort among the different fishing gears.

Mean spatial patterns of all variables and pairwise Spearman correlation coefficients are provided in *Supplementary material* (Fig. S1, S2). Several explanatory variables were  $\log_{10}$  transformed to avoid excessive dispersion of model residuals and fulfil the normality assumption of residuals for the linear models (see paragraph 2.5 and see *Supplementary material S1.1*). All variables were normalised by subtracting the mean and dividing by the standard deviation. For consistency among explanatory variables, we considered a shorter time series from 2000 to 2016 (i.e. including 1014 rectangles over the years) when modelling the contribution of energy, habitat and fishing pressure to the variability of biodiversity indices. For each variable, we considered the linear and quadratic terms, to account for a certain degree of nonlinearity in the response curves in the models. We used elastic-net regularised generalised linear models (Elastic-net GLMs: Zou & Hastie, 2005) to select the most influential variables related to energy, habitat and fishing pressure separately for each of the 11 biodiversity metrics, before further modelling. This approach is useful when large numbers of potentially correlated variables with limited effect are available. Additional details about this approach are provided in *Supplementary material S1.2*.

## 2.4. Inferring spatio-temporal patterns

### 2.4.1. Regional scale

At the regional scale (i.e. BoB and CS), we estimated the temporal change of average SR, abundance and evenness per rectangle and the average pairwise values among all ICES rectangles for  $\beta_{\text{jac}}$ ,  $\beta_{\text{jtu}}$ ,  $\beta_{\text{jne}}$  and  $\beta_{\text{ratio}}$  (see flowchart of the analytical steps in Fig. S5). We applied a generalised additive model (GAM) to better detect non linear temporal trends by using the general equation:

$$Y = a + f(\text{year}) + \varepsilon,$$

where  $Y$  is the response variable (i.e. the different biodiversity indices),

$a$  is the intercept,  $f(\text{year})$  is a smooth function (thin plate regression spline) of the fixed effect “year” limited to a maximum of 3 basis dimensions to avoid overfitting and  $\varepsilon$  represents residuals. We considered a gaussian error and an identity link function for the average SR, abundance and evenness because we modelled the average values over the 100 resampled communities which are all positive continuous variables truncated at 0, and a Beta error distribution and a logit link function for the average values of  $\beta$  diversity indices because they take values between 0 and 1 (i.e. see Fig. 1). The relatively short time series (maximum 21 years) leads to a small sample size and thus limits the statistical power to test for temporal trends (positive vs negative). Considering the strong relationships between p.value and sample size, we adapted the significance threshold to the sample size (Pérez & Pericchi, 2014; Betensky, 2019). Thus, we reported weak evidence (Muff et al., 2022) for a positive or a negative temporal trend (the p.value of the temporal slope  $< 0.1$ ). In contrast, all temporal slopes associated with a p.value  $> 0.1$  were considered as stable. Moreover, to assess general interdecadal trends we estimated the slope of generalised linear models (GLM) with year as explanatory variable and biodiversity indices as response variables, considering the same error distributions and link functions as for GAMs.

### 2.4.2. Local scale

We next explored the spatial and temporal patterns of biodiversity indices at the local scale ( $1^\circ$  longitude  $\times$   $0.5^\circ$  latitude, ICES rectangle). For each rectangle we averaged across years SR, abundance, evenness and local  $\beta$  diversity indices (LBD.jac, LBD.jtu, LBD.jne, LBD.ruz, LBD.ruz.bal, LBD.ruz.gra, see Fig. S5). Then, to test for temporal trends, we estimated the slope of a GLM, which represents a summary statistic of the temporal trend with year as explanatory variable and biodiversity indices as response variable according to the following equation:

$$Y = a + B * \text{year} + \varepsilon,$$

where  $Y$  are biodiversity indices,  $a$  is the intercept,  $B$  is the linear slope of the “year” effect and  $\varepsilon$  represents residuals. Gaussian errors and identity links were considered for SR, abundance and evenness and a Beta error with logit link function for LBD indices. To avoid boundary problems with the logit link (i.e. response values of 0 or 1), the response variable was transformed following the recommendation by Cribari-Neto & Zeileis (2010) as  $(y * (n - 1) + 0.5)/n$ , being  $n$  the sample size. To investigate temporal trends, 71 rectangles sampled at least five years were retained. We considered spatial differentiation and homogenisation of communities over time as soon as weak evidence (p.value of slope  $< 0.1$ , Muff et al., 2022) of either positive or negative temporal linear slopes respectively were reported for LBD indices. In addition, we also assessed the variability of species composition within a rectangle over time, the so called temporal  $\beta$  diversity (TBI; Albouy et al., 2012), using both Jaccard and Ruzicka indices and their respective components (see methodological details in *Supplementary material S1.3*, and Fig. S3 for the pairwise relationships among temporal trends for all biodiversity indices).

### 2.4.3. Partitioning space and time variations

For the full data set of 1242 rectangles sampled from 1997 to 2018, we used a variance partitioning approach based on the Moran Eigenvector Map (MEM) method (Dray et al., 2012) to test the relative importance of spatial and temporal variability of biodiversity patterns (Legendre and Gauthier, 2014; for more details see *Supplementary material S1.4*; Fig. S5).

### 2.4.4. Partitioning diversity variations among energy, habitat and fishing pressure

We applied a steady-state linear mixed effects model (LMM) considering time (i.e. year) as a random effect, to test the relative influence of energy, habitat and fishing pressure on SR, abundance,

evenness and LBDs indices. Only the most influential variables previously retained with the Elastic-net GLMs (see paragraph 2.3) for the three groups of variables were included as fixed effects in the full LMM. We used average values of 100 resampled biodiversity indices (i.e. species richness is not an integer anymore but can be a decimal value) and we considered a large data set of 1014 rectangles sampled between 2000 and 2016. Therefore, the central limit theorem justifies the use of a gaussian error model, which we combined with an identity link for all biodiversity indices. Based on these full LMM, a variance partitioning approach (Legendre & Legendre, 1998) was performed to estimate the independent and shared contributions of the three groups of variables for each biodiversity index.

The general equation of the full LMM including the best set of variables related to energy, habitat and fishing was as follows:

$$Y_i = a + B_{\text{energy}} * x_{\text{energy } i} + B_{\text{habitat}} * x_{\text{habitat } i} + B_{\text{fishing}} * x_{\text{fishing } i} + Z_i^* b_i + \varepsilon_i,$$

where  $Y_i$  are the biodiversity index in year  $i$ ,  $a$  is the intercept,  $B_{\text{energy}}$ ,  $B_{\text{habitat}}$  and  $B_{\text{fishing}}$  are the slopes of the energy, habitat and fishing variables respectively,  $Z_i$  is a design matrix (identity matrix for the random intercept model) associated with the random year effect  $b_i$  and  $\varepsilon_i$  represents model residuals. For each biodiversity index, the best set of explanatory variables for energy, habitat and fishing retained in the full LMM model for variance partitioning are available in *Supplementary material S4 Table S2*. We estimated the marginal  $R^2$  (Nakagawa et al., 2017) as a proxy for the variance explained by fixed effects. To test for potential lack of fit of the LMMs due to complex nonlinear relationships, we conducted the same approach using generalised additive mixed models (GAMM) using the same general equation, except that we associated fixed effects with smoothing functions. Normality and homogeneity assumptions of the GAMM and LMM residuals were assessed for each model through visual inspection (histogram, qqplot, plot of the fitted vs residuals) and shapiro tests (Shapiro & Wilk, 1965). The list of R packages used for variance partitioning is available in *Supplementary material S1.5*.

#### 2.4.5. Determining variables importance within energy, habitats and fishing pressure

For each biodiversity index, we used a model selection approach to select the most parsimonious model and assess the relative importance of the main variables within the three groups of explanatory variables included in the LMMs presented in 2.5. First, we performed a multi-model inference approach based on information theory running all possible models (Grueber et al., 2011). We retained the most parsimonious model based on the Bayesian Information Criteria (BIC) among the best set of models that have less than 2 BIC units difference with the best model with the lowest BIC. Second, we computed the semi-partial marginal  $R^2$  as a proxy of explained variance for each variable retained in the most parsimonious model (Jaeger et al., 2017; Nakagawa et al., 2017). In addition, for the most parsimonious LMM we also considered alternative models to investigate the existence of temporal and/or spatial autocorrelation in residuals (Zuur et al., 2009, additional details are provided in *Supplementary material S1.6*). To assess the goodness-of-fit of these alternative models we used the Pseudo- $R^2$  (Efron, 1978) which is defined as the coefficient of determination of the linear relationships between the observed and fitted values.

#### 2.4.6. Testing for temporal effects, time lag and environmental forcings

For each biodiversity index, we also investigated the temporal variation of the environmental-biodiversity relationships by testing 1) the significance of temporal effects in the most parsimonious models presented in 2.6, 2) for time lag effects of 1 and 2 years between the biodiversity indices and explanatory variables and 3) the relationships between environmental forcing and temporal trends of biodiversity indices. All methodological details related to these three approaches are provided in *Supplementary material S1.7, S1.8 and S1.9 respectively* (see

Fig. S5 for the flowchart of the analytical steps).

### 3. Results

#### 3.1. Temporal patterns at regional scale

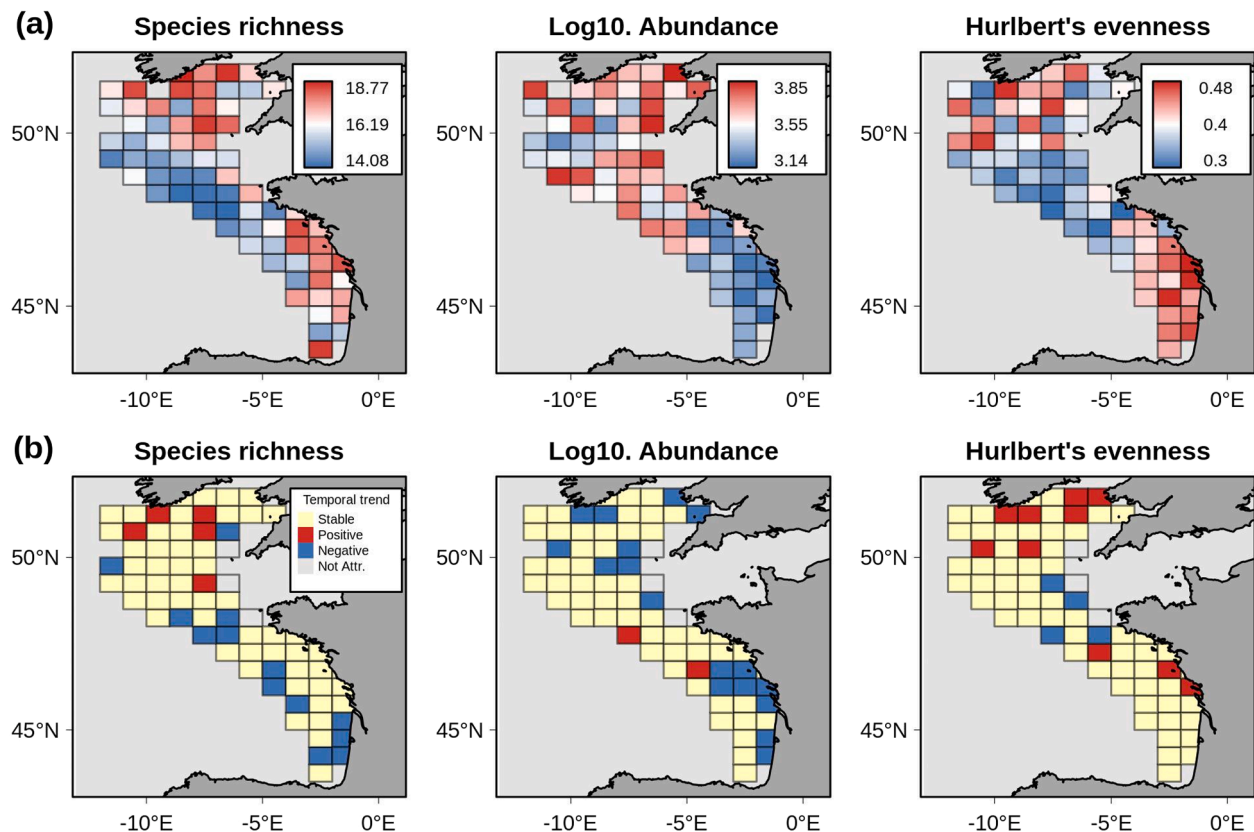
At the regional scale, as expected, abundance-based biodiversity indices displayed clearer temporal changes than incidence-based indices. Species richness remained stable in the Bay of Biscay (BoB) and Celtic Sea (CS) between 1997 and 2018 (GAM, edf = 1.65,  $p = 0.37$ , Fig. 1b), while overall abundance declined (GAM, edf = 1,  $p = 0.01$ , GLM slope =  $-0.01$ ,  $p = 0.01$ ). The incidence-based  $\beta$  diversity was dominated by species turnover. While  $\beta_{\text{jac}}$  increased significantly over time (GAM, edf = 1,  $p = 0.06$ , GLM slope =  $0.004$ ,  $p = 0.05$ ), none of its components,  $\beta_{\text{jtu}}$ ,  $\beta_{\text{jne}}$  and  $\beta_{\text{ratio}}$ , had a significant time trend (Fig. 1b). In contrast, overall abundance-based  $\beta$  diversity ( $\beta_{\text{ruz}}$ ) as well as its two components and  $\beta_{\text{ruz.ratio}}$  showed clear significant time trends (Fig. 1b).  $\beta_{\text{ruz}}$  increased significantly since 2005 (GAM, edf = 1.87,  $p = 0.01$ ). This increase is mainly driven by balanced variation in abundance, i.e. compensation between species ( $\beta_{\text{ruz.bal}}$ : GAM, edf = 1.88,  $p = 0.01$ ;  $\beta_{\text{ruz.ratio}}$ : GAM, edf = 1.81,  $p = 0.01$ ). The abundance gradient component made a smaller contribution, remaining stable from 1997 to 2005 and decreasing thereafter (GAM, edf = 1.78,  $p = 0.02$ , Fig. 1b; see Fig. S6-S9 for patterns including small pelagic species).

#### 3.2. Spatio-temporal patterns at local scale

At the local scale, contrary to our expectation, geographic patterns were clearer for incidence-based than for abundance-based biodiversity indices and revealed a pattern of taxonomic homogenization in the CS and differentiation in the southern BoB. SR averaged over time showed two local “hot-spots” (SR = 17–19 species per ICES rectangle), one in the CS along the coasts of Ireland and the UK and the other one in the BoB along the coast of France, from Brittany to the Basque country (Fig. 2a). The average abundance pattern revealed a geographic division ( $t$  test = 5.2,  $p < 0.001$ ) between the CS and the BoB showing higher (log10 (abund), mean = 3.6, standard deviation  $\pm 0.13$ ) and lower (log10 (abund) mean = 3.42  $\pm 0.16$ ) abundances, respectively (Fig. 2a). The average pattern of evenness was driven by SR (Fig. 2a). At the local scale, in 75% of rectangles ( $n = 53$ ), SR remained stable during the study period, while 18% ( $n = 13$ ), mostly located on the outer-shelf and in coastal areas of the southern Bay of Biscay, lost species (Fig. 2b). The 7% of rectangles ( $n = 5$ ) gaining species over time were located in the northern part of the Celtic Sea. Similarly, abundance in 73% of rectangles ( $n = 52$ ) had a stable temporal trend, and 23% ( $n = 17$ ) showed a significant loss of individuals. The latter rectangles were located both in the CS and the BoB, mostly near the coast (Fig. 2b). The pattern of temporal changes of evenness was inverted in comparison to abundance patterns ( $r_{\text{Spearman}} = -0.49$ ,  $p < 0.001$ , Fig. 2b).

For incidence-based local  $\beta$  diversity (LBDs), we retained 190 km as the spatial distance maximising the number of rectangles with a significant temporal trend of taxonomic differentiation/homogenisation to build local  $\beta$  diversity indices (Fig. S4a). Average geographic patterns for LBDs indices were dominated by the turnover component ( $\beta_{\text{jtu}}$ ) and showed strong north/south and coastal/offshore patterns (Fig. 3a). LBD.jac and LBD.jtu indicated similar spatial patterns ( $r_{\text{Spearman}} = 0.78-0.98$ ) with high values along the coast of the BoB and low values in the central CS (Fig. 3a). The nestedness component had a limited contribution to the jaccard index, and LBD.jne displayed a reversed pattern ( $r_{\text{Spearman}} = -0.93$ ,  $p < 0.001$ ; Fig. 3a). The spatial pattern of temporal changes of LBD.jac revealed a significant decrease (27% of rectangles,  $n = 17$ ) in compositional dissimilarity over time in the offshore part of the southern CS (Fig. 3b), while the coastal communities in the south of the Bay of Biscay and along the Welsh coast became more dissimilar (Fig. 3b). The LBD.jac pattern was mostly driven by species turnover (LBD.jtu) reinforcing a pattern of taxonomic homogenization (31% of rectangles,





**Fig. 2.** Species richness, abundance (log10 transformed), and the Hurlbert's evenness patterns of the demersal fish assemblages of the Bay of Biscay and the Celtic Sea for the period 1997–2018. The row (a) represents the mean species richness (SR), the mean abundance (log10(abundance)) and the mean evenness (Hurlbert's index) over the period 1997–2018. The row (b) shows the trends of the temporal evolution of SR, abundance and Hurlbert's evenness. The beige colour indicates a stable trend (slope not significantly different from 0, with a  $p$ -value  $> 0.1$ ), while positive and negative trends are in red and blue, respectively.

mean slope =  $-0.03 \pm 0.001$ ) in the north (Fig. 3b) and taxonomic differentiation (15% of rectangles, mean slope =  $0.04 \pm 0.014$ ) mostly in the south (Fig. 3b).

For abundance-based LBD indices, average geographic patterns were dominated by balanced variations in abundance (LBD.ruz.bal,  $r_{\text{Spearman}} = 0.76$ ,  $p < 0.001$ ) and showed a more patchy spatial pattern than incidence-based indices (Fig. 4a). A distance of 290 km maximising the number of rectangles with a significant temporal trend of taxonomic differentiation/homogenisation was retained to investigate abundance-based LBDs (Fig. S4b). Spatial patterns for the two components LBD.ruz and LBD.ruz.bal were similar ( $r_{\text{Spearman}} = 0.76$ ), with higher values (0.73–0.8) in the northern part of the Celtic Sea and along the coast of the Bay of Biscay (Fig. 4a), while LBD.ruz.gra showed an inverted spatial pattern ( $r_{\text{Spearman}} = -0.95$ ,  $p < 0.001$ ; Fig. 4a, additional details in Supplementary material S2.1). The temporal trend of the spatial patterns for abundance-based LBD indices revealed an increase in LBD.ruz.bal (23% of rectangles, mean slope =  $0.03 \pm 0.01$ ) and a decrease in LBD.ruz.gra (18% of rectangles, mean slope =  $-0.02 \pm 0.01$ , Fig. 4b) for both the entrance of the St George Channel in the Celtic Sea and the southern coast of the Bay of Biscay. The temporal  $\beta$  diversity (TBI) patterns based on both incidence and abundance-based indices were consistent with the identified LBD patterns (see Supplementary material S2.1 Fig. S3, S10a,b, S11a,b).

### 3.3. Partitioning space and time variations

Overall, partitioning the variance between space and time revealed that the spatial dimension explained more than double of the variability ( $7.6 \pm 2.5\%$ ) than time ( $3.3 \pm 1.26\%$ ) for all biodiversity indices except LBD.jne (Table S1).

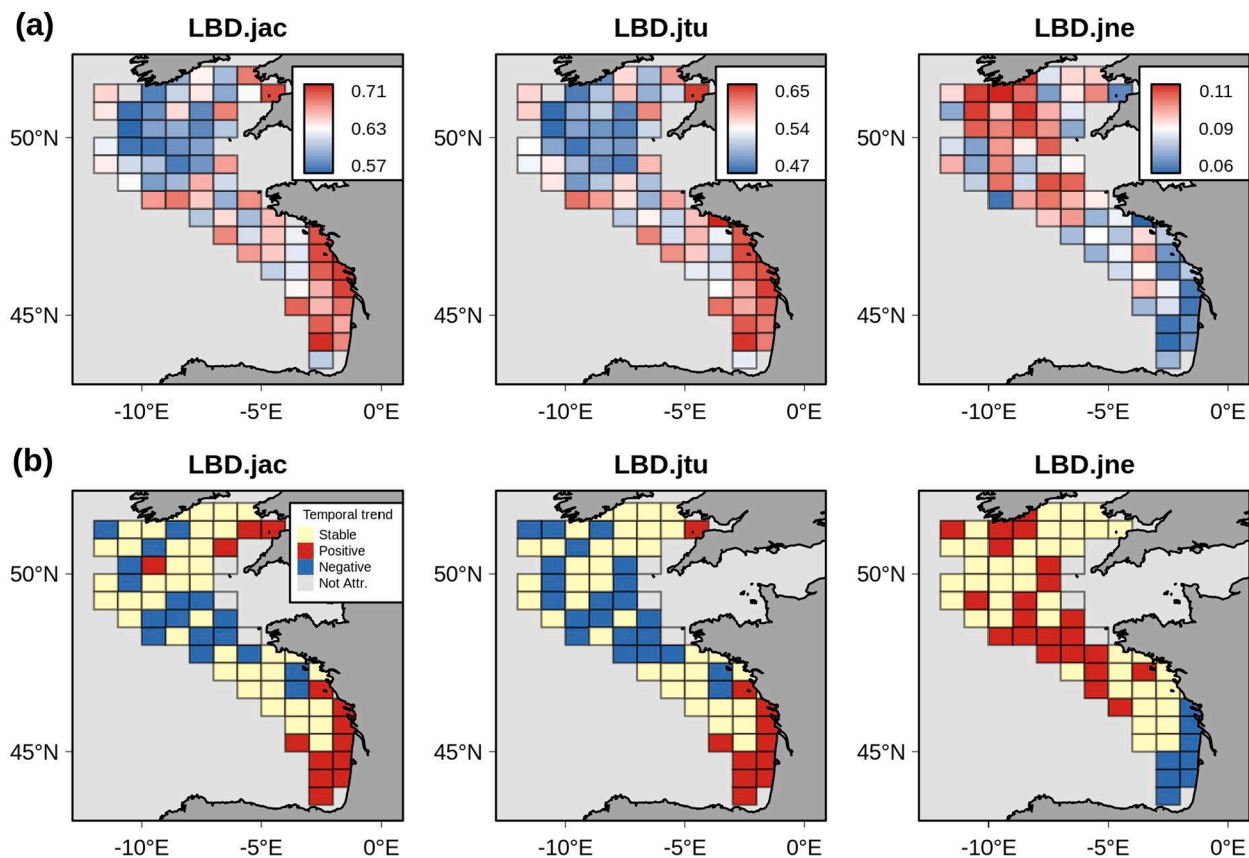
### 3.4. Partitioning diversity variations among energy, habitat and fishing pressure

Contrary to our expectation, we found that energy (temperature and trophic resources) had a greater influence on spatio-temporal biodiversity variations than habitat or fishing. The steady-state LMMs based on the four best explanatory variables for energy, habitat and fishing pressure (see Table S2 for the selection of the explanatory variables for each biodiversity metric) explained on average a small proportion of variance (mean =  $15.4 \pm 6.53\%$ , Table 2). The explained variance (for the fixed effects) was smallest for the evenness model (4.4%), moderate for SR (12.5%), LBD.jne (11%) and all abundance-based LBD indices (11.7–16%) while variations in abundance (20.3%), LBD.jac (23.2%) and LBD.jtu (25%) were best explained (Table 2). Energy explained the highest proportion of variance ( $8.1 \pm 5.5\%$ ), followed by habitat ( $1.6 \pm 0.8\%$ ) and fishing pressure ( $0.9 \pm 0.8\%$ , Table 2). The largest fraction of shared variance was attributed among the three categories ( $2.2 \pm 1.7\%$ ), followed by energy and habitat ( $1.1 \pm 0.6\%$ ; Table 2). The contribution of energy alone was particularly high for abundance (14.7%), LBD.jac (14.8%), and LBD.jtu (14.9%). Variance partitioning performed with GAMMs showed very consistent results with the results obtained using LMMs indicating that the relationships were well captured by simple linear and quadratic terms (i.e. second order polynomial; Table S3).

### 3.5. Importance of variables within energy, habitats and fishing pressure

Model selection revealed that SR and the abundance of the nine small pelagic species (i.e. productive energy related to trophic resources) were two of the most important variables for explaining variability in





**Fig. 3.** Local  $\beta$  diversity of incidence-based indices of the demersal fish assemblages in the Bay of Biscay and Celtic Sea for the period 1997–2018. The first row (a) shows the mean local Jaccard index (LBD.jac), mean local species turnover (LBD.jtu), and mean local nestedness (LBD.jne) over the period 1997–2018. The second row (b) shows the trends of the temporal evolution of LBD.jac, LBD.jtu and LBD.jne. The beige colour indicates a stable trend (slope not significantly different from 0, with a  $p$ -value  $> 0.1$ ), while positive and negative trends are in red and blue, respectively.

biodiversity indices (Table S3–S11). Species richness of small pelagics had the highest or second highest semi-partial marginal  $R^2$  for abundance (5.6%), LBD.jac (8%), LBD.jtu (10.5%) and LBD.jne (5.2%). It was positively related to evenness, LBD.jac, LBD.jtu, LBD.ruz and LBD.ruz.bal and negatively to abundance, LBD.jne and LBD.ruz.gra (Table S5–S12). The abundance of small pelagics achieved the highest or the second highest, though still small, semi-partial marginal  $R^2$  for SR (5.5%), abundance (5.8%), LBD.jac (10.8%), LBD.jtu (9.7%), LBD.ruz (6.3%), and was negatively related to SR and positively related to abundance, LBD.jac, LBD.jtu, and LBD.ruz. Distance to the coast, minimum thickness of the mixed layer depth (MLD.min), and bathymetry were the most important habitat variables, though they only explained a low percentage of variation in diversity indices when they were retained (1.3–6%, Table S4–S12). Fishing pressure and its heterogeneity were retained for the SR models, while they had limited explanatory power for the different incidence and abundance-based LBD indices (0.8–4.5%) (Table S3, S7–S12). Overall, accounting for the remaining spatial or temporal autocorrelation in the model residuals did not affect the importance of the main variables described above but improved the explained variance of the models and even more so when both spatial and temporal autocorrelation were simultaneously accounted for (pseudo- $R^2 = 58\% \pm 25$ ), in comparison to accounting only for spatial (53%  $\pm 8$ ) or temporal correlations (50%  $\pm 14$ ), (see Supplementary material S4. Table S4–S12 for model outputs). Only marginal improvements were obtained by testing for temporal effect by including time as fixed effect, or lagged variables, or testing for relationships between environmental forcings and temporal trends of biodiversity indices (more detailed results are available in Supplementary material in Table S4–S12 for temporal effect, for lag effect see results in paragraph

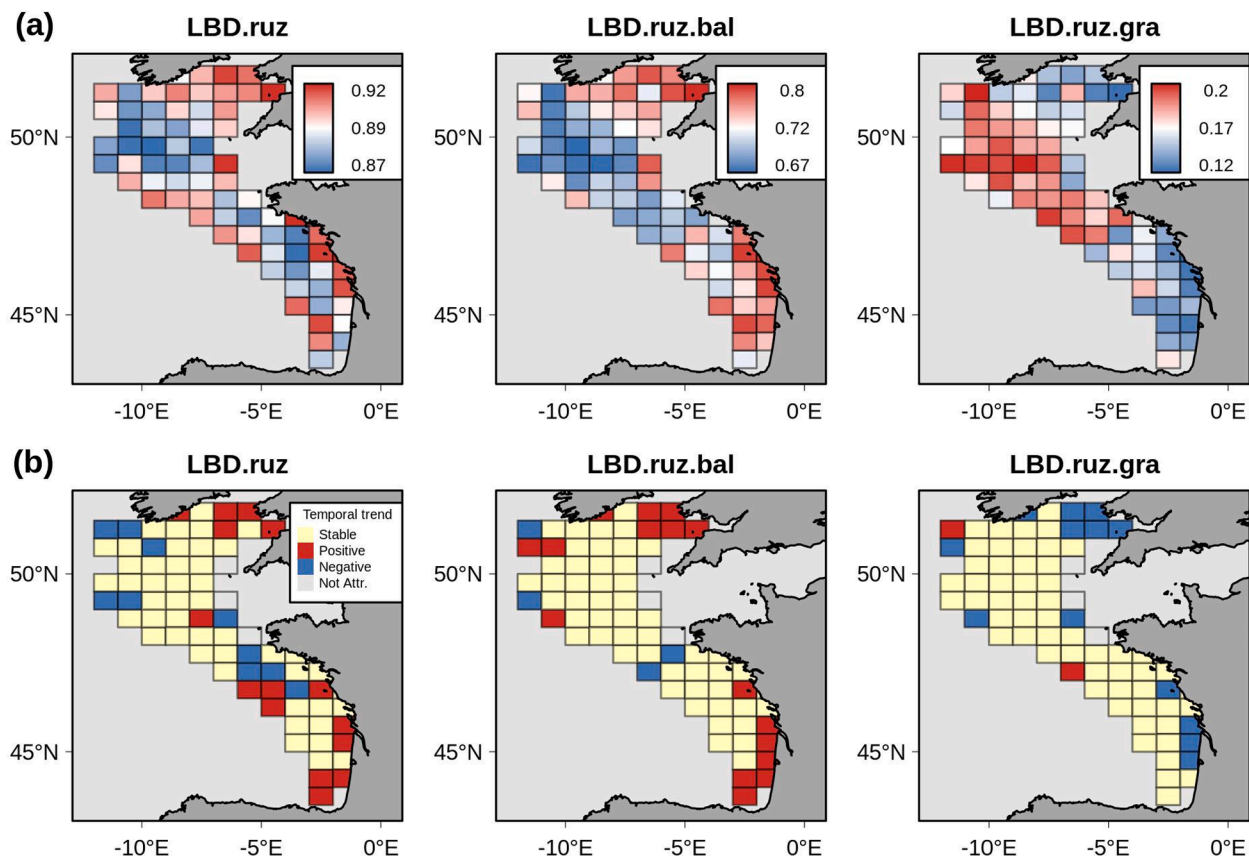
S2.2 and Table S13–S22, for environmental forcing see results in paragraph S2.3, Fig. S12 and Table S23–S24).

#### 4. Discussion

In this study, we investigated the spatio-temporal changes of demersal marine ray-finned fishes in the Bay of Biscay and in the Celtic Sea and assessed the relative contribution of energy, habitat and fishing pressure, during the last two decades by using long-term scientific surveys. We found that species richness weakly changed over time, while compositional dissimilarity showed contrasted patterns of taxonomic homogenization in the Celtic Sea and differentiation in the southern Bay of Biscay, where local assemblages were becoming more similar and dissimilar over time, respectively. In agreement with our first expectation, the temporal trends of the abundance-based indices showed stronger relationships than incidence-based indices at regional scale while the latter indices provided clearer patterns at local scale. In contrast to our second expectation, we showed that the contrasted spatio-temporal changes of demersal fish assemblages were best explained by productive energy funnelled through the dynamics of small pelagic species, whereas effects of environmental forcing and most notably fishing pressure were limited.

##### 4.1. Incidence-based biodiversity patterns

One of the striking results of this study was the different temporal dynamics of communities situated in the offshore regions of the Celtic Sea (CS) and the southern coast of the French part of the Bay of Biscay (BoB). Indeed, our investigation at the local scale of  $\beta$  diversity (up to



**Fig. 4.** Local  $\beta$  diversity of abundance-based indices of the demersal fish assemblages in the Bay of Biscay and the Celtic Sea for the period 1997–2018. The first row (a) shows the mean local Ruzicka index (LBD.ruz), mean local balance variation in abundance (LBD.ruz.bal), and mean local abundance gradient (LBD.ruz.gra) over the period 1997–2018. The second row (b) shows the trends of the temporal evolution of LBD.ruz, LBD.ruz.bal and LBD.ruz.gra. Only 71 ICES rectangles sampled at least 5 times were retained. The beige colour indicates a stable trend (slope not significantly different from 0, with a p.value > 0.1), while positive and negative trends are in red and blue, respectively.

**Table 2**

Variance partitioning based on linear mixed models (LMM) including time (i.e. Year effect) as a random intercept, for species richness (SR), abundance, Hurlbert's evenness (evenness), and all local  $\beta$  diversity indices (LBD, see text for the meaning of LBD indices), considering contemporaneous explanatory variables, for the demersal fish assemblages of the Bay of Biscay and the Celtic Sea. E: energy, H: habitat, F: fishing pressure. Values correspond to the percentage of explained variance. In abbreviations, energy E, habitat H, and fishing pressure F.

Biodiversity index	Explained(%)	E (%)	H(%)	F (%)	Shared.E.F.	Shared.E.H.	Shared.H.F.	Shared.E.H.F
SR	12.5	6.5	3	0.7	0.3	2	0.5	0 <sup>a</sup>
Abundance	20.3	14.7	2.1	0.3	0.2	0.7	1.2	1.2
Evenness	4.4	1.7	1.1	0.6	0 <sup>a</sup>	0.3	0.5	0.4
LBD.jac	23.2	14.8	1.1	1	1.6	1.1	0.4	3.3
LBD.jtu	25	14.9	1.8	1.2	1.6	1.1	0.7	3.8
LBD.jne	11	5.9	0.6	0.9	0.7	0.4	0.8	1.7
LBD.ruz	14.3	8.4	1.4	0.2	0.3	1.5	0.3	2.1
LBD.ruz.bal	16	4.2	2.8	0.4	0.4	1.6	1.8	4.7
LBD.ruz.gra	11.7	1.7	1	2.7	0.2	1.6	1.4	3.1

<sup>a</sup> Negative values were converted to 0 (Legendre and Legendre, 1998), as such the sum of the variance of the individual categories might not add-up to the total explained variance.

200 km) showed spatially contrasting patterns of either taxonomic homogenization or differentiation among communities that compensated each other at the regional scale. Contrary to our expectation, these patterns of homogenization and differentiation were better detected by incidence-based indices at the local scale and indicated that variations of species assemblages over time can display different signals when analysed at different spatial scales (Chase et al., 2019). In the Celtic Sea, SR was stable or increased over time while local  $\beta$  diversity (LBD) driven by species turnover decreased, indicating that local communities were becoming more homogenous. A similar pattern of taxonomic homogenization for the last three decades has been found for demersal fish

communities off the west coast of Scotland (Magurran et al., 2015). The stability of SR suggests that taxonomic homogenization on the west coast of Scotland is mostly due to community re-organisation of existing species. However, in our results the only locations (7% of rectangles) significantly gaining species (*Agonus cataphractus*, *Pleuronectes platessa*, *Trisopterus esmarkii*, *Callionymus reticulatus*) were located in the CS suggesting that taxonomic homogenization is the result to both spatial re-organisation of the communities, with species getting less spatially segregated (more dispersal), and the arrival of new taxa within multiple communities (Olden 2006). In contrast, on the south coast of the BoB, communities tended to lose species while the temporal increase of the

local  $\beta$  diversity was mostly influenced by species turnover. Taken together, these results showed spatial differentiation of communities and confirmed that temporal dynamics of assemblages can drastically vary over short spatial distances (Leprieur et al., 2008).

Another striking result is that the southern BoB is losing species over time, despite southern newcomers having been detected (Iglésias & Lorance 2016). In this region the species turnover increased in recent years among local communities (LBD.jtu), potentially due to an increase in patchiness of species populations. The loss of species was counterintuitive, as we expected that species range shifts and arrival of southerly species would increase species richness (Dornelas et al., 2019) if the tempo of immigration is higher than extirpation (Chase et al., 2019). Several species were becoming rarer, such as *Trisopterus minutus*, *Hippoglossoides platessoides*, *Melanogrammus aeglefinus*, *Merlangius merlangus* or *Lophius piscatorius*, while others were becoming more frequent (e.g. *Scomber colias*, *Spondyliosoma cantharus*, *Trigla lyra*, *Boops boops*, *Trachinus draco*, *Dicentrarchus labrax*, *Liza ramada*). Additional results showed that at regional scale, incidence-based biodiversity indices had weak temporal variation when averaged over space, and species richness remained stable. These results confirmed that global species range shifts of marine species do not necessarily translate into species richness variation over time (Dornelas et al., 2014) or into taxonomic homogenization of communities (McKinney and Lockwood, 1999).

#### 4.2. Abundance-based biodiversity indices

Temporal trends of abundance-based diversity patterns revealed contrasted pictures at regional and local scale. At regional scale, in agreement with our expectation, abundance-based indices provided clear temporal trends. Abundance of the demersal communities decreased over the time series and abundance-based dissimilarity measures indicated a differentiation among communities, which was mostly driven by the balanced variation of abundance. This implies that abundant species in one community were replaced by other species in other communities and this mechanism of replacement increased over the years. The balanced variation in abundance has been previously investigated through the compensation mechanism explained by the replacement of the most sensitive species to a disturbance (such as fishing) by less sensitive species (Rochet et al., 2013). In a spatial context, an increasing compensation mechanism may be related to increasing variation in abundance among species present in different locations. Over large spatial and temporal scales, such patterns might be caused by fishing and predator–prey interactions that generate fluctuating abundance among prey and predators such as suggested between hake and horse mackerel in the BoB (Moullec et al., 2017).

On the other hand, at local scale, abundance-based patterns were more patchy than incidence-based patterns and we did not detect clear ecosystem dynamics as expected. Higher abundances were detected in the CS compared to the BoB (for similar results see Moullec et al., 2017), abundances remained stable over time for most rectangles (73%) and a majority of species (72%) showed stable abundances over the study period (see Table S25). We noticed that our simple estimate of the general temporal trend of the abundance can differ from the more detailed trends reported by ICES for several commercial stocks on larger spatial scales than considered here using additional data sets (e.g. *Lophius budegassa* and *L. piscatorius*, ICES, 2020). However, despite EVHOE surveys might have different catchability for part of the population (adults or juveniles) of certain species, our results, based on abundance, are in line with published results showing that overall fish biomass of most European seas has not yet recovered during the last two decades (Gascuel et al., 2016). Over time, the balanced variation in abundance among communities increased in coastal rectangles of the southern BoB and along the Welsh coast of the CS, showing an increasing exchange of individuals belonging to different species among communities. However, it remains unclear how much of this increase is also driven by the influence of species turnover on the balanced variation in

abundance as the two components are not independent (Baselga, 2013; Baselga, 2017). Disentangling the contributions of balanced variations in abundance and abundance gradients to species turnover and nestedness is beyond the scope of this study but merits further research. Finally, not only incidence but also abundance-based indices revealed greater spatial than temporal variation of community dynamics, which confirmed previous findings for the Celtic Sea (Mérillet et al., 2020) and the Bay of Biscay (Poulard et al., 2003). Overall, the local patterns may have suffered from high variability in the sampling process (see section 4.4), which is unlikely to be improved if bottom trawl remains the main sampling technique as it is influenced by meteorological conditions while sampling (Poulard & Trenkel, 2007).

#### 4.3. Evidence for trophic drivers of regional and local-scale biodiversity patterns

Observed spatial patterns of community re-organisations were mainly explained by variables describing energy (14.9% Table 2) rather than habitat and fishing. These results contradict our second expectation, even though the variance explained by these models remained low (25% Table 2). Accounting for the remaining temporal and spatial autocorrelation improved the predictive power of all models (Table S4–S14) which suggests that we may be currently missing covariates, or that fine scale variability has not yet been captured. Considering the huge source of uncertainty (see section 4.4 for details) associated with long-term ecological surveys (Cauvy-Fraunié et al., 2019), what looks at first as a deceptive model fit, could yet provide first insights into the main drivers.

We found that among energy variables, both diversity and abundance of the small pelagics were the most important variables, while temperature and primary production had limited explanatory power. These results suggest that productive energy, especially the benthopelagos trophic link (Cury et al., 2000) could be an important driver of the studied demersal community dynamics. The increasing diversity of small pelagic species and their abundance favoured the differentiation among demersal communities, while the abundance of small pelagics was positively related to the abundance of demersal species. These results may be related to positive predator–prey interactions allowing demersal predators to increase in abundance following increasing pelagic abundance (Moullec et al., 2017). These predator–prey interactions might be partly driven by the strong recovery of *Engraulis encrasicolus* since 2005 (Fig. S13) and the high biomass of pelagic species in general in the BoB supported by high pelagic primary production (Cresson et al., 2020). If pelagic species constitute a large proportion of trophic resources consumed by the demersal community, variation in pelagic species abundance could significantly affect the variations in the abundance of demersal species as well. An indirect relationship driven by the productivity of benthic communities (Lassalle et al., 2011) is also possible but could not be tested here. Our results do not confirm the role of rising temperatures as the main driver of taxonomic re-organisation as suggested for ecosystems elsewhere (Magurran et al., 2015; McLean et al., 2019). However, our analysis of environmental forcing on temporal variations of LBD.jtu revealed that decreasing temperature seasonality favoured taxonomic differentiation (southern BoB), while increasing temperature seasonality favoured taxonomic homogenization (CS; Fig. S13 and additional results in Supplementary material S2.3). Nevertheless, because the temporal trends in temperature seasonality remained non-significant, such results might be too preliminary to be attributed to global change yet (see Fig. S14).

Concerning habitat, we confirmed that bathymetry, water stratification (mixed layer depth), and distance to the coast were important drivers of the spatial distribution of marine biodiversity, specifically the importance of shallow coastal habitat with a thin mixed layer depth (Ray, 1991; Poulard et al., 2003; Leathwick et al., 2006; Tittensor et al., 2010; Seitz et al., 2014).

The limited contribution of fishing pressure might be explained by

the long fishing history that may have selected the most resilient species and shaped adaptable communities (Blanchard et al., 2004; McLean et al., 2019). Indeed, the BoB and the CS have been impacted by fishing for over a century (Quéro & Cendrero, 1996; Thurstan et al., 2010; Moullec et al., 2017) and this constant pressure on species communities may have been detectable at the beginning of the exploitation (Pauly, 1995; Lotze & Worm, 2009) but difficulties to pinpoint fishing as the main driver based on recent (i.e. two decades) scientific surveys is common for areas with a long fishing history (Farriols et al., 2017; Mérillet et al., 2020). Indeed, BoB ecosystem components in the early 1990s were considered widely impacted by fishing and locally by other human activities (Lorance et al., 2009; Gascuel et al., 2016).

Overall, the negligible effect of the tested time lags for environmental variables suggests a rapid biological response of communities to the environment, as previously shown for small pelagic species (Huret et al., 2018). One exception though was the two year lag for the minimum thickness of the mixed layer depth (MLD.min) for LBD indices suggesting a multiannual effect of water stratification on the change in species abundance among communities (LBD.ruz.bal), though the causal mechanism remains unknown.

#### 4.4. Some limitations of long-term ecological surveys

Long-term ecological surveys (LTES) are key to document temporal dynamics (Kuebbing et al., 2018), but their drawbacks should also be considered. First, variations in sampling effort over time or space are likely especially for LTES carried out over large spatial or temporal scales such as fish stock surveys (Trenkel & Cotter, 2009). For the EVHOE time series, it was crucial to use a sample-based rarefaction approach with resampling (e.g. Dornelas et al., 2014; Magurran et al., 2015; Blowes et al., 2019; Antão et al., 2020), to avoid temporal sampling bias that might lead to an artificial increase in species richness. Second, variations in species identification due to inherent progress in taxonomy, and/or knowledge differences among scientific staff represent another source of bias that must be accounted for. Here, we homogenised the species list over the time series by lumping taxa that could have been misidentified during the early years of the survey. As a consequence, all detected patterns are expected to be robust and may have been even stronger if a greater precision in species identification would have been available from the start of the time series. Finally, the accumulation of sources of uncertainty in LTES often leads to weak signal to noise ratios (Cauvy-Fraunié et al., 2019). For example, the EVHOE survey is carried out during a transitional period, shifting from autumn to winter conditions with storms and high wind stress. These climatic conditions can affect the variation in catchability among species (Poulard & Trenkel, 2007) and thus impact species composition and abundance of the catch. Changes in gear catchability creating a biased representation of communities and species abundance is a frequent concern of bottom trawl surveys such as EVHOE (Poulard & Trenkel, 2007). Further, trawl selectivity is size-dependent (Krag et al., 2014). However, the main advantage of these surveys is that sampling is standardised and constant throughout the time series. Indeed, the sampling period (October–December), gear (GOV 36/47), tow duration (30 min) and trawl speed ( $7.4 \text{ km.h}^{-1}$ ) remained the same during the whole campaign and over the years (Laffargue et al., 2021). Hence, we believe that the identified strong multi-annual trends convey a genuine biological signal of change. The EVHOE data set has already been used (e.g. Mérillet et al., 2020), as have other similar surveys, to derive indicators of diversity (including abundance), and ecological status (e.g. Rufino et al., 2018; Mahé et al., 2018). Despite those different sources of uncertainty and bias, the different conservative solutions applied in this study enabled us to detect spatio-temporal variations of community composition and reassert the crucial role of standardised LTES to understand community dynamics in a fast-evolving environment.

#### 4.5. Conclusion

A suite of complementary biodiversity indices based on scientific surveys allowed us to capture spatio-temporal community dynamics at different spatial scales. The stability of species richness, and the increasing composition dissimilarities at regional scale for abundance-based indices, hid a spatially contrasted pattern of taxonomic homogenization and differentiation for communities within the Celtic Sea and the southern Bay of Biscay, respectively. Abundance-based indices showed stronger temporal patterns at regional scale and confirmed higher abundance in the Celtic Sea than in the Bay of Biscay. However, at a local scale, abundance-based indices might be powerful to detect early changes in community dynamics only if new sampling approaches (e.g. environmental DNA; Stoeckle et al., 2020) can control and reduce the variability in the sampling process. Our modelling approach revealed greater spatial than temporal variation and a larger contribution of energy, followed by habitat, while fishing pressure had a very limited contribution. Furthermore, we showed that the benthic-pelagic trophic link (Moullec et al., 2017; Cresson et al., 2020) had a greater influence on community dynamics of demersal species than changes in sea temperature (Magurran et al., 2015). By applying methods inspired by biogeography and community ecology to a scientific survey data set, our study paved the way to better disentangle and explain the subtle dynamics of communities and their drivers for ecosystems providing crucial services.

#### CRedit authorship contribution statement

**David Eme:** Data curation, Conceptualization, Methodology, Investigation, Formal analysis, Writing – original draft, Writing – review & editing, Visualization, Project administration, Funding acquisition. **Marta M. Rufino:** Data curation, Conceptualization, Methodology, Writing – review & editing, Project administration. **Verena M. Trenkel:** Data curation, Writing – review & editing. **Youen Vermard:** Data curation, Resources, Writing – review & editing. **Pascal Laffargue:** Data curation, Resources, Writing – review & editing. **Pierre Petitgas:** Funding acquisition, Writing – review & editing. **Loïc Pellissier:** Methodology, Writing – review & editing. **Camille Albouy:** Data curation, Conceptualization, Methodology, Visualization, Resources, Writing – review & editing, Project administration, Funding acquisition.

#### Declaration of Competing Interest

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

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#### Data availability statement

The original biological data as DATRAS files are available at: <https://>



//www.ices.dk/data/data-portals/Pages/DATRAS.aspx.

The curated data set used in this study is available on figshare at: 10.6084/m9.figshare.19573354.

## Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pocean.2022.102788>.

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