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# **RESEARCH ARTICLE**

# Understanding the local drivers of beta-diversity patterns under climate change: The case of seaweed communities in Galicia, North West of the Iberian Peninsula

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# Abstract

**Aim:** To understand spatial-temporal changes (beta-diversity) in coastal communities and their drivers in the context of climate change. Coastal ecosystems are extremely exposed and dynamic, where changes in seaweed assemblages have been associated with changing water temperatures. However, at local scale, the effects of changes in the upwelling events and related stressors seek further exploration.

Location: Galicia rías, North West of the Iberian Peninsula.

**Methods:** Using data collected in 42 sampling localities in Galicia rias and over two time periods (1998 and 2014), we analysed changes in the seaweed community's composition through time and space. We calculated the temporal beta-diversity index and spatial beta-diversity as the pairwise composition differences between sampling localities. We use generalized dissimilarity models, to identify local environmental drivers of spatial and temporal beta-diversity.

**Results:** We found a significant change in seaweed communities of Galicia rias, between 1998 and 2014 (temporal beta-diversity). They were mostly related to species loss rather than to species replacement. The dissimilarity among localities (spatial beta-diversity) was significantly higher in 2014 than in 1998. Nitrate concentration was consistently predicted as the main driver of both temporal and spatial betadiversity patterns.

**Main conclusions:** Unlike other studies in marine ecosystems, our results suggest that observed changes in the structure of perennial seaweed assemblages in Galicia Rias might lead to a local biotic heterogenization, indirectly linked to climate change through changes in nutrients availability and the upwelling intensity. Changes in Galicia seaweed communities call scientific attention to the importance of local stressors in climate change studies.

#### KEYWORDS

coastal ecosystems, GDM, nestedness, nitrates, turnover, upwelling, warming

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# 1 | INTRODUCTION

Unprecedented climate changes are globally altering every ecosystem on Earth. Climate fluctuations are pointed as important driving forces of complex and unanticipated changes in biodiversity (Burrows et al., 2014; Parmesan & Yohe, 2003). Most research has focussed on understanding changes in species abundance and/or distribution, from regional to global scales. The observed distribution shifts have often followed the same trajectories as species thermal affinities (Burrows et al., 2019; Mieszkowska, 2015). However, heterogeneity in species responses to changes has been also documented, even within the same community (Lima et al., 2007). For instance, a temperature increase may negatively affect coldadapted species while benefiting warm-adapted ones in the same location (eg. Mieszkowska & Sugden, 2016; Muguerza et al., 2020; Wernberg et al., 2011). For this reason, recent research has shifted. and increasing attention is being paid to understanding the extent of change in communities' composition between localities or time instances (beta-diversity; Crabot et al., 2019; Fitzpatrick et al., 2013). Beta-diversity changes over time and space and can be influenced by shifts in species ranges and local extinctions (Magurran et al., 2015). Indeed, measures of beta-diversity can provide valuable insights into local and regional biodiversity patterns and underlying processes (Crabot et al., 2019), and on climate change impacts on biodiversity (Tingley & Beissinger, 2013). Despite recent advances in the understanding of communities' changes at different spatial scales (e.g. Bué et al., 2020; Leclerc, 2018; Robuchon et al., 2017), further exploration of beta-diversity patterns and the underlying in situ environmental drivers is needed, particularly in highly dynamic ecosystems.

Climate change impacts are particularly severe in coastal biomes. They are extremely dynamic ecosystems where high levels of biodiversity and key climate regulating processes are vulnerable to changes in both ocean and land environmental pressures (He & Silliman, 2019). The increasing temperature of both air and water at a rough rate of 0.1°C -0.2°C per decade is one of the main threats to coastal ecosystems (IPCC, 2014). Notwithstanding, changes in upwelling events, acidification and/or anthropogenic local stressors are also involved (Allison & Bassett, 2015; Mineur et al., 2015). Adjustments in species distributions, abundance and community compositions have been globally reported and associated with these climate-related changes (eg. García Molinos et al., 2015; Hawkins et al., 2009; Mieszkowska, 2015; Mieszkowska et al., 2005; Mieszkowska & Sugden, 2016; Poloczanska et al., 2016; Smale et al., 2019). Studies focussing on temporal and spatial variations in the composition of communities (expressed as beta-diversity) have shown an increasing homogenization (Dornelas et al., 2014; Magurran et al., 2015; Piazzi & Ceccherelli, 2020). Although coastal communities' changes have been associated with the predicted warming (Bué et al., 2020), beta-diversity is still poorly explored to understand climate change impacts on marine communities' homogenization (Dornelas et al., 2014; Magurran et al., 2015; Piazzi & Ceccherelli, 2020). While recent studies have investigated the spatial scale dependency of biodiversity patterns and processes

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(Leclerc, 2018; Robuchon et al., 2017), temporal changes in betadiversity patterns remain overlooked. Assessments of both temporal and spatial beta-diversity could provide a more sensitive indicator of community changes.

In coastal ecosystems, seaweeds play a central role as they are ecologically important primary producers. However, they are vulnerable to physical and chemical changes in the marine environment (Harley et al., 2012). In the last decades, dramatic changes in seaweed assemblages have been linked to climate change (eg. Barrientos et al., 2020; Gallon et al., 2014; Lima et al., 2007; Piñeiro-Corbeira et al., 2016; Smale & Wernberg, 2013; Wernberg, Russell, et al., 2011; Wernberg, Thomsen, et al., 2011). Major changes have been observed in temperate areas, including increases of warm water adapted species and retreats or disappearances of the cold-adapted ones (Barrientos et al., 2020; Casado-Amezúa et al., 2019; Díez et al., 2012; Lima et al., 2007; Muguerza et al., 2020: Piñeiro-Corbeira et al., 2016: Wernberg, Thomsen, et al., 2011). Occasionally, these changes have a major impact on the submarine landscape, such as when complex three-dimensional kelp forests have been replaced by structurally simpler systems dominated by algal turfs (Filbee-Dexter & Wernberg, 2018; Wernberg et al., 2019). Even though changing water temperature has been linked to these changes, other factors (e.g. waves, currents and nutrient concentrations) deserve further attention as they might also play an important role, particularly at local scales (e.g. Mabin et al., 2019; Mancuso et al., 2018; Piñeiro-Corbeira et al., 2019; Robuchon et al., 2017; Smale & Wernberg, 2013; Straub et al., 2019).

The number of studies linking seaweed assemblage shifts to climate change has been growing in the last years. Still, there are knowledge gaps, particularly in overlooked regions where environmental conditions may not be directly comparable to those in neighbouring areas. Located in the North West of the Iberian Peninsula, Galicia is a region characterized by several large inlets (drowned river valleys known as rías) that provide a heterogeneous environment and shelter for many species. Further, marine productivity is remarkably high thanks to the strong influence of a large upwelling system (Bode et al., 2011; Sydeman et al., 2014). These unique conditions mean that the Galician coast is home to a high diversity of seaweeds, being the southern edge of the range of many cold-temperate species (Bárbara et al., 2005; Hoek & Breeman, 1990). Recent studies have reported an impoverishment of the intertidal seaweed's communities in Galicia rias (Barrientos et al., 2020; Piñeiro-Corbeira et al., 2016). The increase of the air and seawater temperatures, frequency of strong waves and the slight decrease in some nutrients were suggested as potential causes for this loss (Piñeiro-Corbeira et al., 2016). However, further analyses are still required to accurately discriminate the main threats to these communities. In addition, since decreases in local richness can be followed by increased beta-diversity (Socolar et al., 2016), it is important to understand whether and how the changes in the number of species per locality may have altered the patterns of beta-diversity in Galicia.

To better understand what might make seaweed assemblages in Galicia vulnerable to future climate change, we investigated the spatial and temporal responses of seaweed communities to in situ Diversity and Distributions

environmental changes. Using data collected in 42 sampling localities over two time periods (1998 and 2014) (Piñeiro-Corbeira et al., 2016), we tested whether the observed decrease in species frequency was accompanied by changes in the community structure (as temporal beta-diversity) and, if so, whether they could be linked to sea surface temperature changes (Piñeiro-Corbeira et al., 2016). Additionally, we investigated whether the spatial beta-diversity changed in 1998 and 2014, and whether there are differences in the environmental variables determining the spatial and temporal beta-diversity, respectively.

## 2 | MATERIALS AND METHODS

## 2.1 | Study area

The study area is North West Iberia, Galicia (Figure 1), where the coastline is characterized by open coast sections interrupted by

sheltered rias, and an alternation of rocky cliffs and sandy beaches (Piñeiro-Corbeira et al., 2016). Sea water temperature ranges from 11 °C in winter to 18 °C in summer (Bárbara et al., 2005). Coastal upwelling has a strong influence on primary production in spring-summer, bringing nutrients from the Eastern North Atlantic Central Water mass to near the coast and even inside the rias (Alvarez et al., 2011). In winter, downwelling retains water inside the rias and nutrients are depleted (Varela et al., 2004).

#### 2.2 | Seaweed data

We use data collected and published by Piñeiro-Corbeira et al., 2016. Seaweed communities were surveyed in forty-two intertidal localities along Galicia rias in 1998–9 and re-surveyed in 2014 applying the same methodology to ensure comparable datasets (Figure 1; Piñeiro-Corbeira et al., 2016). Sampling localities were chosen to (a) ensure



FIGURE 1 Study area and sampling localities in green (some reference names in balloons). Rías names. Small inset of the study area location in the European context

appropriate hard subtract for intertidal seaweeds; (b) minimize human pressures (e.g. far from harbours, villages, aquaculture plants; Piñeiro-Corbeira et al., 2016); and (c) provide an appropriate sampling of the levels of wave exposure found in the region (exposed, semi-exposed, semi-protected and protected; see Cremades et al., 2004 and Piñeiro-Corbeira et al., 2016, for details). In each sampling locality, the same transect sampling approach was replicated in the two time periods (Piñeiro-Corbeira et al., 2016). The presence/absence of 39 seaweeds (Table S1) was recorded by local inspection of a 10 m wide transect (from the supralittoral fringe to the infralittoral one) for one hour (Piñeiro-Corbeira et al., 2016). Species were selected based on (a) perennial character to avoid seasonality confounding effect; (b) narrow range of wave exposure conditions (stenoecious) to disregard the potential effect of wave intensity in these species' distributions; and (c) identifiability (Cremades et al., 2004; Piñeiro-Corbeira et al., 2016). Based on authors' expert knowledge, literature (Lüning, 1990) and biogeographic affinity (Guiry & Guiry, 2021), the selected species were grouped according to thermal affinities for further analysis (Table S1).

## 2.3 | Environmental variables

In situ environmental variables were used to investigate the drivers of both temporal and spatial beta-diversity patterns in Galicia Rías (Figure S1) weekly water column recording of seawater temperature, and nitrate and phosphate concentrations. Data were provided by Instituto Tecnoloxico para o Control de Medio Mariño de Galicia (INTECMAR, Vilagarcía de Arousa, Spain), which runs a network of sampling stations where water samples are collected on a weekly basis at depth intervals 0-5 m, 5-10 m and 5-15m. In this study, we used in situ data from 43 sampling stations to produce a continuous yearly average of the surface of seawater temperature, nitrate and phosphate concentrations at 0.005 degree of resolution, using the Inverse Distance Weighting interpolation (IDW) model. IDW outperforms other interpolation methods in spatial interpolation for seawater temperature (Kusuma et al 2018). We used in situ measurements of the average water temperature in the upper 5 m layer as a surrogate for sea surface temperature (SST), as it matched the warming trend observed in satellite-derived SST data (Piñeiro-Corbeira et al., 2016). Due to its high correlation with other variables, water temperature between 5 and 10m was excluded from the analysis. The remaining variables had correlation coefficients below 0. 505 in 1998 and 0.574 in 2014.

# 2.4 | Data analysis

We analysed trends in the seaweed community compositions in Galicia by looking at spatial and temporal differences in taxa richness and beta-diversity. We performed analyses for all taxa and for species grouped by empirical thermal affinity. Species richness for each sampling locality was calculated as the number of the observed seaweed species. Temporal changes in species richness were measured **Diversity** and **Distributions** 

through the difference between 2014 and 1998 in each location and its significance was tested using a Wilcoxon Signed-Rank Test.

To study the change in seaweed community composition through time (from 1998 to 2014), we calculated the temporal betadiversity index (TBI, Legendre, 2019). The Sørensen index was used as TBI because it is the presence-absence equivalent of the Bray-Curtis dissimilarity index. TBI was computed for each sampling locality by measuring the change in species composition between the first (1998) and second surveys (2014). TBI was decomposed into the species loss (B) and gain (C) components of these dissimilarities (Legendre, 2019). We tested for significant changes, to identify localities that have changed in composition. We tested the null hypothesis  $(H_0)$  that species assemblage at a given locality i (i.e. sampling locality) was not different between 1998 and 2014, compared to the assemblages that could have been observed at the same two times in each sampling locality (Legendre, 2019). We applied a bootstrap method to randomly recompute TBI 999 times, and a *p*-value was calculated for the TBI difference between 1998 and 2014 at each sampling locality. Analyses were performed using the TBI.R function available in the R package "adespatial" (Dray et al., 2018). Two additive components were calculated: turnover (Simpson index of dissimilarity, βsim) and nestedness (nestedness resultant index of dissimilarity, ßsne) (Baselga, 2010). This was made because variation in species composition may be caused by turnover (species replacement from site to site or year to year) or nestedness (species loss from site to site, or year to year) (Baselga, 2010). They were computed using the betapart package in R (Baselga & Orme, 2012).

To analyse the spatial variation of seaweed communities, we calculated the spatial beta-diversity as the pairwise composition differences between sampling localities for each sampling year. We measured beta-diversity by calculating the presence-absence Sørensen dissimilarity index ( $\beta$ sor), turnover (Simpson index of dissimilarity,  $\beta$ sim) and nestedness (nestedness resultant index of dissimilarity,  $\beta$ sne) components (Baselga, 2010). Significance was tested with a *t* test after 100 iterations of resampling of 50% of all sampling units. Analyses were performed using the betapart package in R (Baselga & Orme, 2012).

We use generalized dissimilarity modelling (hereafter, GDM, Ferrier et al., 2007), to evaluate the role of environmental changes in the observed patterns. GDM is a nonlinear matrix regression technique for analysing spatial patterns in the compositional dissimilarity between (previously calculated) pairs of locations or temporal dissimilarities as a function of environmental dissimilarity and geographical distance (Ferrier et al., 2007). To fit GDMs, we constructed site-by-species and site-by-environment matrices for each year (1998 and 2014) and between years, where sites are the localities where species were observed. In addition to temperature, phosphates and nitrates, the environmental matrices included the geographical coordinates for the localities. It is from these predictors that GDM derives sets of I-splines and calculates distances between all possible pairs of sites. We tested variable significance using Monte Carlo permutation (Ferrier et al., 2007). All analyses were performed in R v. 2.12.2. All previous analyses were replicated **VILEY** Diversity and Distributions

# 3 | RESULTS

# 3.1 | Quantification of seaweed communities

In 1998, 39 species of seaweed were observed in the 42 sampling localities. This number decreased to 37 in 2014, as two species were not observed, namely Cystoseira nodicaulis and Gracilaria gracilis. (Figure 2, Figure S2). There were significant differences in the total number of species observed per locality from 1998 to 2014 (W = 678.5, p < .05). There was a general decrease in the total number of species observed per locality during the study period (in ~81% sampling localities). An increase in the number of species was only observed in three localities, namely Punta Del Castro, Santa Cruz and Punta Bazar. The same pattern was observed when looking at species by their thermal affinity (Figure 2, Figure S2). Regardless of the thermal affinity, the number of species observed per locality decreased significantly (W cold =642, p < .05 and W warm = 622, p <.05, respectively). One species of each thermal affinity went unrecorded in 2014 (the warm-affinity C. nodicaulis and the coldaffinity G. gracilis). The number of warm-adapted species increased

in five localities of Central and Northern Rías (Punta de Arnela, Punta Lens and Punta Bazar in Rías Baixas, Santa Cruz, Barizo and Punta do Castro) while the number of cold-adapted species increased in three localities of the Southern Rías (Punta Bazar, Punta Batuda and Punta Redondelo).

#### 3.2 | Temporal patterns of beta-diversity

Overall, there were changes in seaweed community compositions between 1998 and 2014. Species loss was the main component of temporal beta-diversity between 1998 and 2014 (t = -0.21, p < .05, Figure 3, and Table S2), and this also happened when each thermal affinity group was examined separately (t warm = -0.27, p < .05, t cold = -0.24, p < .05, Figure 3). Seaweed community's lost species in 35 localities, for instance *Gigartina pistillata* and *Himanthalia elongata* were absent in 15 localities in 2014, compared to 1998 (Table S1 and S2). With all species taken together and with just the cold-water set, there were significant differences in ~14% of sampling localities between 1998 and 2014 (TBI > 0.06, *p*-value < .05; Table S2), while this value increased to 17.5% when only warm-adapted seaweeds were taken into consideration (Table S2).

Changes in nitrate concentrations and water temperature from 1998 to 2014 were the major drivers of the observed patterns of



**FIGURE 2** Boxplots of species richness and spatial beta-diversity (Sorensen dissimilarity index) each year (1998 and 2014) for all seaweeds and with seaweeds grouped by thermal affinity



FIGURE 3 Plot of seaweed survey data for 1998 and 2014, where 42 localities were plotted (yellow dots) using species gains (C) against species losses (B) - B-C plot. Dot size proportional to the temporal beta-diversity value (Sorensen index) between 1998 and 2014. Green line is where gains are equal to losses while the red line has the slope of the green line but passes through the centroid of the points. Red line position indicates the direction of communities' composition changes from 1998 to 2014 (loss of species)

TABLE 1 Coefficients of GDMs predictors of spatial beta-diversity and its components (replacement and species loss) in 1998 and 2014 and of TBI				Geographic	[Phosphate]	[Nitrate]	Temp.	Temp.
	All Taxa	Beta-diversity	1998	0.00	0.13	0.95*	0.07	0.16
			2014	0.00	0.15	1.01*	0.07	0.10
			2014 TDI	0.00	0.00	1.01	0.01	0.23
			1000	-	0.00	1.07	0.50	0.00
		species loss	1998	0.07	0.03	0.00	0.01	0.00
			2014	0.13	0.04	0.00	0.11	0.08
			IBI	-	0.01	0.35	0.13	0.00
		Replacement	1998	0.00	0.13	0.7	0.19	0.07
			2014	0.00	0.00	1.01	0.01	0.23
			TBI	-	0.00	0.00	0.00	0.00
	Warm Affinity	Beta-diversity	1998	0.01	0.53	1.70	0.27	0.12
			2014	0.00	0.20	2.43	0.00	0.61
			TBI	-	0.10	2.41	0.42	0.00
		Species loss	1998	0.09	0.07	0.00	0.00	0.00
			2014	0.17	0.11	0.00	0.04	0.08
			TBI	-	0.00	0.47	0.25	0.00
		Replacement	1998	0.00	0.31	0.39	0.77	0.23
			2014	0.00	0.16	0.21	0.00	0.00
			TBI	-	0.00	0.00	0.00	0.00
	Cold Affinity	Beta-diversity	1998	0.00	0.00	0.83*	0.02	0.14
			2014	0.00	0.00	0.70	0.11	0.13
			TBI	-	0.59	0.73	0.42	0.00
		Species loss	1998	0.00	0.03	0.00	0.08	0.05
			2014	0.00	0.00	0.70	0.11	0.13
			TBI	-	0.00	0.01	0.18	0.00
		Replacement	1998	0.00	0.00	0.76 <sup>*</sup>	0.01	0.13
			2014	0.00	0.00	0.70 <sup>*</sup>	0.11	0.13
			TBI	-	0.07	0.98	0.00	0.00

Note: Note The most important predictors are shown in bold.

\*Statistically significant (p < .05).

temporal beta-diversity and the associated species loss (Table 1, Figure S1, S3). On the other hand, the change in phosphate concentrations also contributed to the pattern observed for the cold-water group (Table 1, Figure S1).

# 3.3 | Spatial patterns of beta-diversity

There was a significant correlation between the observed values of spatial beta-diversity in 1998 and 2014 (Mantel statistic = 0.67 p < .05). VILEY— Diversity and Distributions

Both spatial replacement (turnover) and species loss (nestedness) components were also significantly correlated between years (Mantel statistic=0.64 and 0.24, p = .001 and .004, respectively). The dissimilarity among localities (spatial beta-diversity) was significantly higher in 2014 than 1998 (Figure 2; t = 15.693 p < .05). The same was also observed for the spatial replacement (t = 14.02, p < .05) and species loss components of beta-diversity (t = 5.91, p < .05). Similar patterns were observed when looking at species by their thermal affinities. There was a significant increase of beta-diversity and its components from 1998 to 2014 (Figure 2 and Figure S2) except for nestedness (species loss) in cold-water species (t = 1.02, p > .05, Figure 2 and Figure S2).

Nitrate concentration was consistently predicted as the main driver of spatial patterns in Galicia rías in each vear (Table 1. Figure S4). It was significantly related to spatial beta-diversity and replacement in 1998 and in 2014 for all species as well as for coldadapted species spatial beta-diversity in 1998 and replacement in both time periods (Table 1, Figure S4). Although not significant, nitrate concentration was related to warm-adapted species spatial beta-diversity and replacement in 1998 or 2014 (Table 1). Water temperature, particularly at the surface (<5 m), was the second most important driver of beta-diversity patterns for all taxa in both time periods. The same was also observed independently for each thermal affinity group, although changes in phosphate concentrations were also important for the warm-affinity group (Table 1, Figure S4). Geographic distance and phosphate concentration were the most important drivers of species loss among localities for all species and for species with warm affinity (Table 1, Figure S1, Figure S4).

# 4 | DISCUSSION

Understanding spatial-temporal changes in ecological communities of coastal ecosystems are crucial in the context of climate change. Our study is pioneering in exploring how in situ recorded environmental variables may affect the structure of the perennial seaweed assemblage over space and time in the rocky intertidal of NW Iberian Rías. Our results show that seaweed assemblages changed significantly between 1998 and 2014 (temporal beta-diversity), and these changes were linked to species loss rather than to species replacement. Therefore, our results support the initial hypothesis that the decrease in species recorded between 1998 and 2014 came with changes in the community structure. Nonetheless, our results diverge from observations in other marine assemblages (e.g. fishes) where the temporal beta-diversity was linked to species replacement rather than species loss (Dornelas et al., 2014; Magurran et al., 2015). These studies suggested an increase in spatial homogenization as the species identity of colder northern localities increasingly resembles that of warmer southern localities (Magurran et al., 2015). Similarly, many studies with seaweeds across the European Atlantic have reported range shifts as well as some replacement of cold-affinity species by warm-affinity ones (eg. Díez et al., 2012; Gallon et al., 2014; Lima et al., 2007; Muguerza et al., 2017, 2020). In our study, however, species losses outweighed gains in both cold-affinity and

warm-affinity species suggesting that water warming may not be the only factor explaining temporal beta-diversity patterns. In fact, our analysis suggests that the changes in nitrate concentration have greater explanatory power for the temporal beta-diversity variation in Galician rías than water warming. Another alternative hypothesis for the observed pattern is a mismatch between changes in environmental and species responses: while some cold-adapted species might disappear in one locality, warm-adapted ones might not have the time to arrive. Therefore, we acknowledge that caution should be taken in the interpretation of our results as we have only tested two-time instances. Longer time series will be needed to determine the true extent of the relative importance of nutrient and temperature changes to the perennial seaweed assemblage.

Temperature has often been identified as the main driver of temporal and spatial changes in many marine communities (Burrows et al., 2019). However, a range of abiotic and biotic factors are known to be drivers of change in the marine realm (Bulleri et al., 2020). Environmental factors other than temperature may be equally important in accounting for community changes at local scales, such as nutrient inputs, storms or habitat destruction (Jackson, 2008). Nitrogen and phosphorus are common limiting nutrients for seaweeds; for example, growth can be simultaneously limited by both (Hurd et al., 2014). On the other hand, different seaweed species show different nitrogen usage, suggesting that more diverse communities enhance nitrate uptake (Bracken & Stachowicz, 2006). In fact, laboratory experiments suggest that nutrient limitation may more strongly constrain seaweed performance than warming, in both warm and cold-affinity temperate species (Piñeiro-Corbeira et al., 2019). Nonetheless, disentangling the relative importance of temperature and nutrients from field data can be challenging because high temperatures often correlate with low concentrations of inorganic nutrients in temperate marine ecosystems (Gerard, 1997). This relationship is particularly relevant in areas such as Galicia where a seasonal coastal upwelling pumps colder nutrient-rich deeper water to the surface, thus fuelling a great primary production (Alvarez et al., 2017). Climate change is altering the intensity of eastern boundary upwelling (Sousa et al., 2017; Sydeman et al., 2014). Although somewhat contentious, and unlike other large upwelling systems worldwide, there is evidence that the Iberian upwelling may have weakened in recent times (Sydeman et al., 2014). A weaker upwelling would be largely consistent with the environmental changes observed between 1998 and 2014 and here reported, as it would involve warmer, nutrientpoor waters. Moreover, the spatial variability of the temporal trends of some environmental variables (e.g. nitrates, temperature) might also be related to the spatial variability of the upwelling system since upwelling events are more frequent and intense along the western coast of Galicia than along the northern one (Alvarez et al., 2011). Obviously, a weakened upwelling might not be the only mechanism behind the environmental changes recorded in Galicia. A detailed analysis of water temperature seasonal trends suggests that much of the warming happens in autumn (Piñeiro-Corbeira et al., 2016), a time of year when upwelling events typically occur less frequently (Alvarez et al., 2011). Similarly, changes in other human activities on the nearby coast may also be related to the variation recorded for some nutrients over time

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(e.g. nitrates). Nonetheless, it still seems plausible to suggest that the change in the intensity of the Iberian upwelling could be an ultimate driver of at least some of the variation in the perennial seaweed assemblage recorded in Galicia between 1998 and 2014.

The prevalence of species losses over gains between 1998 and 2014 led to a higher spatial beta-diversity in seaweed assemblages in 2014. This could be a consequence of the fact that the estimates of dissimilarity between sites may increase even though the number of different species between two sites does not change if the sites to be compared have fewer species in total (Legendre, 2019). Nevertheless, it does not counteract our inference that rather than the biotic homogenization reported elsewhere for other marine assemblages (Magurran et al., 2015), the assemblage of intertidal perennial seaweeds of Galician coasts became more spatially variable in 2014. Regardless of the year, species turnover rather than nestedness was the main component of spatial beta-diversity. This is hardly surprising for the intertidal seaweed assemblage, as wave exposure is a major determinant of the presence/absence of many species at a given site (Barrientos et al., 2020). Although we believe that the potential effect of wave exposure was mitigated by the sampling methodology, its importance is indubitable (Robuchon et al., 2017), particularly in the intricate coast of Galician rias. As such, the hypothesis that the observed spatial beta-diversity and spatial replacement might be also related to the differences in wave exposure among sites will possibly need further exploration. Indeed, nitrate concentration is consistently predicted as the variable that best predicts the spatial beta-diversity, and our data show that the sites within the rias tend to have higher nutrient concentrations and those sites usually are less exposed to the waves.

# 5 | CONCLUSION

Undoubtedly, global climate change is leading to changes in communities. In Galicia rias, the structure of perennial seaweed assemblage has changed over space and time, leading to an apparently biotic heterogenization. The observed pattern is apparently linked to nitrates concentrations, which might be explained by a strong influence of changes in the intensity of the Iberian upwelling. Despite countercurrent, our results highlight the importance of exploring local and indirect climate change effects.

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#### CONFLICT OF INTEREST

Authors declare there is no conflict of interest.

#### DATA AVAILABILITY STATEMENT

The data on seaweeds presence/absence in 1998 and 2014 (Table S1) are provided at the DRYAD data repository (https://doi. org/10.5061/dryad.s4mw6m96f).

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#### BIOSKETCH

This study is part of the project of SEEINGSHORE (PTDC/BIA-BMA/31893/2017) which combines several approaches to better understand and predict the impact of climate changes on the structure of coastal ecosystems. The work was developed using seaweed information of Galicia rias, in North West of the Iberian Peninsula. Cândida G Vale is a postdoc researcher, working on the application of modelling tools for studying spatial and temporal dynamics of biodiversity, particularly linked to climate change effects. Francisco Arenas is team leader of Benthic Ecology Team and researcher at the Laboratory of Coastal Biodiversity at CIIMAR. His research focussed on experimental approaches to understand and predict the effects of global changes on coastal populations and ecosystems. Rodolfo Barreiro is team leader of BioCost Research Group. His research is focussed on the study of environmental conservation from various approaches focussing on the effects of global change on coastal ecosystems, with special attention on seaweeds. Cristina Piñeiro-Corbeira is a postdoc researcher working on the study of short- and long-term changes in intertidal macroalgae communities and their relationship to increased natural and anthropogenic disturbances at both global and local scales.

Authors Contributions: Cândida Gomes Vale: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft. Francisco Arenas: Funding acquisition, Writing - review & editing. Rodolfo Barreiro: Funding acquisition, Writing - review & editing. Cristina Piñeiro-Corbeira: Conceptualization, Data collection, Investigation, Writing - original draft.

#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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