Marine Environmental Research 202 (2024) 106743

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Functional traits of ecosystem engineers as predictors of associated fauna

Javier Jiménez Herrero [a,*], Andrea Desiderato [b,c], Pedro Emanuel Vieira [c], Ana Mafalda Tavares [a], Henrique Queiroga [c], Rui Santos [a]

[a] *Marine Plant Ecology Research Group, CCMAR, Centre of Marine Sciences, University of Algarve, Gambelas, 8005-139, Faro, Portugal*
[b] *Department of Invertebrate Zoology and Hydrobiology, University of Lodz, Banacha 12/16, 90-237, Lodz, Poland*
[c] *Centre for Environmental and Marine Studies (CESAM), Department of Biology, University of Aveiro, Campus Universitário de Santiago, 3810-193, Aveiro, Portugal*

ARTICLE INFO

Keywords:
Beta diversity
Biogeography dynamics
Environmental variables
Functional traits
Intertidal communities
Latitudinal gradient

ABSTRACT

The ongoing combination of global warming and increased anthropogenic pressure is causing latitudinal shifts in marine species, potentially impacting community composition, local richness, and marine trophic webs. This study investigates the factors influencing the distribution and diversity of intertidal seaweed and associated peracarid communities, including their functional traits, and explores various facets of beta diversity (taxonomic and functional). We hypothesize that: 1) abiotic factors such as temperature and anthropogenic pressure significantly influence seaweed distribution and diversity shifts, and 2) changes in seaweed functional diversity have an impact on the diversity and functioning of its associated peracarid communities. The sampling was conducted along a wide latitudinal gradient in the NE Atlantic (27°N - 65°N), encompassing three distinct ecoregions: Northern European coasts, the Iberian Peninsula, and Macaronesia. The identified seaweed and peracarid species were classified functionally, and taxonomic and functional diversity were analysed on a large geographic scale. The northern region exhibited large brown canopy seaweeds and epibiotic isopods, while Macaronesia featured small red, highly branched, and calcareous crust seaweeds with burrower and tube-building tanaids. The Iberian Peninsula acted as a transitional zone, showcasing a mix of green, red, and brown seaweeds, along with Amphipoda peracarids found across all ecoregions. Our findings underscore the impact of geographic distance on total beta diversity, revealing distinct seaweed and peracarid communities across spatial gradients. Environmental variables, particularly pH and maximum sea surface temperature, emerged as significant factors influencing beta diversity patterns of seaweeds, indicating the potential impact of acidification and heat waves on community composition. In addition, seaweed functional traits were shown to be significant in shaping the diversity and abundance of associated peracarid assemblages, impacting both taxonomic and functional beta diversity. These findings provide crucial insights into the factors influencing the biogeography and biodiversity dynamics of intertidal seaweeds and associated peracarids, offering essential implications for conservation and management strategies amid ongoing environmental changes.

1. Introduction

Under the current global warming and the increase of anthropogenic pressure, marine species are shifting their latitudinal ranges (e.g., Mineur et al., 2015) which may alter community composition and local richness patterns, leading to local extinctions and/or invasions (Pinsky et al., 2020) and thus change marine trophic webs. The study of distribution patterns and abundance of species provides a better understanding of organism assemblages (Underwood, 2000), as well as being an important tool for the identification, selection, and designation of Marine Protected Areas (MPAs) (Dinter, 2001). However, the delimitation of these ecological boundaries typically varies significantly between flora and fauna, benthic or pelagic organisms, or different taxonomic groups. The study of the changes in the geographical distribution of marine species can also help to assess how climate change may affect the structure and functioning of ecosystems (Blanchette et al., 2008; Hawkins et al., 2009; Adey and Hayek, 2011). Although climate is thought to be a major driver of species distribution (Grinnell, 1917), biotic interactions, habitat complexity, or food choice can have an impact on species' spatial patterns (Bascompte, 2009; van Dam, 2009). Species distribution shifts in the coastal ocean have been documented in several studies (Hawkins et al., 2009; Poloczanska et al., 2013; Gervais

---

[*] Corresponding author.
E-mail address: jjherrero@ualg.pt (J. Jiménez Herrero).

https://doi.org/10.1016/j.marenvres.2024.106743
Received 29 April 2024; Received in revised form 3 September 2024; Accepted 4 September 2024

et al., 2021), however, the factors that drive organism distribution and diversity patterns remain poorly understood.

The Temperate North-Eastern Atlantic Region can be divided into Lusitanian and Northern European seas provinces (Dinter, 2001). The province of Lusitania circumscribes the warm-temperate waters of the Iberian Peninsula and the Azores, Madeira, and the Canary Islands (Toonen et al., 2016). However, some studies (Almada et al., 2013; Vieira et al., 2022) have argued that the Macaronesian archipelagos are highly distinct from the mainland coasts of the Lusitanian Province, proposing that Macaronesia should be considered a separate ecoregion (Spalding et al., 2007). The Northern European Seas province encompasses the waters from the Norwegian archipelago and Barents Sea to the southern entrance of the English Channel, including Iceland and the Faroe Islands (Toonen et al., 2016). Several studies have investigated the species distribution of seaweed and benthic communities in this area of the Atlantic on a small scale (Díez et al., 2012; Sangil et al., 2014a; Sangil et al., 2018). At larger biogeographic scales, however, research primarily consists of broad descriptions of biota, with little focus on abundance data. These extensive studies are useful for describing biogeographic regions (Ekman, 1953; Briggs, 1974; Gaines and Lubchenco, 1982; Liuzzi et al., 2011), as well as for evaluating latitudinal and longitudinal patterns of richness and diversity (Tuya and Haroun, 2009).

The organisms that occupy the intertidal at the edge of both the marine and terrestrial environment are exposed to extreme environmental conditions and therefore they are most sensitive to the effects of climate change (Harley et al., 2006), thus being used as bioindicators of climate-driven changes (Southward et al., 1995). Seaweeds are the major autotrophic biomass in the intertidal zone, particularly on rocky coastlines, and serve an important structural and functional role in a variety of habitats. Changes in the composition of seaweed communities will have an impact on entire coastal ecosystems (Mineur et al., 2015). Recent changes in seaweed distributions, as well as those associated organisms, have been suggested to be related to rising temperatures caused by climate change (Wernberg et al., 2011; Martínez et al., 2018; Casado-Amezúa et al., 2019). Temperature alters the distribution of seaweeds by affecting survival, recruitment, growth, and reproduction (Breeman 1988), but also biotic interactions such as predation and food availability, indirectly affect species distribution (Ockendon et al., 2014). Chlorophyll levels, indicative of primary productivity and often linked to upwelling conditions, can also affect species shifts by modifying carrying capacities, population densities, and diversity in marine fauna (Field et al., 1998; Huston and Wolverton, 2009). High productivity in seaweeds influences both the seaweeds and associated organisms (Cole and McQuaid, 2010). In turn, climate-induced salinity changes can influence seaweed species richness, thereby habitat complexity and impacting higher trophic levels (Takolander et al., 2017). Furthermore, anthropogenic pressures are increasing in parallel with global warming, which can also cause a change in the distribution of organisms (Beaugrand et al., 2003; Richardson and Schoeman, 2004; Harley et al., 2006; Pörtner and Knust, 2007). Human disturbance and destruction of coastal habitats are likely to have a greater effect on marine ecosystems than global warming (Bugnot et al., 2021). However, for the moment many studies fail to establish limits on the distribution of marine organisms, and therefore to discriminate against many of the ecological responses registered because of anthropogenic disturbances.

Intertidal seaweeds are important habitat-forming organisms harbouring sessile and mobile associated fauna which are mainly peracarid crustaceans such as amphipods, isopods and tanaids (Guerra-Garcia et al., 2011). Macroalgal mats serve as microhabitats by providing a trophic resource and shelter for peracarids, one of the most diverse taxa associated with seaweeds (Zakhama-Sraieb et al., 2006a). This group has been the focus of numerous biogeography studies (Chavanich and Wilson 2000; Thiel 2002; Page et al., 2018; Iwasa-Arai et al., 2021), mainly because the lack of pelagic larvae and their capacities for long-distance movement is limited in adults (Izquierdo and Guerra-García, 2011), being good indicators of environmental changes (Guerra-García et al., 2009). It has been demonstrated that the presence of vegetation is correlated with the distribution of this zoobenthos (Yoshimura and Maeto, 2006). Additionally, variations in the architecture of seaweed and their functional composition have been found to have a major impact on the diversity and abundance of the associated epifaunal assemblages (Leite et al., 2007a; Buza Jacobucci et al., 2014. Functional groups classify organisms based on characteristics related to their biology (body plan, size, behavior, life strategy). Littler and Littler (1984) related seaweed functional-groups to environmental disturbances and discovered that, depending on disturbance levels known from their morphology, community compositions could be predicted. The variation in seaweed morphology (Christie et al., 2009) makes these organisms great candidates for assessing how structural complexity affects ecological assemblages. In particular, greater structural complexity (e.g., higher degree of branching) creates a three-dimensional matrix where various environmental stresses are reduced, providing protection and space for associated species against larger predators (Bulleri et al., 2016), thereby supporting higher diversity (Veiga et al., 2014) Consequently, distribution models of these organisms, and their traits variation, are powerful tools for tracking and forecasting changes in coastal systems (Martínez et al., 2012).

The spatial structure of communities is linked with ecological processes by beta diversity, and therefore it can be defined as the variation in species composition among communities across space or time (Anderson et al., 2011). Besides, this measurement of diversity provides a better understanding of how ecological processes operate along environmental gradients (Qian and Ricklefs, 2007). Beta diversity can be divided into two components: turnover (replacement of species) and nestedness or richness (species richness differences being due to species gain or loss) (Baselga, 2016), showing the ecological processes acting on communities. Ecological research including functional diversity is increasingly growing to better explain patterns such as species occurrence, species competitive capacities, and the impact of biological communities on ecosystem functioning. Exploring both taxonomic and functional diversity enables us to clearly illustrate the main drivers of change in a community and how they affect it, as well as provide details on the process of trait selection (Best and Stachowicz, 2013).

Data for predicting species distribution and habitat shifts is essential for biodiversity assessment and conservation. However, identifying the set of factors that may determine future species occurrence and spatio-temporal dynamics under variable habitat conditions is challenging (Brown and Knowles, 2012). Understanding both the current and projected distribution of marine organisms is crucial for evaluating their vulnerability to climate change. There are several studies focused on the distribution of seaweeds (Robin South, 1987; Fernández, 2016; Vieira et al., 2022), peracarids (Guerra-García et al., 2009; Arfianti and Costello, 2020) and the role of seaweeds as determinants of epifauna diversity (Chemello and Milazzo, 2002; Leite et al., 2021). However, knowledge of the biogeography of seaweeds and peracarids in the Northeast (NE) Atlantic, and especially including oceanic islands, is still fragmentary. Limited research has been conducted to explore the relationship between geographical variations in seaweed composition and the diversity patterns of associated macroinvertebrates (Arrontes and Anadón, 1990; Pereira et al., 2006; Guerra-Garcia et al., 2011). Moreover, these studies did not address the functional aspects of the communities, which are typically inferred by examining the traits of species. Experimental studies have shown that within-community diversity in functional traits ('functional diversity'; Díaz and Cabido, 2001; Tilman, 2001; Petchey and Gaston, 2006) is linked to ecosystem functioning. It has also been found that functional diversity frequently drives ecosystem functioning, which sometimes can be masked by studying only the taxonomic diversity (Tilman et al., 1997; Hooper and Dukes, 2004.

Here, we hypothesize that: 1) abiotic factors such as temperature and anthropogenic pressure significantly influence seaweed distribution and diversity shifts, and 2) changes in seaweed functional diversity have an impact on the diversity and functioning of its associated peracarid communities. To test these hypotheses, we investigated the functional and taxonomic aspects of seaweeds and associated peracarid communities along an extensive latitudinal gradient in the NE Atlantic (27°N-65°N). The selection of functional traits was based on the prediction that they significantly influence the diversity and composition of peracarid communities by providing varying structural complexity, resource availability, and habitat conditions in general. Additionally, to examine deterministic niche-based processes such as environmental filtering, responses to abiotic conditions and biological interactions like competition and predation, we analysed all levels of beta diversity (i.e., total, richness, and replacement) across two facets of biodiversity (taxonomic and functional). Our goal is to identify the best predictors of variation in seaweed and associated peracarid communities among geographic, climatic, environmental, anthropogenic, and functional factors.

2. Material and methods

2.1. Study area

This study encompasses the NE Atlantic region. Samples were taken at nine coasts that comprise 27 stations along a wide latitudinal gradient from Reykjavik in Iceland (65° 59′ 59.985″ N, 21° 19′ 10.776″ W) to Canary Island (Spain) in the south of the NE Atlantic region (27° 59′ 8.714″ N, 15° 22′ 30.756″ W) (Fig. 1). The stations were selected in locally sheltered locations (low wave exposure), covering a great range of latitudinal environmental variation. The primary goal of the sampling design at each coast (n = 3 stations) was to cover all relevant habitats in the intertidal zone to maximize diversity sampling. Four habitats were sampled along the intertidal vertical distribution, which was divided into upper, middle, and lower zones. This division was based on tidal levels: the lower zone ranged from the low tide at spring tides to the low tide at neap tides, the middle zone encompassed the tidal range under neap tide conditions, and the upper level extended from the high tide at neap tides to the high tide level at spring tides. Within each level, the interaction of light exposure and air exposure was considered, resulting in four sampled conditions: Immersed-Shade, Immersed-Sunny, Emersed-Shade, and Emersed-Sunny.

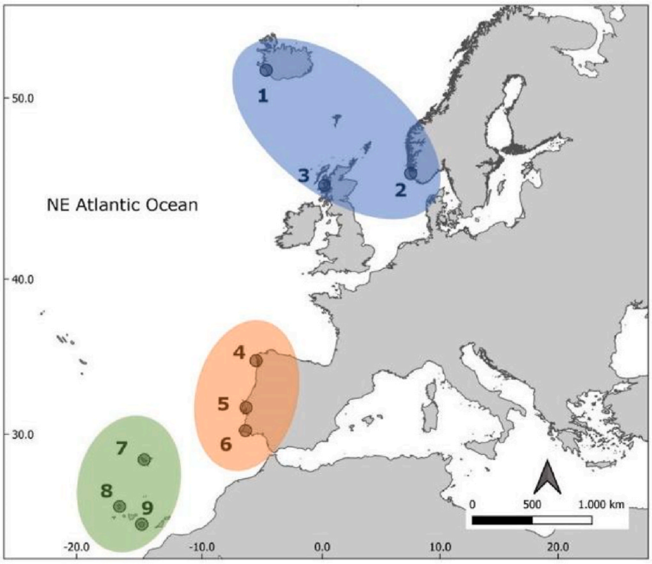

Fig. 1. Study area showing the coasts where the sampling was carried out. 1) Iceland (stations 1–3), 2) Norway (stations 4–6), 3) Scotland (United Kingdom) (stations 7–9), 4) North Spain (stations 10–12) 5) West Portugal (stations 13–15), 6) South Portugal (stations 16–18), 7) Madeira (Portugal) (stations 19–21), 8) La Palma (Spain) (stations 22–24) and 9) Gran Canaria (Spain) (stations 25–27). Colours represent the ecoregions: North (blue), Iberian Peninsula (orange), Macaronesia (green).

2.2. Environmental data

The environmental variables used in the present study were selected due to the important role that they play in the distribution of marine organisms. Sea surface temperature (SST), salinity and chlorophyll (as a proxy of ocean productivity) can drive the distribution and the occurrence of marine organisms (Gaston, 2000). At the local shore level, other abiotic factors, such as wave fetch, tidal amplitude and insolation are critical to the structure of marine communities (Gambi et al., 2016). As well, human disturbances and ocean acidification can act both on small and large scales, affecting the distribution of organisms (Brierley and Kingsford, 2009). Consequently, the latitudinal gradient along the sampling stations was characterized by the following environmental variables: fetch, air temperature, chlorophyll-a (chla), SST, insolation, precipitation which were obtained from Bio-ORACLE data set (Tyberghein et al., 2012; Assis et al., 2017); aragonite saturation and pH values were obtained from NOAA Dataset ("https://sos.noaa.gov/catalog/datasets/ocean-acidification-saturation-state/"). The Ocean Health Index (OHI) developed by Halpern et al. (2012) was also included as it encompasses different human impacts. The OHI score is the weighted sum of ten goal-specific index scores such as 1) food provision, 2) artisanal fishing opportunity, 3) natural products, 4) carbon storage, 5) coastal protection, 6) tourism and recreation, 7) coastal livelihoods and economies, 8) sense of place, 9) clean waters and 10) biodiversity.

2.3. Sampling and sample processing

Sampling was conducted from April to October of 2011. Quadrats of 20 cm × 20 cm were laid within each habitat (n = 3) in the intertidal zone of each site during the day at low tide. The rock surface within each quadrant was scraped and organisms were completely removed. In the laboratory, the seaweed samples were immersed in fresh water for 5 min and agitated to release the fauna, without specifying its host seaweeds. Then, the seaweeds were removed, the water was sieved through a 500-micra mesh and the peracarids were collected and preserved in 96% alcohol for later identification. The seaweed species were immediately identified whenever possible. Cryptic species were preserved in KEW solution (40% salt water, 40% ethanol at 70%, 10% glycerin, 10% formalin at 4%) and identified later. Firstly, seaweed abundances were standardized using a scale ranging from 0 to 4, with 0 - absent, 1 - present or rare, 2 - not very abundant, 3 - common, and 4 - very abundant. Subsequently, these values were further adjusted to conform to the DAFOR scale. Peracarids were quantified using count data and then it was adapted to the DAFOR scale so that abundances of seaweed and peracarids could be expressed in a common scale. DAFOR scale was presented as D - dominant, A - abundant, F - frequent, O - occasional and R – rare, and in the case of the peracarids the limits used for each class of abundance as a percentage were 100, 50, 30, 15, 5, respectively. In the last step, different traits were used to describe the functional ecology of these communities. The classification was done according to specialised literature and if no information was available, expert's opinion. According to Petchey and Gaston (2006), the selection of functional traits should focus on those that influence the ecological processes under study. Therefore, the functional traits of seaweeds and peracarids were selected based on their ecological significance and potential to influence community dynamics through various mechanisms. For seaweeds, five morpho-functional traits adapted from Littler and Littler (1980) were included and subdivided into categories (Supplementary Material, Table 1): 1) Thalli growth, which included the categories apical, diffuse, kelp type, and marginal; 2) degree of branching, categorized into three levels from low to high; 3) external morphology, which included the categories foliose, delicately branched, upright, thick blades, calcareous, and encrusting; 4) texture, categorized into soft, fleshy-wiry, leathery, and stony; 5) size, categorized into four levels from <0.03 to >10 cm. Seaweed traits such as thalli growth type, degree of branching, external morphology and texture may influence associated fauna assemblages by affecting microhabitat's physical properties and resource distribution (Gallardo et al., 2021; Gutiérrez et al., 2022). These traits determine the structural complexity of seaweeds, which provide different habitats and refuges for peracarids, thereby influencing their diversity and abundance. Functional traits related to the productivity and decomposition of seaweeds (e.g., size) may alter the detrital food web dynamics (Vilas et al., 2020), thus impacting the feeding groups and functional diversity of peracarid communities. For peracarids, traits adapted from Ashford et al. (2018) were used (Supplementary Material, Table 1): 1) Maximum adult length, in millimeters, divided into five modalities; 2) Maximum fecundity (i.e., number of eggs), also divided into 5 modalities; 3) Feeding group (i.e., Deposit feeder, Suspension feeder, Active predator (including grazing), Scavenger, Parasitic); 4) Habitat space, the location relative to the substrate of the organism (i.e., Infaunal, Epibenthic, Epibiotic-benthic); 5) Living habit, (i.e., Free, Tube/burrow dweller, Parasite/direct commensal); 6) Motility (i.e., Fast swimmer, Slow swimmer/crawler, Crawler/limited swimmer, Crawler-no swim, Burrower); 7) Bioturbation/sediment transport potential (i.e., Limited, Low-level incidental diffusive mixing, Active significant sediment transport); 8) Sociability (i.e., Solitary, Gregarious). The predation was classified similarly for carnivores and herbivores (i.e., ignoring the identity of the prey) as ecologically they are similar (i.e., reducing the number of preys). Functional traits such as maximum adult length and fecundity influence peracarids' reproductive success and population dynamics in seaweed habitats while feeding strategies indicate their ecological roles and reliance on seaweed-derived resources. Traits related to habitat use and living habits delineate how peracarids occupy ecological niches potentially shaped by seaweed characteristics. Their motility and bioturbation abilities further influence interactions with sediment and organisms, thereby shaping community structure. Additionally, sociability traits impact peracarid interactions and resource utilization within seaweed environments. These traits collectively define how peracarids interact with seaweeds and contribute to ecosystem dynamics in marine habitats. The degree to which each taxon displayed each of these characteristics was then assessed using a "fuzzy coding" procedure (Chevene et al., 1994). To account for intraspecific variations in trait expression (Castella and Speight, 1996; Charvet et al., 2000), fuzzy coding enables taxa to exhibit trait categories to varying degrees (Chevene et al., 1994). A scale of 0–3, with 0 representing no affinity to a trait category and 3 representing absolute affinity, was chosen.

2.4. Data analysis

Based on the abundance dataset, a matrix (samples x species) was constructed for both taxa (combined), only seaweed and another for peracarids, with a total of 320 seaweed and 80 peracarids. To assess biogeographic ecoregions based on presence-absence dataset, a cluster analysis using UPGMA (unweighted pair group method using arithmetic averages), based on Jaccard's similarity index was done. To choose the optimal number of clusters (or K-means), the so-called "Elbow method" was used (Aggarwal and Sharma, 2019). The analyses were performed (*hclust* function) and visualized in R with the packages "cluster" v.2.1.4. (Maechler, 2018), "vegan" v. 2.6.4 (Oksanen, 2017) and "stats'' v.4.3.0 (R core team 2020) as default. To assess the functional space occupied by the organisms found, a Fuzzy Principal Component Analysis (FPCA) was performed for both the seaweeds and the peracarids separately using the function *dudi.fpca* of the package "ade4" v.1.7.22 (Dray and Dufour, 2007). For the seaweeds, functional groups were estimated using the function *dbFD* and kmeans of the package "FD" v.1.0.12.3 (Laliberté and Legendre, 2010). To evaluate if the number of functional traits affects the quality of functional space, we followed the methodology outlined by Maire et al. (2015). Initial functional distances using Gower's distance were calculated and a Principal Coordinates Analysis (PCoA) was carried out to provide a multidimensional representation of the data, with distances standardized to the maximum value of the initial distance matrix in the functional space. The congruence between these initial and standardized distances was assessed using the mean squared deviation (mSD) metric, where lower mSD values indicate better alignment of the original trait-based distances in the functional space.

The relationships between taxonomic and functional diversity were assessed by a Redundancy Analysis (RDA) (*rda* function) using the package 'vegan' (Oksanen, 2017). We employed the Bray Curtis dissimilarity coefficient to illustrate both taxonomic and functional beta diversities (referred to as Btotal), along with their corresponding replacement (Brepl) and richness difference (Brich) components. All components of beta diversity were calculated using the 'beta' function within the R package BAT (Cardoso et al., 2015). In addition, the relation between taxonomic and functional richness was examined using a linear regression model (*lm* function) from the R package "stats" (version 4.3.0, R Core Team, 2020). The variation in seaweed assemblage composition along spatial and environmental gradients, as well as, the variation in peracarid assemblage composition along seaweed traits were modelled using Generalized Dissimilarity Modelling (GDM; Ferrier et al., 2007) using the dissimilarity matrices of beta diversity components (i.e. total, replacement, and richness) for the diversity facets (taxonomic and functional) as response matrices. While other statistical assessments of pairwise dissimilarities (e.g., Mantel test, nMDS) in which the difference between pairs is related linearly to differences in space or environment, GDM can handle the nonlinearities common in eco-geographical datasets. Variables such as aragonite saturation, mean precipitation, insolation, minimum SST, and mean and minimum chla were removed after multicollinearity testing, using Pearson correlation coefficient (i.e., correlation >0.7) as indicated by Dormann (2012). For seaweeds only environmental and climatic predictors were used, while for peracarids also the RDA axes (i.e., axes explaining more than 1%) of seaweeds were included as predictors (i.e., their loadings). The functions *gdm* and *gdm.varImp* in the package "gdm" v.1.5.0.9.1 of R (Fitzpatrick et al., 2020). were used to run GDM models and plot the I-splines (i.e. monotone cubic spline functions) to evaluate the impact of predictor variables on the total, replacement, and richness components of taxonomic and functional dissimilarity matrices. Null model testing was used to assess the significance of the observed patterns by comparing them to patterns generated under random or null hypotheses.

3. Results

A total of 12,654 specimens were sorted and examined, out of which more than 74% were seaweeds. In this study, 320 species of seaweeds were identified, 61% of Rhodophyta, 19% of Chlorophyta, and 20% of Ochrophyta. As well, 80 different species of peracarids were found, of which 62 % were Amphipoda, 31 % were Isopoda, and 7 % were Tanaidacea.

For the combined dataset, three main sampling station clusters were differentiated with a 0.6 dissimilarity threshold (Fig. 2). One included the northern European coasts of Iceland, Norway and Scotland (stations 1 to 9, except station 6), a second included the Iberian Peninsula coast (stations 10 to 18) and a third with Macaronesia coasts of Madeira and Canary Islands (stations 19 to 27). Seaweeds showed similar clustering (Fig. 2), nevertheless, it is worth highlighting that stations 6 in Norway and 14 in Portugal did not group to any cluster according to this dissimilarity threshold. The results for peracarids also showed a clustering into three biogeographical regions, however, stations in southern Portugal (stations 16 to 18) presented a species composition more similar to the Macaronesian stations than to the rest of the Iberian Peninsula (Fig. 2).

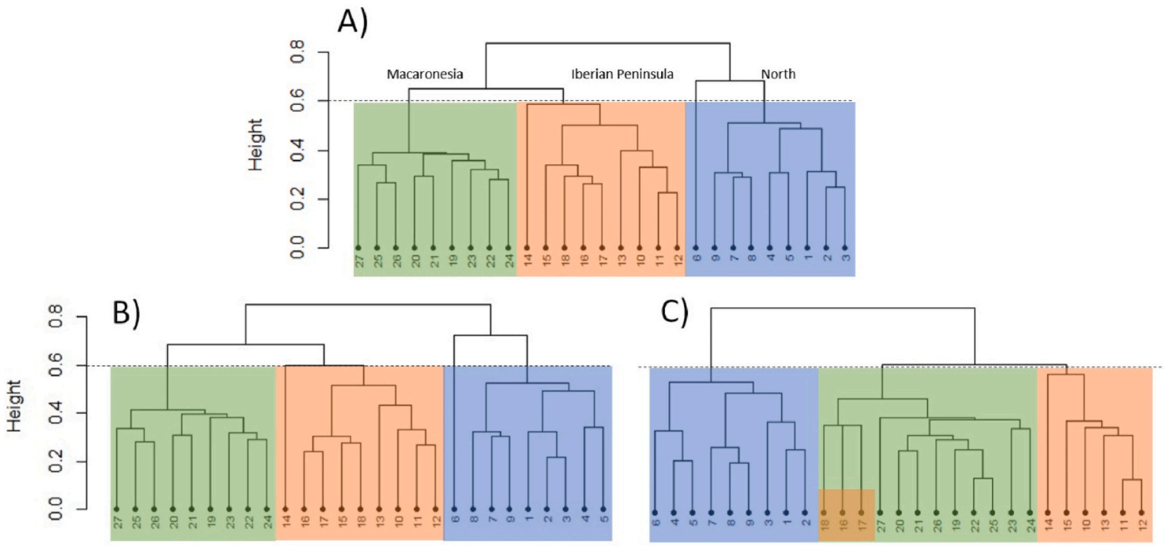

Fig. 2. Dendrogram of UPGMA cluster analysis of sampling stations for a) combined dataset (up), b) seaweeds (down left) and c) peracarids (down right). Colours represent the different biogeographic regions: North (blue), Iberian Peninsula (orange) and Macaronesia (green). The dotted line marks the dissimilarity threshold.

3.1. Functional space

The seaweed species were divided into 5 functional groups according to their traits (Fig. 3A). The traits contributing most to the first axis (FPC1), capturing 32.5% of the variation, were the degree of branching (DB2 and 3), soft and fleshy wiry textures (TX1 and 2)), apical growth (TG1) and delicately branched morphology (EM2). The second axis (FPC2) captured 13.4% of the variation in function trait space and the traits that contributed the most were the size (S4 and 2). In addition, the third axis (FPC3) captured 12.5% of the variation and was mainly driven by low branching (DB2) (Supplementary Material, Table 2A). Despite the overlapping positions of some genera, such as *Ulva*, most seaweed orders occupied distinct regions of trait space. In the FPCA (Fig. 3), “Canopy Formers” (functional group 2) was distinguished mainly by brown seaweeds of the Laminariales, Fucales and Gigartinales orders, characterized by soft texture, foliose morphology and low branching. “Large Ceramiales” (functional group 1),” Medium Ceramiales” (functional group 4) and “Small Ceramiales” (functional group 5) were characterised by red seaweeds of the Ceramiales order, distinguished by a fleshy wiry texture, high degree of branching and hair-like morphology. The “Mixed Traits” group (functional group 3) includes a mixture of species from different orders marked by diverse traits and overlaps with the other functional groups. For peracarids, the family level was utilized and represented according to their traits (Fig. 3B). Nevertheless, the FPCA did not reveal any clearly defined clustering. The traits with the greatest contribution to the first axis (FPC1) included solitary (S.so), burrow dweller (Lh.tb), gregarious (S.li), and epibiotic (H.eb), explaining 30.5% of the variation. The second axis (FPC2) accounted for 17.6% of the variation in the functional trait space, with major contributions from burrow dweller (Lh.tb), free (Lh.f), and crawler (M.c) behaviour. Additionally, the third axis (FPC3) captured 10.8% of the variation and was primarily influenced by low fecundity (i.e., F.l, Supplementary Material, Table 2B). While the families of the order Amphipoda were distributed across the entire functional space, those belonging to the Tanaidacea order (Leptocheliidae, Leptognathiidae, Apseudidae) were distinguished by positive values along the first axes (FPC1) and were infaunal, burrower-dwelling organisms. The Isopoda order (Munnidae, Joeropsididae, Janiridae, Sphaeromatidae families), on the other hand, was primarily differentiated by negative values along the second axes (FPC2) and were epibenthic, free-living organisms with crawler motility. The species corresponding to each group are listed in Table 3 of the Supplementary Material. Furthermore, low mSD values (0.002 for seaweed and 0.001 for peracarids) indicated a high quality of functional space, according to the number of traits selected.

3.2. Community analysis

The RDA (Fig. 4) explored the relationship between the species assemblages for seaweed and peracarids, with their corresponding traits. Based on the significance of the models (p-value <0.05) we can conclude that the ordination was not arbitrary. For seaweed, the functional traits represented by the constrained inertia significantly explained 25% of the total correlation. The RDA reflected the geographic structure of the biota, grouping them into the three regions sampled: North, Iberian Peninsula and Macaronesia (Fig. 2). The variables positively correlated (>0.5) with the first axis of variation, which explained 8.9% of the total variance, included fleshy-wiry texture (TX2) and small size (S2) distinguishing the Macaronesia region. Conversely, marginal thalli growth (TG4), leathery texture (TX3) and large size (S4) traits were negatively correlated (<-0.5) and differentiated the North region. The second axis, explaining 5.3% of the total variance, was mostly correlated with thick blades (EM4) (-0.58) and high branching (DB3) (0.44), separating the North from the Iberian Peninsula. The third axis explained only 1.9% of the total variance and was negatively correlated (-0.48) with the delicately branched trait (EM2) (Supplementary Material; Table 3A).

The constrained inertia representing the functional traits for peracarids explained 71% of the total correlation. Despite a less distinct illustration of the geographical structure, spatial differentiation was evident across the three studied regions. Traits such as high fecundity (F.h), scavenger feeding (Fg.s), fast swimming (M.fs), crawling (Mss) and epibiotic habits (H.eb) showed negative correlations (<-0.60), while burrowing (M.b) exhibited a positive correlation (0.84) to the first axis of variation, accounting for 18% of the total variance. On the second axis, which accounts for 13.4% of the total variance, active predation (Fg.ap), suspension feeding (Fg.sf) and parasitic behavior (Lh.p) (0.58, -0.60 and -0.73, respectively) were the functional traits showing the strongest correlation. The third axis was positively correlated (0.87) with parasitism (Fg.p) and explained 7% of the total variation (Supplementary Material; Table 3B).

The GDMs for seaweed explained more than 40% of the total dissimilarity for taxonomic and functional diversity (~58 and 45 respectively) (Fig. 5A1). The same pattern but with lower values was found in the richness (~22 and ~21 for taxonomic and functional

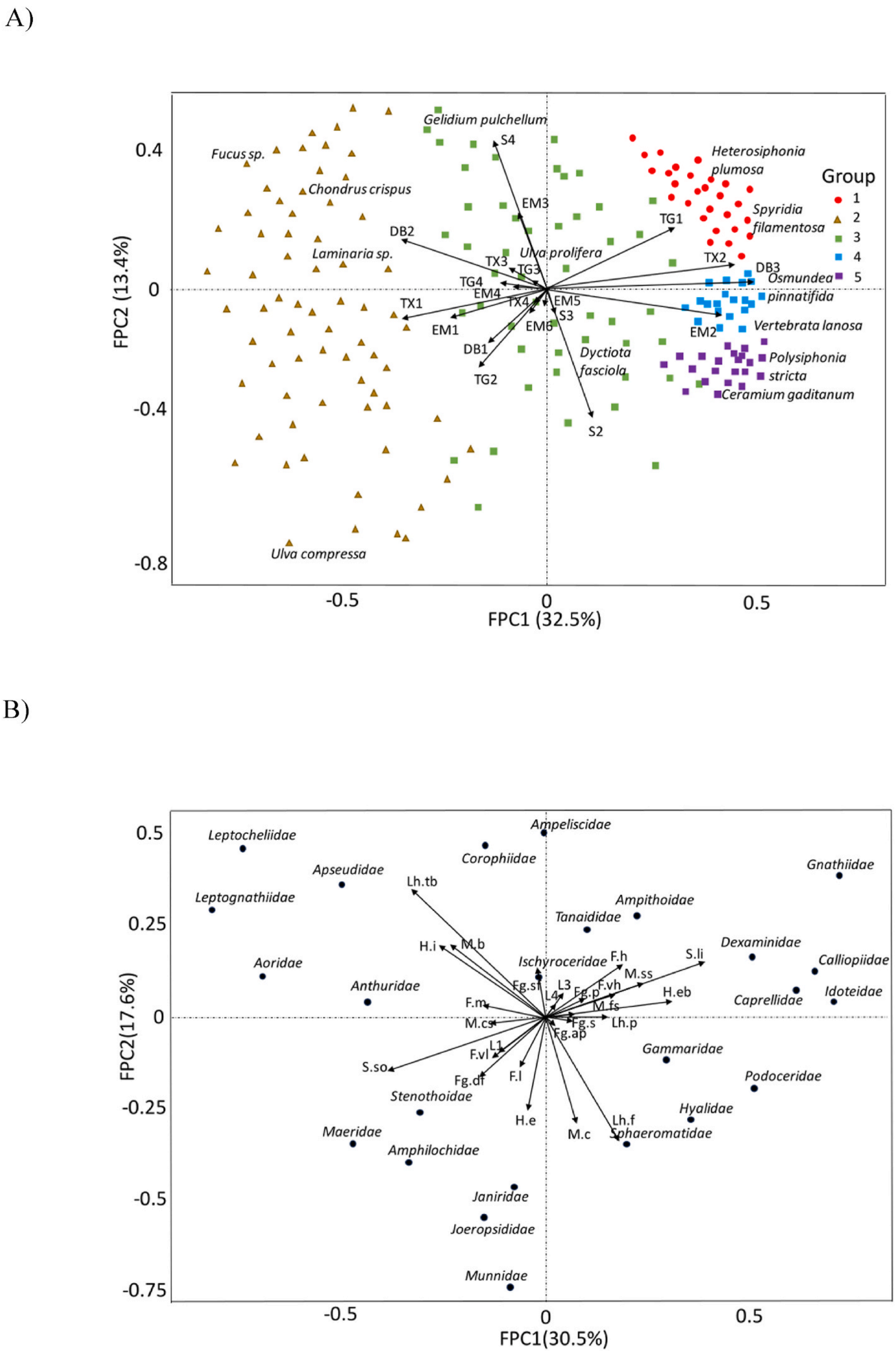

Fig. 3. Fuzzy Principal Component Analysis of the traits of seaweeds (A) and peracarids (B). Points displaying the position of each species (for seaweeds) or family (for peracarids) in their functional space. Vectors showing the correlation of each trait with the functional space. Ellipses in A showing the 95% confidence intervals. Colours in A) refers to the different functional groups.

respectively) (Fig. 5A2) and replacement (~17 and ~14 for taxonomic and functional respectively) (Fig. 5A3). For every GDM, the relationship between observed compositional dissimilarity of each pair of samples and the predictor of the regression equation was increasingly monotonic and, in some cases, linear (Fig. 5B). For the total dissimilarity, the greatest degree of compositional change occurred along the pH gradient in the functional diversity and the geographic distance in the taxonomic diversity with a marked increase after the 20° (Fig. 5C1). The pH was the only significant predictor for both taxonomic and functional richness (Fig. 5C2). In the replacement, SST max was the most important predictor for the functional diversity, while pH was for the taxonomic showing a slight increase at the end of the gradient (after pH 8.15). The curves followed a logistic increment reaching a plateau before half of the gradient for the total (only functional) and richness (functional and taxonomic) (Fig. 5C1-2) but, reached the plateau at the end of the gradient for the replacement (Fig. 5C3). The pH was significant for the three facets of biodiversity studied, total (only functional), richness (functional and taxonomic) and replacement (only taxonomic) (Fig. 5. C1). The geographic distance was shown to be significant for the total (functional and taxonomic) beta diversity (Fig. 5.C2), while the SST max was the only significant predictor for the replacement (functional) (Fig. 5.C3). The I-splines of non-significant predictors included in the

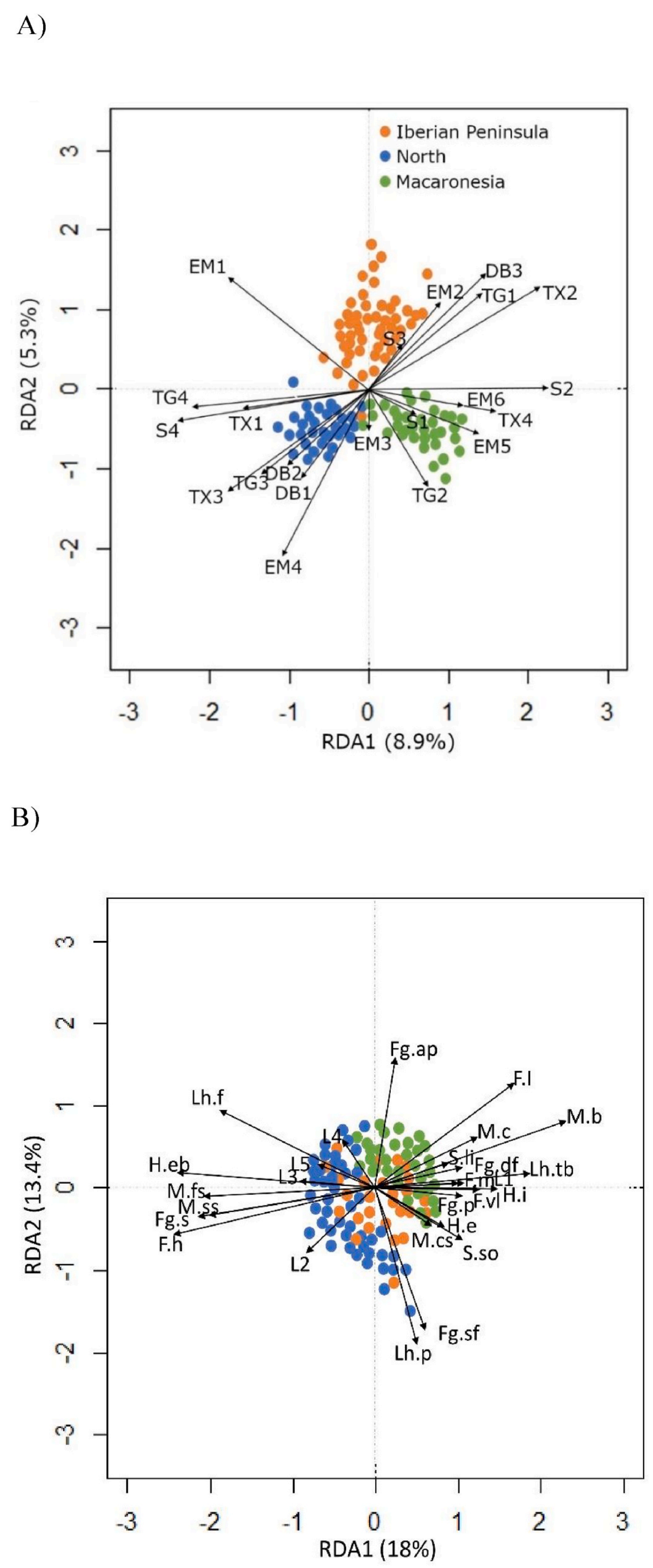

Fig. 4. Results of the RDA showing the relationship between species assemblages and their functional traits (arrows) along the first two axes for A) seaweed and B) peracarids. Colours represent the three ecoregions sampled.

model are displayed in the Supplementary Material (Fig. 1A).

For peracarid assemblages, the GDMs accounted for 45 and 44 of the total dissimilarity for taxonomic and functional diversity, respectively (Fig. 6A1). The replacement showed the same pattern but with lower values (25 and 23 for taxonomic and functional, respectively) (Fig. 6A3), whereas in the richness the functional diversity explained more of the dissimilarity than the taxonomic (15 and 16 for taxonomic and functional, respectively) (Fig. 6A2). Every GDM exhibited an increasing monotonic and, in most cases, linear relationship between the predictor of the regression equation and the observed compositional dissimilarity of each pair of samples (Fig. 6B). The functional and taxonomic diversity along the RDA2 gradient, mostly characterised by highly branched seaweeds (DB3) (positively) and thick blades (EM4) (negatively) (Supplementary Material, Table 4), displayed the greatest degree of compositional change for the total dissimilarity. Geographical distance had a significant impact on total taxonomic and functional diversity beyond 20°. Taxonomic diversity followed a sigmoidal curve along RDA1, negatively represented by marginal thalli growth, leathery texture and large size (TG4, TX3 and S4), and positively represented by fleshy-wiry texture and small size (TX2 and S2) (Supplementary Material, Table 4) (Fig. 6C1). Seaweed traits (RDA2 and RDA3) emerged as the only significant predictor for both taxonomic and functional richness of peracarids. RDA2 significantly increased from zero, while RDA3, negatively represented by delicately branched (EM2) and positively by stony texture (TX4)) (Supplementary Material, Table 4), exhibited a slight increase from −0.2 (Fig. 6C.2).

RDA1 was the most important predictor of functional and taxonomic diversity in the replacement, with the latter explaining more dissimilarity and a higher increase at positive RDA1 values. Geographic distance (for taxonomic and functional diversity) showed a significant increase after 20° (Fig. 6.C3). The I-splines of non-significant predictors included in the model are displayed in the Supplementary Material (Fig. 1B).

4. Discussion

Our study shows how even over large geographical scales the functional traits of seaweeds are the main drivers of the associated peracarids and their traits. The climatic variables are shaping the diversity of the seaweeds supporting the distinction in three different ecoregions for the NE Atlantic coasts. The strong latitudinal gradient is also correlated with the change in the function and structure of the intertidal communities shaping the complexity of the habitat formers (i.e., seaweeds), resulting in traits supporting a more interstitial life habit and more generalist niche in general. This intricate relationship between seaweeds and peracarids highlights the importance of functional traits in understanding and predicting the responses of intertidal ecosystems to environmental changes.

Based on the sampling design and the cluster analysis (Fig. 2), we identified three distinct ecoregions according to the taxonomic distribution of seaweeds and peracarids: Northern Europe, the Iberian Peninsula, and Macaronesia. These findings are consistent with earlier studies conducted by Spalding et al. (2007) and Alvarez et al. (1988), with some discrepancies observed for Norway, Scotland, and Iceland. Notably, Almada et al. (2013) and Vieira et al. (2022) proposed a differentiation between the Iberian Peninsula and Macaronesia based on fish and peracarids, respectively, a classification that aligns with our results on seaweeds. However, a nuanced perspective emerges when considering peracarids, which reveals a greater similarity between the stations in southern Portugal and Macaronesia, contrary to the anticipated divergence. Pereira et al. (2006) and Ardré (1971) emphasized the geographical distinctions in crustacean and seaweed assemblages between the Iberian Peninsula and Macaronesia. However, they included the idea that the Iberian Peninsula functions as a transition zone, facilitating the coexistence of warm-water and cold-water species along the continental Portuguese coast. This could explain the similarity found in

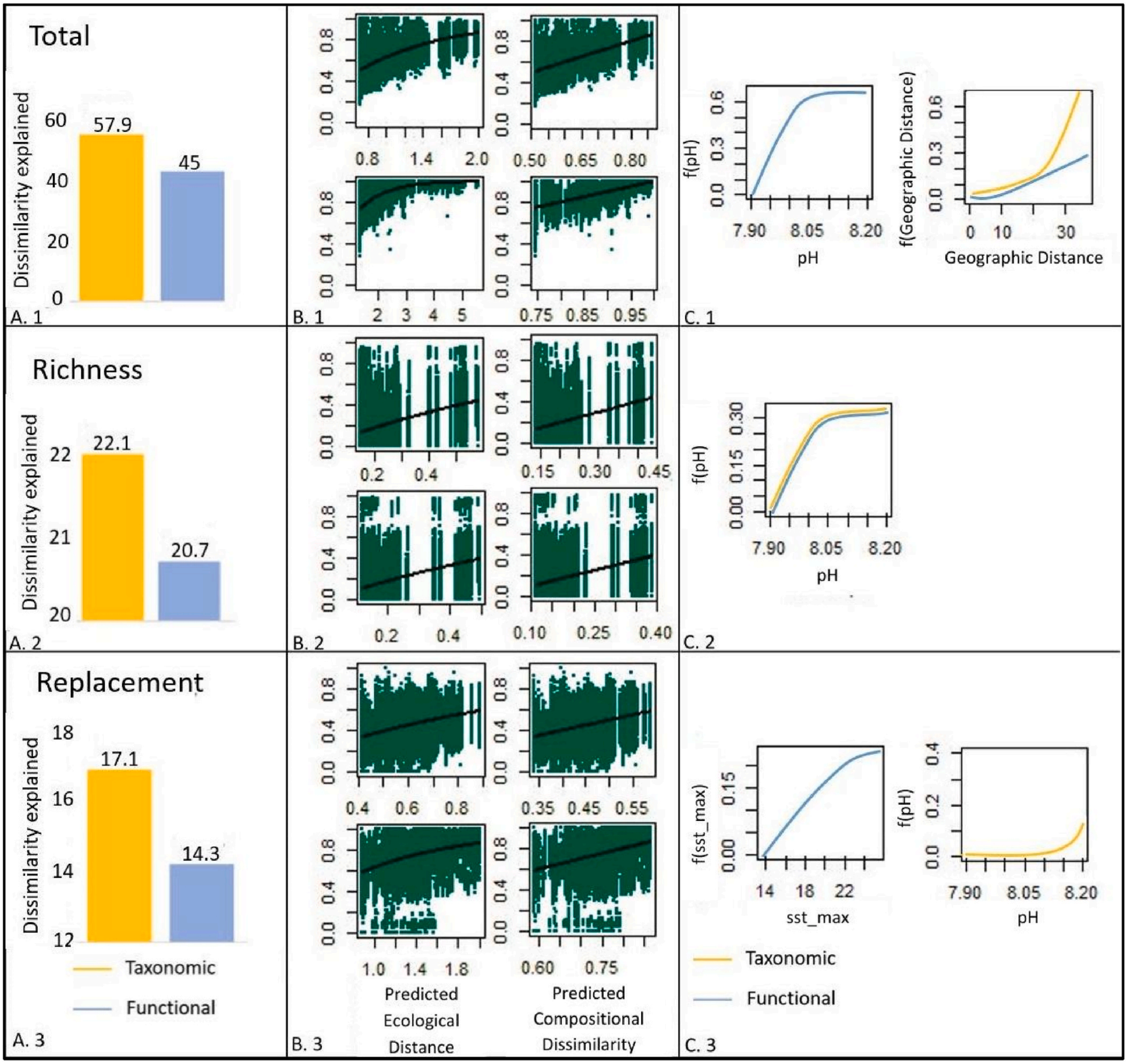

Fig. 5. Results of the GDMs for seaweed and environmental variables as predictors (on top). A: percentage of dissimilarity fitted by the model for the taxonomic (orange) and functional (blue) diversity for each level of beta diversity (Total, Richness and Replacement, 1-2-3 respectively). B: on the left, scatter plot of observed compositional dissimilarity of each community pair and the linear predictor of the regression equation from GDM (predicted ecological distance between pairs of sampling points). On the right, scatter plot reflecting the general agreement between observed and calculated values of dissimilarity. For both, from the top results for taxonomic and functional beta diversity. C: I-splines of the predicted ecological distance explained by the value of the significant variables (p-value<0.05) for each diversity (different colours). The maximum height reached by each curve indicates the total amount of compositional turnover associated with that variable and its relative importance in explaining beta diversity.

peracarid composition between Southern Portugal and Macaronesia. Our findings emphasize the complexity of biogeographic patterns in the NE Atlantic, indicating that factors beyond those associated with latitude may contribute to the observed distribution patterns, likely influencing biodiversity.

To understand the global mechanisms underlying biodiversity responses to environmental change, functional trait analysis has been suggested (Liu et al., 2019). Similar to the variation in taxonomic distribution and composition, the variation in biological traits distribution we found can be partly attributed to latitude. The FPCA and RDA (Figs. 3 and 4) show region differentiation, with large brown seaweeds (mainly Lamiraliales, Gigartinales, Fucales) dominating, alongside Isopoda peracarids in the north, and smaller red seaweeds with calcareous crusts, Tanaidacea peracarids in Macaronesia. The Iberian Peninsula acts as a transition zone with diverse seaweed groups (Chlorophyta, Rodophyta, Ochrophyta) and Amphipoda peracarids, the most abundant group across all regions. For seaweeds, the RDA (Fig. A) showed that the first three axes explained a limited proportion of the variation (16.1% in total), indicating that seaweed distribution is likely influenced by other factors (e.g. environmental variables) beyond the functional traits.

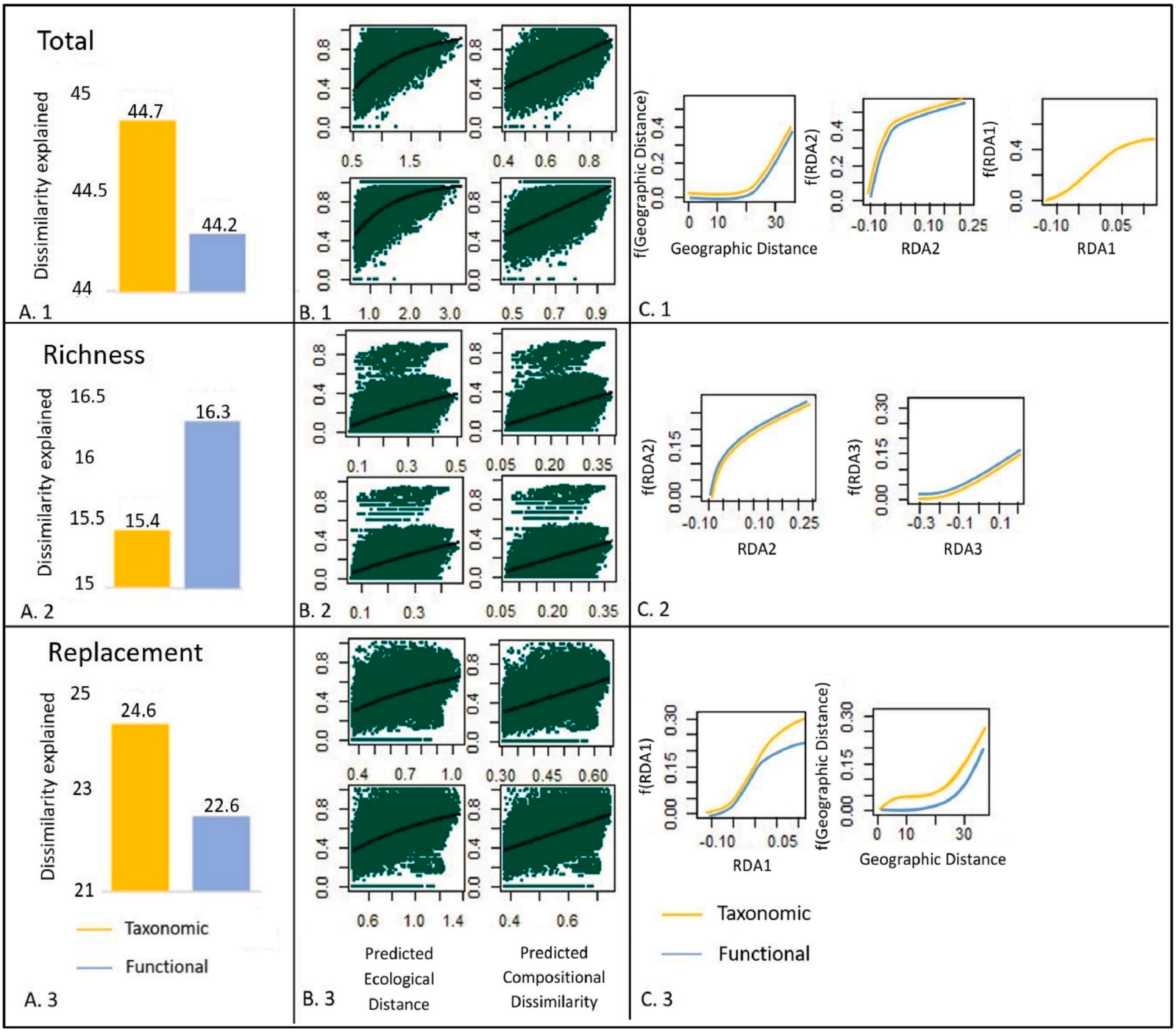

Fig. 6. Results of the GDMs for peracarids with seaweed traits and environmental variables as predictors. A: percentage of dissimilarity fitted by the model for the taxonomic (orange) and functional (blue) diversity for each level of beta diversity (Total, Richness and Replacement, 1-2-3 respectively). B: on the left, scatter plot of observed compositional dissimilarity of each community pair and the linear predictor of the regression equation from GDM (predicted ecological distance between pairs of sampling points). On the right, scatter plot reflecting the general agreement between observed and calculated values of dissimilarity. For both, from the top results for taxonomic and functional beta diversity. C: I-splines of the predicted ecological distance explained by the value of the significant variables (p-value<0.05) for each diversity (different colours). The maximum height reached by each curve indicates the total amount of compositional turnover associated with that variable and its relative importance in explaining beta diversity.

Additionally, peracarids exhibit a segregation of functional traits (Supplementary material; Table 2B) indicating a high functional variability between communities. This global seaweed distribution pattern, where brown seaweeds dominate temperate and arctic zones, red seaweeds exhibit increased abundance from the poles to the tropics, and green seaweeds show high variability, has been reported before (i.e., Santelices et al., 2009). Gaspar et al. (2017) observed a similar latitudinal variation along the Portuguese coast, noting an increase in thick leathery morpho-functional groups in the north as fleshy and calcareous structures were more abundant in the south. Concerning peracarids, temperature might be one of the drivers shaping their distribution as suggested by Izquierdo and Guerra-García (2011) for the Iberian Peninsula. However, their affinity for different morpho-functional groups of seaweeds may be more relevant. For instance, the preference of Idotea genus species for brown seaweeds, particularly *Fucus* sp (Leidenberger et al., 2012). Isopods' preference for large brown seaweeds such as Kelps, has been mainly attributed to their stronger attachment to these seaweeds (Starko et al., 2016), while the association of tanaids to corallinae turf mats, may be linked to sediment trapping (Bueno et al., 2016). Although additional research on peracarid preferences for seaweed traits is needed, our results imply that peracarid distribution, beyond latitude, may be associated with various morpho-functional seaweed groups.

One of the central macroecological and biogeographical patterns that have been thoroughly investigated (Willig et al., 2003; Mittelbach et al., 2007) is the latitudinal gradient of diversity. Numerous investigations validate the observed increase in species richness from polar to tropical regions (Brown and Lomolino 1998; Willig et al., 2003) with some exceptions (Pyron and Burbrink, 2009). Beta diversity and the geographic turnover of species composition have received far less study. Nonetheless, it seems that another common characteristic of the latitudinal gradient of diversity is a higher beta diversity in the tropics (Wang et al., 2009; Kraft et al., 2011). Our findings underscore a noteworthy influence of geographic distance in the total beta diversity (taxonomic and functional), highlighting the distinctiveness of seaweed and peracarid communities across a spatial gradient (Figs. 5 and 6; C1). Moreover, the high proportion of functional beta diversity (i.e., 55% for total diversity) shown in our results emphasizes the influential role of functional traits in shaping diversity within these communities. While evaluating various facets of beta diversity (taxonomic and functional) for seaweeds, geographic distance was only significant in total beta diversity, indicating the existence of other drivers independent of spatial location. GDMs for seaweed revealed pH as a significant factor explaining variations in total beta diversity (functional) and species richness (functional and taxonomic). The pH effect reached a plateau after attaining approximately 8.05, with low pH contributing to a decline in functional and taxonomic diversity (Fig. 5; C1 and C2), as previously observed in benthic communities affecting primarily calcified organisms (Teixidó et al., 2018). Various studies (Porzio et al., 2011; Peña et al., 2021) investigated the impact of acidification on seaweeds, showing a decrease in the diversity of both taxonomic and morphology groups, with a reduction of coralline seaweeds mainly calcified and turf seaweed mats as acidification increased, while specific non-calcified species gained dominance. Additionally, our results indicated maximum sea surface temperature as a significant predictor of seaweed diversity (replacement), suggesting the potential impact of heatwaves in inducing a greater loss of seaweed. This may lead to a subsequent species shift, potentially favouring the succession of fast-growing opportunistic species and, consequently, not affecting the total number of species. Hillebrand et al. (2010) investigated the effects of heat waves on macroinvertebrates, benthic diatoms, and macrophytes. They observed that while temperature had minimal impact on the overall number of species, there was a notable increase in species replacement with rising temperatures. Recently, Chaudhary and Costello (2023) revealed an inverse correlation between species richness and replacement, particularly in equatorial regions, suggesting a link to thermal stress. As highlighted by several studies (Smale and Wernberg, 2013; Wernberg et al., 2016; McPherson et al., 2021), heat waves may contribute to the decline of large canopy seaweeds and an increase in turf-forming seaweeds. Therefore, we suggest that heatwaves could lead to a regime shift from kelp forests to seaweed turfs, predominantly affecting the temperate Iberian Peninsula and the cold-temperate North ecoregions Contrary to our hypothesis, anthropogenic pressures assessed through the OHI did not significantly influence seaweed diversity patterns suggesting that at such large scale its effect is hidden by the stronger climatic and environmental variables (Supplementary Material, Fig. 1A). Nevertheless, our findings suggest that climate change, particularly global warming and acidification, may exert a more pronounced impact on these patterns compared to direct human activities (e.g., fishing, pollution, etc)

Our results (Fig. 6) indicate that seaweed functional traits played a more crucial role than environmental variables in explaining the diversity patterns of associated peracarids. Specifically, higher values of RDA2, characterized by foliose and highly branched seaweeds from the Iberian Peninsula, explained an increase in beta diversity. Conversely, the Macaronesia and North ecoregions exhibited lower diversity compared to the Iberian Peninsula, possibly attributed to the upwelling zone along the west coast of the latter ecoregion. Furthermore, the area functions as a transition zone, facilitating the coexistence of warm-water and cold-water species (Pereira et al., 2006), thereby promoting more diverse communities. Additionally, oceanic islands such as Macaronesia and Iceland tend to have fewer species due to their isolation (Costello et al., 2017), which could explain the lower beta diversity observed in these regions.

GDMs showed an increase in both functional and taxonomic beta diversity as the geographic distance expanded, aligning with the latitudinal gradient elucidated by seaweed traits in the RDA1. Lower values of RDA1, characterized by kelp-type seaweeds corresponding with the North ecoregion, explained less beta diversity of peracarids than Macaronesia (high RDA1 values), which was characterised by crustose and non-crustose calcified and highly branched red seaweeds. This finding suggests a latitudinal gradient of beta diversity of peracarids mainly correlated with the functional traits of seaweed hosts. Dworschak (2000) studied 516 taxa of decapods, observing a strong latitudinal increase in the number of species from high latitudes toward the equator in both hemispheres. Other studies (i.e. Kerswell, 2006) have found a peak of algal richness in temperate regions, decreasing toward the tropics and poles. Our results indicated that there was a rise in the species richness of peracarids as RDA2 increased, corresponding to seaweed functional traits specific to the Iberian Peninsula. Additionally, there was an increase in species richness associated with the occurrence of articulated and crustose calcareous seaweeds (RDA3), which are distinctive features of the Macaronesia region. Various studies (Adey and Hayek 2011; Chenelot et al., 2011; Adey et al., 2013) have shown that crustose coralline seaweeds host a variety of grazing and burrowing infauna, with thicker crusts hosting a greater diversity of infauna (Steneck and Paine, 1986). Anandavelu et al. (2013) studied the quantitative distribution of epifaunal communities associated with seaweeds in South Andaman. The study found that *Galaxura* sp. and *Halimeda tuna* (calcareous seaweeds) supported higher faunal density compared to other seaweeds. The diversity and abundance of the macroalgal epifauna have been linked to the structural complexity of the algal habitat in several studies (Gee and Warwick, 1994a; Veiga et al., 2014). These studies demonstrate that seaweeds with higher structural complexity host more invertebrate species, individuals, and biomass than seaweeds with lower structural complexity. Probably, the Macaronesia ecoregion characterized by small red calcareous seaweeds encrusting or articulated and the Iberian Peninsula characterized by a mix of green, red and brown with foliose morphology and highly branched hold a more diverse associated peracarid communities since their higher structural complexity. The diverse functional traits of seaweeds in these ecoregions could increase habitat complexity which may result in the reduction of competition (Marx and Herrnkind, 1985), predation (Coull and Wells, 1983; Warfe and Barmuta, 2004) and wave stress (Gregg and Rose, 1982) and, in turn, increase food resources (Orav-Kotta and Kotta, 2004). Additionally, the sediment retention capacity of seaweeds may play a crucial role in shaping the assemblage of peracarids communities of these ecoregions, characterized by tube-building, burrower mobility and deposit-feeding behaviours.

The significant impact of seaweed functional traits (RDA2) on the replacement of taxonomic and functional beta diversity, coupled with geographic distance, underscores the crucial role of seaweed functional traits in shaping the latitudinal diversity patterns of associated peracarids. This leads to a higher turnover of peracarid species and functional groups associated with small red, highly branched, and calcareous seaweeds in the Macaronesia ecoregions. This turnover could be an indirect consequence of seaweed loss due to environmental variables such as increased pH and maximum SST, as indicated by the GDMs for seaweeds. Cruz-Motta et al. (2020) studied latitudinal gradients of beta diversity for intertidal seaweeds and associated fauna, observing an increase in beta diversity primarily attributed to replacement toward the tropics. They suggested that SST gradient and spatial scale play crucial roles in explaining the latitudinal diversity gradient. Certain seaweeds are recognized as foundation species or ecosystem engineers (El-Khaled et al., 2022; Shelamoff et al., 2020), and the loss of these species is likely to lead to escalating changes in the diversity of associated communities. This aligns with various studies, such as Lilley and Schiel (2006), which demonstrated that the removal of foundational seaweed species resulted in a significant reduction in the number of invertebrate taxa.

5. Conclusion

This study examines the taxonomic distribution of intertidal seaweeds and peracarids across three ecoregions in the NE Atlantic. Similarities between peracarid communities in southern Portugal and Macaronesia challenge the anticipated divergence, emphasizing the Iberian Peninsula's transitional role. Seaweed functional traits significantly explain peracarid communities' diversity variations, challenging assumptions about peracarid diversity patterns being solely influenced by latitude. Environmental factors such as pH and SST influence seaweed diversity. This research advances our understanding of marine ecology, biogeography, and biodiversity dynamics in the NE Atlantic, with implications for conservation and management strategies amid ongoing environmental changes.

Data availability statement

The data will be made available on request.

CRediT authorship contribution statement

Javier Jiménez Herrero: Writing – original draft, Formal analysis, Data curation. **Andrea Desiderato:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Pedro Emanuel Vieira:** Writing – review & editing, Data curation. **Ana Mafalda Tavares:** Writing – review & editing, Data curation. **Henrique Queiroga:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **Rui Santos:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

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.

Data availability

Data will be made available on request.

Acknowledgments

This study received Portuguese national funds from FCT - Foundation for Science and Technology through projects UIDB/04326/2020, UIDP/04326/2020 and LA/P/0101/2020.

This work was supported by the project "DiverseShores - Testing associations between genetic 242 and community diversity in European rocky shore environments (PTDC/BIA-BIC/114526/2009 and UIDB/04326/2020)" funded by the Fundação para a Ciência e Tecnologia (FCT) under the COMPETE programme supported by the European Regional Development Fund. We thank Ragnhildur Siguedardottir for hosting our sampling mission in Iceland. We thank Bruno Bellisario for the help with statistical analyses. Thanks to FCT/MCTES are also due for financial support to CESAM (UIDP/50017/2020+UIDB/50017/2020), through national funds. FCT also supported a Ph. D. grant to P. E. V. (SFRH/BD/86536/2012). Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) provided a Ph. D. grant to A. D. (process No 141565/2017-9).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2024.106743.

References

Adey, W., Hayek, L., 2011. Elucidating marine biogeography with macrophytes: quantitative analysis of the North Atlantic supports the Thermogeographic model and demonstrates a distinct Subarctic region in the Northwestern Atlantic. Northeast. Nat. 18, 1–128. https://doi.org/10.1656/045.018.m801.

Adey, W.H., Halfar, J., Williams, B., 2013. The coralline genus *Clathromorphum* Foslie emend. Adey: biological, physiological, and ecological factors controlling carbonate production in an Arctic-Subarctic climate archive. Smithsonian Contr. Mar. Sci. 40, 1–41.

Aggarwal, D., Sharma, D., 2019. Application of clustering for student result analysis. Int. J. Recent Technol. Eng. 7 (6), 50–53.

Almada, V.C., Toledo, J.F., Brito, A., Levy, A., Floeter, S.R., Robalo, J.I., et al., 2013. Complex origins of the Lusitania biogeographic province and northeastern Atlantic fishes. Frontiers of biogeography 5 (1). https://doi.org/10.21425/F5FBG14493.

Alvarez, M., Gallardo, T., Ribera, M.A., Garreta, A.G., 1988. A reassessment of Northern Atlantic seaweed biogeography. Phycologia 27 (2), 221–223. https://doi.org/10.2216/i0031-8884-27-2-.1.

Anandavelu, I., Jayabarathi, R., Padmavati, G., Jayaraj, K.A., 2013. Epifaunal assemblage on morphologically distinct intertidal seaweeds of Kodiyaghat (South Andaman), India. Proceedings of the International Academy of Ecology and Environmental Sciences 3 (3), 229–237.

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., et al., 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecol. Lett. 14 (1), 19–28. https://doi.org/10.1111/j.1461-0248.2010.01552.x.

Ardré, F., 1971. Contribution a l'etude des algues marines du Portugal II. Ecologie et Chorologie. Bull. Cent. Études Rech. Sci. Biarritz 8, 359–574.

Arfianti, T., Costello, M., 2020. Global biogeography of marine amphipod crustaceans: latitude, regionalization, and beta diversity. Mar. Ecol. Prog. Ser. 638, 83–94. https://doi.org/10.3354/meps13272.

Arrontes, J., Anadón, R., 1990. Distribution of intertidal isopods in relation to geographical changes in macroalgal cover in the Bay of Biscay. J. Mar. Biol. Assoc. U. K. 70 (2), 283–293. https://doi.org/10.1017/S0025315400035402.

Ashford, O.S., Kenny, A.J., Barrio Froján, C.R., Bonsall, M.B., Horton, T., Brandt, A., et al., 2018. Phylogenetic and functional evidence suggests that deep-ocean ecosystems are highly sensitive to environmental change and direct human disturbance. Proceedings of the Royal Society B 285 (1884), 20180923. https://doi.org/10.1098/rspb.2018.0923.

Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E.A., De Clerck, O., 2017. Bio-ORACLE v2. 0: Extending marine data layers for bioclimatic modelling. Global Ecology and Biogeography. 27 (3), 277–284. https://doi.org/10.1111/geb.12693.

Bascompte, J., 2009. Disentangling the web of life. Science 325 (5939), 416–419. https://doi.org/10.1126/science.1170749.

Baselga, A., 2016. Partitioning abundance-based multiple-site dissimilarity into components: balanced variation in abundance and abundance gradients. Methods Ecol. Evol. 8 (7), 799–808. https://doi.org/10.1111/2041-210x.12693.

Beaugrand, G., Brander, K.M., Alistair Lindley, J., Souissi, S., Reid, P.C., 2003. Plankton effect on cod recruitment in the North Sea. Nature 426 (6967), 661–664. https://doi.org/10.1038/nature02164.

Best, R.J., Stachowicz, J.J., 2013. Phylogeny as a proxy for ecology in seagrass amphipods: Which traits are most conserved? PLoS ONE 8 (3). https://doi.org/10.1371/journal.pone.0057550.

Blanchette, C.A., Melissa Miner, C., Raimondi, P.T., Lohse, D., Heady, K.E., Broitman, B. R., 2008. Biogeographical patterns of rocky intertidal communities along the Pacific coast of North America. J. Biogeogr. 35 (9), 1593–1607. https://doi.org/10.1111/j.1365-2699.2008.01913.x.

Breeman, A., 1988. Relative importance of temperature and other factors in determining geographic boundaries of seaweeds: Experimental and phenological evidence. Helgoländer Meeresuntersuchungen 42 (2), 199–241. https://doi.org/10.1007/bf02366043.

Brierley, A.S., Kingsford, M.J., 2009. Impacts of climate change on marine organisms and ecosystems. Curr. Biol. 19 (14), R602–R614. https://doi.org/10.1016/j.cub.2009.05.046.

Briggs, J.C., 1974. Marine Zoogeography. McGraw-Hill, New York, p. 475p. Publishers.

Brown, J.L., Knowles, L.L., 2012. Spatially explicit models of dynamic histories: examination of the genetic consequences of Pleistocene glaciation and recent climate change on the American Pika. Mol. Ecol. 21 (15), 3757–3775. https://doi.org/10.1111/j.1365-294X.2012.05640.x.

Brown, J.H., Lomolino, M.V., 1998. Biogeography. *Sunderland*, MA: Sinauer, second ed.

Bueno, M., Dena-Silva, S.A., Flores, A.A.V., Leite, F.P.P., 2016. Effects of wave exposure on the abundance and composition of amphipod and tanaidacean assemblages inhabiting intertidal coralline algae. J. Mar. Biol. Assoc. U. K. 96 (3), 761–767. https://doi.org/10.1017/S002531541500123X.

Bugnot, A.B., Mayer-Pinto, M., Airoldi, L., Heery, E.C., Johnston, E.L., Critchley, L.P., et al., 2021. Current and projected global extent of marine built structures. Nat. Sustain. 4 (1), 33–41. https://doi.org/10.1038/s41893-020-00595-1.

Bulleri, F., Bruno, J., Silliman, B., Stachowicz, J., 2016. Facilitation and the niche: implications for coexistence range shifts and ecosystem functioning. Funct. Ecol. 30, 66–74. https://doi.org/10.1111/1365-2435.12528.

Buza Jacobucci, Pereira Leite, F.P., 2014. The role of epiphytic algae and different species of sargassum in the distribution and feeding of herbivorous amphipods. Latin American Journal of Aquatic Research 42 (2), 353–363. https://doi.org/10.3856/vol42-issue2-fulltext-6.

Cardoso, P., Rigal, F., Carvalho, J.C., 2015. BAT–Biodiversity Assessment Tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. Methods Ecol. Evol. 6 (2), 232–236. https://doi.org/10.1111/2041-210X.12310.

Casado-Amezúa, P., Araújo, R., Bárbara, I., Bermejo, R., Borja, Á., Díez, I., et al., 2019. Distributional shifts of canopy-forming seaweeds from the Atlantic coast of Southern Europe. Biodivers. Conserv. 28, 1151–1172. https://doi.org/10.1007/s10531-019-01716-9.

Castella, E., Speight, M.C., 1996. Knowledge representation using fuzzy coded variables: an example based on the use of Syrphidae (Insecta, Diptera) in the assessment of riverine wetlands. Ecol. Model. 85 (1), 13–25. https://doi.org/10.1016/0304-3800(95)00015-1.

Charvet, S., Statzner, B., Usseglio-Polatera, P., Dumont, B., 2000. Traits of benthic macroinvertebrates in semi-natural French streams: an initial application to biomonitoring in Europe. Freshw. Biol. 43 (2), 277–296. https://doi.org/10.1046/j.1365-2427.2000.00545.x.

Chaudhary, C., Costello, M.J., 2023. Marine species turnover but not richness, peaks at the Equator. Prog. Oceanogr. 210, 102941 https://doi.org/10.1016/j.pocean.2022.102941.

Chavanich, S., Wilson, K., 2000. Rocky intertidal zonation of Gammaridean amphipods in long island sound, Connecticut. Crustaceana 73, 835–846.

Chemello, R., Milazzo, M., 2002. Effect of algal architecture on associated fauna: some evidence from phytal molluscs. Marine biology 140, 981–990. https://doi.org/10.1007/s00227-002-0777-x.

Chenelot, H., Jewett, S.C., Hoberg, M.K., 2011. Macrobenthos of the nearshore aleutian archipelago, with emphasis on invertebrates associated with clathromorphum nereostratum (Rhodophyta, corallinaceae). Mar. Biodivers. 41, 413–424. https://doi.org/10.1007/s12526-010-0071-y.

Chevene, F., Doleadec, S., Chessel, D., 1994. A fuzzy coding approach for the analysis of long-term ecological data. Freshw. Biol. 31 (3), 295–309. https://doi.org/10.1111/j.1365-2427.1994.tb01742.x.

Christie, H., Norderhaug, K.M., Fredriksen, S., 2009. Macrophytes as habitat for fauna. Marine ecology progress series 396, 221–233. https://doi.org/10.3354/meps08351.

Cole, V.J., McQuaid, C.D., 2010. Bioengineers and their associated fauna respond differently to the effects of biogeography and upwelling. Ecology 91 (12), 3549–3562. https://doi.org/10.1890/09-2152.1.

Costello, M.J., Tsai, P., Wong, P.S., Cheung, A.K.L., Basher, Z., Chaudhary, C., 2017. Marine biogeographic realms and species endemicity. Nat. Commun. 8 (1), 1057. https://doi.org/10.1038/s41467-017-01121-2.

Coull, B.C., Wells, J.B.J., 1983. Refuges from fish predation: experiments with phytal meiofauna from the New Zealand rocky intertidal. Ecology 64 (6), 1599–1609. https://doi.org/10.2307/1937513.

Cruz-Motta, J.J., Miloslavich, P., Guerra-Castro, E., Hernández-Agreda, A., Herrera, C., Barros, F., et al., 2020. Latitudinal patterns of species diversity on South American rocky shores: local processes lead to contrasting trends in regional and local species diversity. J. Biogeogr. 47 (9), 1966–1979. https://doi.org/10.1111/jbi.13869.

Díez, I., Muguerza, N., Santolaria, A., Ganzedo, U., Gorostiaga, J.M., 2012. Seaweed assemblage changes in the eastern Cantabrian Sea and their potential relationship to climate change. Estuar. Coast Shelf Sci. 99, 108–120. https://doi.org/10.1016/j.ecss.2011.12.027.

Dinter, W.P., 2001. Biogeography of the OSPAR Maritime Area, vol. 167. Federal Agency for Nature Conservation, Bonn, Germany.

Díaz, S., Cabido, M., 2001. Vive la différence: Plant functional diversity matters to ecosystem processes. Trends in Ecology & Evolution 16 (11), 646–655. https://doi.org/10.1016/s0169-5347(01)02283-2.

Dormann, C.F., et al., 2012. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. Ecography 36 (1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

Dray, S., Dufour, A., 2007. The ade4 package: implementing the duality diagram for ecologists. J. Stat. Software 22 (4), 1–20. https://doi.org/10.18637/jss.v022.i04.

Dworschak, 2000. Global diversity in the thalassinidea (Decapoda). J. Crustac Biol. 20, 238–245.

Ekman, S., 1953. Zoogeography of the Sea. Sidgwick and Jackson, London, p. 417p. Publishers.

El-Khaled, Y.C., Daraghmeh, N., Tilstra, A., Roth, F., Huettel, M., Rossbach, F.I., et al., 2022. Fleshy red algae mats act as temporary reservoirs for sessile invertebrate biodiversity. Commun. Biol. 5, 579. https://doi.org/10.1038/s42003-022-03523-5.

Fernández, C., 2016. Current status and multidecadal biogeographical changes in rocky intertidal algal assemblages: the northern Spanish coast. Estuar. Coast Shelf Sci. 171, 35–40. https://doi.org/10.1016/j.ecss.2016.01.026.

Ferrier, S., Manion, G., Elith, J., Richardson, K., 2007. Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. Divers. Distrib. 13 (3), 252–264. https://doi.org/10.1111/j.1472-4642.2007.00341.x.

Field, C.B., Behrenfeld, M.J., Randerson, J.T., Falkowski, P., 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. science 281 (5374), 237–240. https://doi.org/10.1126/science.281.5374.237.

Fitzpatrick, M.C., Mokany, K., Manion, G., Lisk, M., Ferrier, S., Nieto-Lugilde, D., 2020. Gdm: generalized dissimilarity modeling. R package version 1.4.2. https://CRANR-project.org/package=gdm.

Gaines, S.D., Lubchenco, J., 1982. A unified approach to marine plant-herbivore interactions. II. Biogeography. Annu. Rev. Ecol. Systemat. 13 (1), 111–138.

Gallardo, D., Oliva, F., Ballesteros, M., 2021. Marine invertebrate epibionts on photophilic seaweeds: importance of algal architecture. Mar. Biodivers. 51 (1), 16. https://doi.org/10.1007/s12526-020-01151-y.

Gambi, M.C., Musco, L., Giangrande, A., Badalamenti, F., Micheli, F., Kroeker, K.J., 2016. Distribution and functional traits of polychaetes in a CO2 vent system: winners and losers among closely related species. Mar. Ecol. Prog. Ser. 550, 121–134. https://doi.org/10.3354/meps11727.

Gaspar, R., Pereira, L., Neto, J.M., 2017. Intertidal zonation and latitudinal gradients on macroalgal assemblages: species, functional groups and thallus morphology approaches. Ecol. Indicat. 81, 90–103. https://doi.org/10.1016/j.ecolind.2017.05.060.

Gaston, K.J., 2000. Global in biodiversity. Nature 405, 220–227. https://doi.org/10.1038/35012228 patterns.

Gee, J.M., Warwick, R.M., 1994. Body-size distribution in a marine metazoan community and the fractal dimensions of macroalgae. Journal of experimental marine biology and ecology 178 (2), 247–259. https://doi.org/10.1016/0022-0981(94)90039-6.

Gervais, C.R., Champion, C., Pecl, G.T., 2021. Species on the move around the Australian coastline: a continental-scale review of climate-driven species redistribution in marine systems. Global Change Biol. 27 (14), 3200–3217. https://doi.org/10.1111/gcb.15634.

Gregg, W.W., Rose, F.L., 1982. The effects of aquatic macrophytes on the stream microenvironment. Aquat. Bot. 14, 309–324. https://doi.org/10.1016/0304-3770(82)90105-X.

Grinnell, J., 1917. Field tests of theories concerning distributional control. Am. Nat. 51 (602), 115–128.

Guerra-García, J.M., Sánchez, J.A., Ros, M., 2009. Distributional and ecological patterns of caprellids (Crustacea: Amphipoda) associated with the seaweed *Stypocaulon scoparium* in the Iberian Peninsula. Marine Biodiversity Records 2, e151. https://doi.org/10.1017/S175526720999073X.

Guerra-Garcia, J.M., Cabezas, M.P., Baeza-Rojano, E., García-Gómez, J.C., 2011. Spatial patterns and seasonal fluctuations of intertidal macroalgal assemblages from Tarifa Island, southern Spain: relationship with associated Crustacea. J. Mar. Biol. Assoc. U. K. 91 (1), 107–116. https://doi.org/10.1017/S0025315410001219.

Gutiérrez, J.L., Hacker, S.D., Coombes, M.A., Wild, C., Pereira-Filho, G.H., Palomo, M.G., 2022. Marine hard substrate communities. In: Marine Biology. CRC Press, pp. 232–273.

Halpern, B.S., Longo, C., Hardy, D., McLeod, K.L., Samhouri, J.F., Katona, S.K., et al., 2012. An index to assess the health and benefits of the global ocean. Nature 488 (7413), 615–620. https://doi.org/10.1038/nature11397.

Harley, C., Randall Hughes, A., Hultgren, K., Miner, B., Sorte, C., Thornber, C., 2006. The impacts of climate change in coastal marine systems. Ecol. Lett. 9 (2), 228–241. https://doi.org/10.1890/0012-9658(2003)084[1477:ASAHIT]2.0.CO;2.

Hawkins, S.J., Sugden, H.E., Mieszkowska, N., Moore, P.J., Poloczanska, E., Leaper, R., et al., 2009. Consequences of climate-driven biodiversity changes for ecosystem functioning of North European rocky shores. Mar. Ecol. Prog. Ser. 396, 245–259. https://doi.org/10.3354/meps08378.

Hillebrand, H., Soininen, J., Snoeijs, P., 2010. Warming leads to higher species turnover in a coastal ecosystem. Global Change Biol. 16 (4), 1181–1193. https://doi.org/10.1111/j.1365-2486.2009.02045.x.

Hooper, D.U., Dukes, J.S., 2004. Overyielding among plant functional groups in a long-term experiment. Ecology Letters 7 (2), 95–105. https://doi.org/10.1046/j.1461-0248.2003.00555.x.

Huston, M.A., Wolverton, S., 2009. The global distribution of net primary production: resolving the paradox. Ecol. Monogr. 79 (3), 343–377. https://doi.org/10.1890/08-0588.1.

Iwasa-Arai, T., Siqueira, S.G., Segadilha, J.L., Leite, F.P., 2021. The unique Amphipoda and Tanaidacea (Crustacea: peracarida) associated with the brown algae Dictyota sp. from the oceanic Trindade Island, Southwestern Atlantic, with biogeographic and phylogenetic insights. Front. Mar. Sci. 8, 641236 https://doi.org/10.3389/fmars.2021.641236.

Izquierdo, D., Guerra-García, J.M., 2011. Distribution patterns of the peracarid crustaceans associated with the alga *Corallina elongata* along the intertidal rocky shores of the Iberian Peninsula. Helgol. Mar. Res. 65, 233–243. https://doi.org/10.1007/s10152-010-0219-y.

Kerswell, A., 2006. Global biodiversity patterns of benthic marine seaweeds. Ecology 87 (10), 2479–2488. https://doi.org/10.1890/0012-9658(2006)87[2479:GBPOBM]2.0.CO;2.

Kraft, N.J., Comita, L.S., Chase, J.M., Sanders, N.J., Swenson, N.G., Crist, T.O., Stegen, J. C., Vellend, M., Boyle, B., Anderson, M.J., Cornell, H.V., Davies, K.F., Freestone, A. L., Inouye, B.D., Harrison, S.P., Myers, J.A., 2011. Disentangling the drivers ofdiversity along latitudinaland elevational gradients. Science 333, 1755–1758.

Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91 (1), 299–305. https://doi.org/10.1890/08-2244.1.

Leidenberger, S., Harding, K., Jonsson, P.R., 2012. Ecology and distribution of the isopod genus Idotea in the Baltic Sea: key species in a changing environment. J. Crustac Biol. 32 (3), 359–389. https://doi.org/10.1163/193724012X626485.

Leite, F.P.P., Tanaka, M.O., Gebara, R.S., 2007. Structural variation in the brown alga Sargassum cymosum and its effects on associated amphipod assemblages. Braz. J. Biol. 67, 215–221. https://doi.org/10.1590/S1519-69842007000200006.

Leite, F.P., Bottcher, C., Lewinsohn, I.D., Siqueira, S.G., Mansur, K.F., Longo, P.A., Vieira, E.A., 2021. Asymmetric effects of changes in the habitat-forming algae Sargassum on different associated mobile faunas along São Paulo coast, Brazil. Mar. Ecol. 42 (3), e12649 https://doi.org/10.1111/maec.12649.

Lilley, S.A., Schiel, D.R., 2006. Community effects following the deletion of a habitat-forming alga from rocky marine shores. Oecologia 148, 672–681. https://doi.org/10.1007/s00442-006-0411-6.

Littler, M.M., Littler, D.S., 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: Field and laboratory tests of a functional form model. The American Naturalist 116 (1), 25–44. https://doi.org/10.1086/283610.

Littler, M.M., Littler, D.S., 1984. Relationships between macroalgal functional form groups and substrata stability in a subtropical rocky-intertidal system. J. Exp. Mar. Biol. Ecol. 74 (1), 13–34. https://doi.org/10.1016/0022-0981(84)90035-2.

Liu, K., Lin, H., He, X., Huang, Y., Li, Z., Lin, J., et al., 2019. Functional trait composition and diversity patterns of marine macrobenthos across the Arctic Bering Sea. Ecol. Indicat. 102, 673–685. https://doi.org/10.1016/j.ecolind.2019.03.029.

Liuzzi, M.G., López Gappa, J., Piriz, M.L., 2011. Latitudinal gradients in macroalgal biodiversity in the Southwest Atlantic between 36 and 55 S. Hydrobiologia 673, 205–214. https://doi.org/10.1007/s10750-011-0780-7.

Maechler, M., 2018. Cluster: cluster analysis basics and extensions. R package version 2 (0), 7, 1.

Maire, E., Grenouillet, G., Brosse, S., Villéger, S., 2015. How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. Global Ecol. Biogeogr. 24 (6), 728–740. https://doi.org/10.1111/geb.12299.

Martínez, B., Viejo, R.M., Carreño, F., Aranda, S.C., 2012. Habitat distribution models for intertidal seaweeds: responses to climatic and non-climatic drivers. J. Biogeogr. 39 (10), 1877–1890. https://doi.org/10.1111/j.1365-2699.2012.02741.x.

Martínez, B., Radford, B., Thomsen, M.S., Connell, S.D., Carreño, F., Bradshaw, C.J., et al., 2018. Distribution models predict large contractions of habitat-forming seaweeds in response to ocean warming. Divers. Distrib. 24 (10), 1350–1366. https://doi.org/10.1111/ddi.12767.

Marx, J., Herrnkind, W., 1985. Factors regulating microhabitat use by young juvenile spiny lobsters, Panulirus argus: food and shelter. J. Crustac Biol. 5 (4), 650–657. https://doi.org/10.2307/1548242.

McPherson, M.L., Finger, D.J., Houskeeper, H.F., Bell, T.W., Carr, M.H., Rogers-Bennett, L., Kudela, R.M., 2021. Large-scale shift in the structure of a kelp forest ecosystem co-occurs with an epizootic and marine heatwave. Commun. Biol. 4 (1), 298. https://doi.org/10.1038/s42003-021-01827-6.

Mineur, F., Arenas, F., Assis, J., Davies, A.J., Engelen, A.H., Fernandes, F., et al., 2015. European seaweeds under pressure: consequences for communities and ecosystem functioning. J. Sea Res. 98, 91–108. https://doi.org/10.1016/j.seares.2014.11.004.

Mittelbach, G.G., Schemske, D.W., Cornell, H.V., Allen, A.P., Brown, J.M., Bush, M.B., et al., 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecol. Lett. 10 (4), 315–331. https://doi.org/10.1111/j.1461-0248.2007.01020.x.

Ockendon, N., Baker, D.J., Carr, J.A., White, E.C., Almond, R.E., Amano, T., et al., 2014. Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. Global Change Biol. 20 (7), 2221–2229. https://doi.org/10.1111/gcb.12559.

Oksanen, J., 2017. Vegan: an introduction to ordination. Retrieved from. https://cran.r-project.org/package=vegan.

Orav-Kotta, H., Kotta, J., 2004. Food and habitat choice of the isopod Idotea baltica in the northeastern Baltic Sea. Hydrobiologia 514, 79–85. https://doi.org/10.1023/B:hydr.0000018208.72394.09.

Page, T.J., Hughes, J.M., Real, K.M., Stevens, M.I., King, R.A., Humphreys, W.F., 2018. Allegory of a cave crustacean: systematic and biogeographic reality of Halosbaena (Peracarida: thermosbaenacea) sought with molecular data at multiple scales. Mar. Biodivers. 48, 1185–1202. https://doi.org/10.1007/s12526-016-0565-3.

Peña, V., Harvey, B.P., Agostini, S., Porzio, L., Milazzo, M., Horta, P., et al., 2021. Major loss of coralline algal diversity in response to ocean acidification. Global Change Biol. 27 (19), 4785–4798. https://doi.org/10.1111/gcb.15757.

Pereira, S.G., Lima, F.P., Queiroz, N.C., Ribeiro, P.A., 2006. Biogeographic patterns of intertidal macroinvertebrates and their association with macroalgae distribution along the Portuguese coast. Hydrobiologia 555, 185–192. https://doi.org/10.1007/s10750-005-1115-3.

Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9 (6), 741–758.

Pinsky, M.L., Selden, R.L., Kitchel, Z.J., 2020. Climate-driven shifts in marine species ranges: scaling from organisms to communities. Ann. Rev. Mar. Sci 12, 153–179. https://doi.org/10.1146/annurev-marine-010419-010916.

Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P. J., et al., 2013. Global imprint of climate change on marine life. Nat. Clim. Change 3 (10), 919–925. https://doi.org/10.1038/nclimate1958.

Pörtner, H.O., Knust, R., 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. Science 315 (5808), 95–97. https://doi.org/10.1126/science.1135471.

Porzio, L., Buia, M.C., Hall-Spencer, J.M., 2011. Effects of ocean acidification on macroalgal communities. Journal of experimental marine biology and ecology 400 (1–2), 278–287. https://doi.org/10.1016/j.jembe.2011.02.011.

Pyron, R.A., Burbrink, F.T., 2009. Can the tropical conservatism hypothesis explain temperate species richness patterns? An inverse latitudinal biodiversity gradient in the New World snake tribe Lampropeltini. Global Ecol. Biogeogr. 18 (4), 406–415. https://doi.org/10.1111/j.1466-8238.2009.00462.x.

Qian, H., Ricklefs, R.E., 2007. A latitudinal gradient in large-scale beta diversity for vascular plants in North America. Ecol. Lett. 10 (8), 737–744. https://doi.org/10.1111/j.1461-0248.2007.01066.x.

Richardson, A.J., Schoeman, D.S., 2004. Climate impact on plankton ecosystems in the Northeast Atlantic. Science 305 (5690), 1609–1612. https://doi.org/10.1126/science.1100958.

Robin South, G., 1987. Biogeography of the benthic marine algae of the North Atlantic Ocean—an overview. Helgoländer Meeresuntersuchungen 41, 273–282. https://doi.org/10.1007/BF02366192.

Sangil, C., Sansón, M., Clemente, S., Afonso-Carrillo, J., Hernández, J.C., 2014. Contrasting the species abundance, species density and diversity of seaweed assemblages in alternative states: urchin density as a driver of biotic homogenization. J. Sea Res. 85, 92–103. https://doi.org/10.1016/j.seares.2013.10.009.

Sangil, C., Martins, G.M., Hernández, J.C., Alves, F., Neto, A.I., Ribeiro, C., et al., 2018. Shallow subtidal macroalgae in the North-eastern Atlantic archipelagos (Macaronesian region): a spatial approach to community structure. Eur. J. Phycol. 53 (1), 83–98. https://doi.org/10.1080/09670262.2017.1385098.

Santelices, B.E.R.N.A.B.É., Bolton, J.J., Meneses, I.S.A.B.E.L., 2009. Chapter Six Marine Algal Communities. Chicago University Press, Chicago, IL, USA, pp. 153–192.

Shelamoff, V., Layton, C., Tatsumi, M., Cameron, M.J., Edgar, G.J., Wright, J.T., Johnson, C.R., 2020. Kelp patch size and density influence secondary productivity and diversity of epifauna. Oikos 129 (3), 331–345. https://doi.org/10.1111/oik.06585.

Smale, D.A., Wernberg, T., 2013. Extreme climatic event drives range contraction of a habitat-forming species. Proc. R. Soc. B-Biological Sci. 280, 20122829 https://doi.org/10.1098/rspb.2012.2829.

Southward, A.J., Hawkins, S.J., Burrows, M.T., 1995. Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. J. Therm. Biol. 20 (1–2), 127–155. https://doi.org/10.1016/0306-4565(94)00043-I.

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M.A.X., et al., 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. Bioscience 57 (7), 573–583. https://doi.org/10.1641/B570707.

Starko, S., Smyth, C., Kucera, H., 2016. Attachment strength of the herbivorous rockweed isopod, Idotea wosnesenskii (Isopoda, Crustaceae, Arthropoda), depends on properties of its seaweed host. Journal of experimental marine biology and ecology 477, 1–6. https://doi.org/10.1016/j.jembe.2016.01.006.

Steneck, R.S., Paine, R.T., 1986. Ecological and taxonomic studies of shallow-water encrusting Corallinaceae (Rhodophyta) of the boreal northeastern Pacific. Phycologia 25 (2), 221–240. https://doi.org/10.2216/i0031-8884-25-2-221.1.

Takolander, A., Leskinen, E., Cabeza, M., 2017. Synergistic effects of extreme temperature and low salinity on foundational macroalga Fucus vesiculosus in the northern Baltic Sea. J. Exp. Mar. Biol. Ecol. 495, 110–118. https://doi.org/10.1016/j.jembe.2017.07.001.

Teixidó, N., Gambi, M.C., Parravacini, V., Kroeker, K., Micheli, F., Villéger, S., Ballesteros, E., 2018. Functional biodiversity loss along natural CO2 gradients. Nat. Commun. 9 (1), 5149.

Thiel, M., 2002. The zoogeography of algae-associated peracarids along the Pacific coast of Chile. J. Biogeogr. 29 (8), 999–1008. https://doi.org/10.1046/j.1365-2699.2002.00745.x.

Tilman, D., 2001. The Encyclopedia of Biodiversity 3 (0), 109–120. https://doi.org/10.1006/rwbd.1999.0154.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E., 1997. The influence of functional diversity and composition on ecosystem processes. Science 277 (5330). https://doi.org/10.1126/science.277.5330.1300.

Toonen, R.J., Bowen, B.W., Iacchei, M., Briggs, J.C., 2016. Biogeography, marine. Encyclopedia of Evolutionary Biology 166–178. December.

Tuya, F., Haroun, R.J., 2009. Phytogeography of Lusitanian Macaronesia: biogeographic affinities in species richness and assemblage composition. Eur. J. Phycol. 44 (3), 405–413. https://doi.org/10.1080/09670260902836246.

Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., De Clerck, O., 2012. Bio-ORACLE: a global environmental dataset for marine species distribution modelling. Global Ecol. Biogeogr. 21 (2), 272–281. https://doi.org/10.1111/j.1466-8238.2011.00656.x.

Underwood, A.J., 2000. Experimental ecology of rocky intertidal habitats: What are we learning? Journal of Experimental Marine Biology and Ecology 250 (1–2), 51–76. https://doi.org/10.1016/s0022-0981(00)00179-9.

Van Dam, N.M., 2009. How plants cope with biotic interactions. Plant Biol (Stuttg) 11, 1–5.

Veiga, P., Rubal, M., Sousa-Pinto, I., 2014. Structural complexity of macroalgae influences epifaunal assemblages associated with native and invasive species. Mar. Environ. Res. 101, 115–123. https://doi.org/10.1016/j.marenvres.2014.09.007.

Vieira, P., Desiderato, A., Azevedo, S., Esquete, P., Costa, F., Queiroga, H., 2022. Molecular evidence for extensive discontinuity between peracarid (Crustacea) fauna of Macaronesian islands and nearby continental coasts: over fifty candidate endemic species. Marine Biology 169 (5). https://doi.org/10.1007/s00227-022-04051-w.

Vilas, D., Coll, M., Pedersen, T., Corrales, X., Filbee-Dexter, K., Pedersen, M.F., et al., 2020. Kelp-carbon uptake by Arctic deep-sea food webs plays a noticeable role in maintaining ecosystem structural and functional traits. J. Mar. Syst. 203, 103268 https://doi.org/10.1016/j.jmarsys.2019.103268.

Wang, Z., Brown, J.H., Tang, Z., Fang, J., 2009. Temperature dependence, spatial scale, and tree species diversity in eastern Asia and North America. Proceedings of the National Academy of Sciences USA 106, 13388–13392. https://doi.org/10.1073/pnas.0905030106.

Warfe, D.M., Barmuta, L.A., 2004. Habitat structural complexity mediates the foraging success of multiple predator species. Oecologia 141, 171–178. https://doi.org/10.1007/s00442-004-1644-x.

Wernberg, T., Russell, B.D., Moore, P.J., Ling, S.D., Smale, D.A., Campbell, A., et al., 2011. Impacts of climate change in a global hotspot for temperate marine biodiversity and ocean warming. Journal of experimental marine biology and ecology 400 (1–2), 7–16. https://doi.org/10.1016/j.jembe.2011.02.021.

Wernberg, T., Bennett, S., Babcock, R.C., De Bettignies, T., Cure, K., Depczynski, M., et al., 2016. Climate-driven regime shift of a temperate marine ecosystem. Science 353 (6295), 169–172. https://doi.org/10.1126/science.aad8745.

Willig, M., Kaufman, D., Stevens, R., 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annual Review of Ecology, Evolution, And Systematics 34 (1), 273–309.

Yoshimura, M., Maeto, K., 2006. Comparison of an aquatic invertebrate assemblage between an old-growth natural forest and planted coniferous forest basins in a Japanese temperate region: the Kuroson stream in the Shimanto River basin. Landsc. Ecol. Eng. 2 (1), 81–89. https://doi.org/10.1007/s11355-006-0029-1.

Zakhama-Sraieb, R., Sghaier, Y.R., Charfi-Cheikhrouha, F., Societa Italiana di Biologia Marina, Livorno(Italy), 2006. Is amphipod diversity related to the quality of Posidonia oceanica beds? Biol. Mar. Mediterr. 13 (4).