Environmental drivers of spatial variability of Chilean Benthic Marine Invertebrates

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Declaration

I, Loreto Andrea Pino Chandia, the author, confirm that this Thesis is my own work. I am aware of the University's Guidance on the Use of Unfair Means (www.sheffield.ac.uk/ssid/unfair-means). This work has not been previously been presented for an award at this, or any other, university.

Abstract

Chilean benthic ecosystems make an ideal test case for studying macroecological patterns in species distributions. Chile spans ~39° in latitude, an eco-geographical gradient encompassing five marine ecoregions, significant variation in temperature, salinity, oxygen, solar radiation, and primary productivity, all of which are potential factors driving benthic community structure. This thesis aims to understand how key environmental drivers and human activities influence the spatial variability of benthic marine invertebrates along this gradient. I compile a new integrated biodiversity database and use it to calculate diversity metrics related to species richness, taxonomic diversity and functional diversity, and combine this with data on environmental covariates and human activities. Species richness and functional richness peaked between 42°-46° S. Taxonomic diversity increased south 42° S. Functional evenness peaked toward extreme northern and southern latitudes. Major anthropogenic activities related to diversity were aquaculture and human population density; however, contrary to expectation, diversity increased with increasing levels of these human pressures. My results highlight the importance of the Humboldt Current System for functional diversity: environmental stress (depletion of oxygen at maximum bottom depth and increasing sea bottom nitrate) modulates the benthic communities in this region. Hydrographic variability driven by bottom temperature and salinity gradients in the Patagonian fjords system influences taxonomic and functional diversities of benthic communities. My research confirmed the importance of latitudes between 42°-46° S as an area of high diversity of benthic marine invertebrates. Here, diversity is mainly driven by peaks of primary productivity. I argue that benthic invertebrate assemblages are composed of communities presenting a small volume of functional traits space, formed mainly by species tolerant to the environmental conditions, using available resources such as food and space, and presenting lower competition per resource. These communities show moderate levels of resilience to environmental changes and resistance to species loss.

1. Introduction

1.1. Benthic marine ecosystems

In area and volume, the oceans represent the largest habitat on Earth, covering 70.8% of its surface (Snelgrove 2001). They support human wellbeing, being economically important for the local and global economy, being also a source of water, food, clean energy, and helping to reduce the effects of climate change (Duarte et al. 2020). However, oceanic productivity and biodiversity have suffered a catastrophic decline due to climate change in the last 70 years; other human activities are affecting marine life and ecosystems such as hunting, fishing, deforestation (increase of sediment export and coastal damage), habitat loss and pollution (fertiliser, plastic and chemicals; Duarte et al. 2020). Moreover, the rise of the human population by 2050 (~ 9 billion individuals) is expected to generate more demand for seafood and coastal areas (Duarte et al. 2020). A fundamental part of the oceans is the benthic coastal and marine ecosystems, which provide an important range of services (Crowe & Frid 2015) such as source of food, supporting marine food webs, key ecotone areas (Snelgrove 2001). Coastal ecosystems are located in the transition between land and sea, including intertidal and estuarine habitats where benthic species must tolerate a range of environmental variables such as hypoxic conditions, organic input and salinity gradients (Snelgrove 2001). Benthic ecosystems are also vulnerable to many threats because they are close to human populations and their pressures, being affected by fisheries, aquaculture, and the introduction of non-native species (Snelgrove 2001).

Benthic invertebrates are a dominant component of marine benthic ecosystems. These organisms present a wide range of sizes (e.g. from meiofauna < 63um to megafauna > 5cm; Gray & Elliott 2009), feeding habits (e.g. suspension feeder, grazer, surface and subsurface deposit feeder, and carnivore), and life habits (e.g. sessile and mobile; Krumhansl et al. 2016). Benthic invertebrates perform a series of fundamental roles in ecosystems' functioning through their biological traits, including bioturbation, food web regulation, biogeochemical cycles, waste material recycling, and capture of hazardous substances (Cooper et al. 2008). For example, feeding activity of benthic macrofauna (size range from 500um to 5cm; Gray & Elliott 2009) helps in the removal of particles and pollutants from the water column (suspension feeding) and sediment (deposit-feeding), as well capturing organic material from the bottom, for example, detritus, faecal pellets or animal shells (Snelgrove 1998). Benthic invertebrates also play important roles in marine food webs, such as secondary production or food sources for the human population and important economic species (Snelgrove 1998), supporting higher trophic levels in marine life food webs (Gray & Elliott 2009).

At the same time, through their interactions with the environment, benthic invertebrates can modify and influence ecosystems as a consequence of biological processes such as bioturbation and biodiffusion. For example, through bioturbation, the sediments are reworked by the action of burrowing organisms such as polychaetes (e.g. *Arenicola* spp.) and bivalves (e.g. *Macoma* sp.), increasing the depth of the oxygenated layer, as well as the exchange of the water-sediment interface (Gray & Elliott 2009). In addition, benthic invertebrates can also stimulate the microbial nutrient dynamics through different animal-microbe interactions, intensifying the interaction between benthos, pelagic and atmosphere by means of enhanced turnover and nitrogen transport (Stief 2013). Benthic marine invertebrates display a variety of responses to specific environmental pressures (Muniz et al. 2005), such as organic enrichment (Pearson & Rosenberg 1978), meaning that the presence or absence of tolerant species in a community can be used in environmental assessment (i.e. bioindicators; Muniz et al. 2005).

1.1.1. Chilean marine and coastal ecosystems

Chilean marine and coastal ecosystems are particularly rich, contributing 3 to 5% to global capture fisheries landings, including one of the world's most productive fisheries (FAO 2016). Although the major fisheries are pelagic (e.g. Peruvian anchoveta, *Engraulis ringens*), significant benthic fisheries also exist, and these have led to overexploitation of benthic invertebrate species including crustaceans, gastropods (e.g. *Concholepas concholepas*) and sea urchins (e.g. *Loxechinus albus*; Mutschke et al. 2016). This exploitation directly impacts the ecosystem services offered by these benthic marine ecosystems.

Chilean coastal waters are also particularly interesting for the study of macroecological patterns in benthic species distributions. They span ~39° of latitude (18° 30'' to 57° 30'' S; Fernández et al. 2000), forming an eco-geographical gradient encompassing a significant variation in terms of temperature, salinity, oxygen, solar radiation, and primary productivity, all of which have a potential factor driving the benthic community structure. Two main current systems impact the Chilean coastline: the Humboldt Current System (HCS) running towards the Equator (Thiel et al. 2007) and Cape Horn Current System (CHC) running towards the South Pole, which originates from the division of the Antarctic Circumpolar Current at ~42° - 48° S (Silva et al. 2009). The HCS is particularly productive due to the upwelling of cold and nutrient-rich waters (Camus 2001, Thiel et al. 2007). However, productivity is influenced both by seasonality and by El Niño Southern Oscillation (ENSO). Productivity and community structure in the seas further south, in the CHC system, are influenced by inputs of low-nutrient freshwater (Silva et al. 2009, Quiroga et al. 2012, 2016), creating a transitional marine system (Iriarte et al. 2010).

In addition, in Chile the human population, and associated activities, are associated with the coastline and the adjacent continental shelf. These activities are located in defined areas along the latitudinal gradient. Copper and iron mining are mostly developed in the northern zone, causing mineral and other deposits along the coast, increasing turbidity and reducing light (Lancellotti & Stotz, 2004). Aquaculture of salmon (*Salmo salar, Oncorhynchus mykiss,* and *Oncorhynchus kisutch*) and mussels (*Mytilus chilensis*) is mainly developed within the channel and fjord systems in the southern zone, resulting in high inputs of nutrients such as nitrogen, phosphorus, and carbon (Iriarte et al. 2010, Mayr et al. 2015), which causes changes in the food web structure and the biogeochemical composition of water and sediments (Iriarte et al. 2010).

In terms of diversity, the area encompassed by the HCS has been described as poor in species richness of invertebrates (Carrasco & Moreno 2006); despite that, this zone has high productivity because of upwelling centres (Camus 2001). The effect of upwelling on benthic communities is not well understood (Thiel et al. 2007). Mining might also affect the functional structure of benthic communities by increasing deposit-feeding species (Lancellotti & Stotz 2004). Overall, the highest diversity of benthic macroinvertebrate species has been observed south of 42° S (Fernandez et al. 2000), specifically in the Inner Sea of Chiloe (ISCh, ~ 42° S; Valdovinos et al. 2003). The ISCh presents high environmental fluctuations in sediment composition, organic matter, and depth (Cañete 1999), favourable features supporting ecosystem diversity. However, the ISCh has also been more intensively sampled because it is thought to be a diversity hotspot and also because of the increase in aquaculture. These differences in sampling effort have hampered the identification of species distribution patterns throughout the Chilean latitudinal gradient (e.g. Lancellotti & Vásquez 2000, Valdovinos et al. 2003, Häussermann 2006). Other researchers have observed the highest species diversity south of 52° S (e.g. Gambi & Mariani 1999, Rivadeneira et al. 2011, Cañete et al. 2012), due to the diversity of biotopes and the high environmental heterogeneity. Thus, the slight diversity gradient of benthic invertebrate species from north to south (e.g. Hernández et al. 2005, Ibáñez et al. 2009) might be significantly influenced by the differences in sampling effort along the latitudinal gradient of Chile and by the changes in the taxonomic composition and functional structure of benthic communities of marine invertebrates, a product of the intense anthropogenic effect and environmental factors.

1.1.2. Aim and theoretical scope of the thesis

The macroecological approach, encompassing studies of diversity patterns and processes on a large, spatial scale and over a long duration (Witman & Roy 2009, Webb et al. 2009), has not been widely adopted in Chile. This has been attributed to the lack of suitable databases, the concentration of investigations in a few sites and the low sampling intensity of surveys (Fernández et al. 2000). Working in European shelf seas, Renaud et al. (2009) argued that diverse factors and mechanisms might be responsible for generating and supporting the biodiversity of benthic species. Thus, the distribution patterns of species might be used to identify key diversity drivers of benthic marine communities (Renaud et al. 2009). In the Chilean context, Fernández et al. (2000) emphasised the importance of developing studies to understand ecosystem processes (e.g. upwelling), and endemism, as possible factors for generating macro-scale patterns. There has been little progress towards this since 2000, however; subsequent studies have been limited to certain factors such as temperature, shelf area, latitudinal gradient, and to specific taxa such as molluscs (e.g. Valdovinos et al. 2003), polychaetes (e.g. Hernández et al. 2005), and peracarida (e.g. Rivadeneira et al. 2011). Thus, a primary aim of this thesis is to address this shortfall and contribute to the knowledge of diversity patterns of benthic species on a regional scale in the Southern Hemisphere, across all Chilean ecoregions, and using different measures of diversity including species richness, taxonomic diversity and functional diversity, with the final aim to identify key environmental drivers and human activities influencing the observed patterns of diversity.

1.2. Chilean Marine Ecoregions

The coast and continental shelf of Chile covers approximately 4,200 km from north to south (Fernández et al. 2000). Because of the long extension of Chile and for a better understanding of its eco-geographical gradient, in this study I use the Marine Ecoregions of the World system of classification proposed by Spalding et al. (2007). These authors divided the global continental shelf into 62 provinces and 232 ecoregions. The ecoregions were defined as areas with relatively homogeneous species composition (Spalding et al. 2007). The continental area of Chile is represented by two provinces: Warm Temperate Southeastern Pacific (WTS Pacific) and Magellanic Province (Figure 1), and five ecoregions: Humboldtian, Central Chile, Araucanian, Chiloense and Channels and Fjords of Southern Chile (Figure 1). Their limits were defined based on Chilean research developed by Fernández et. al (2000), Ojeda et al. (2000) and Camus (2001).

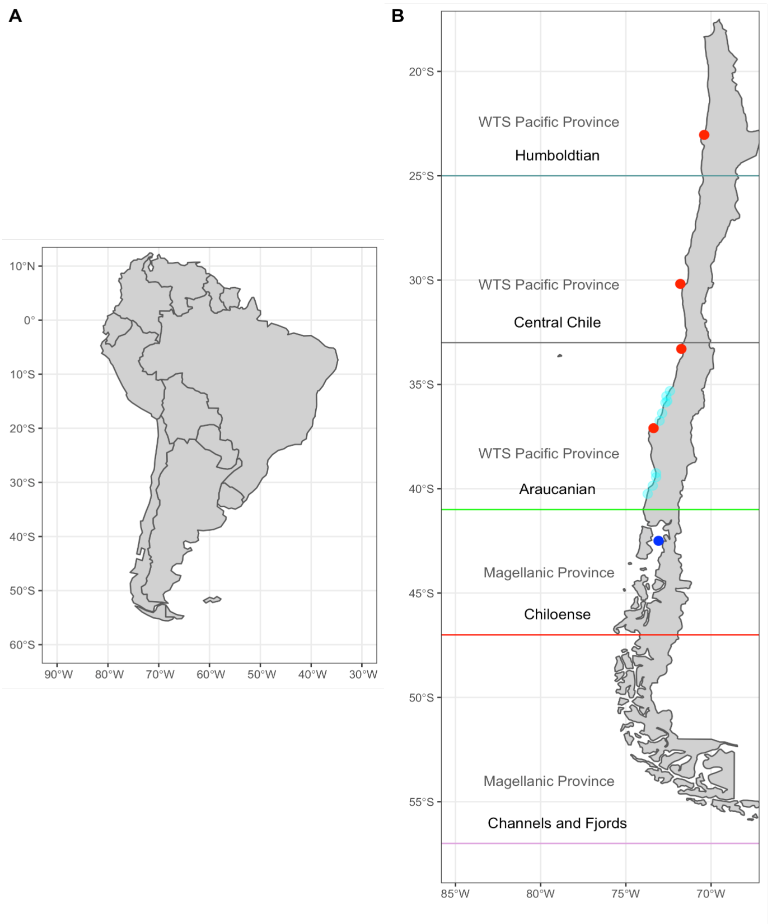

Figure 1. Maps of **A)** South America and **B)** Chile, showing the five ecoregions according to the two provinces (Warm Temperate Southeastern (WTS) Pacific and Magellanic). Some important locations are represented such as upwelling centres (red points), zone of rivers and estuaries (light blue points), and the Inner sea of Chiloe (blue point).

Along the HCS, some areas present levels of dissolved oxygen going from hypoxic to anoxic; these areas are called oxygen minimum zones (OMZs) and influence benthic communities (Thiel et al. 2007). In this reduced environment large mats of large filamentous bacteria *Thioploca* sp. occur (Escribano et al. 2004). OMZs correspond to those layers in the water column with concentrations of oxygen dissolved lower 0.5ml/L (Gooday et al. 2010). The occurrence of El Niño Southern Oscillation (ENSO) events adds complexity to the predictions of ecological processes towards northern latitudes of Chile (Thiel et al. 2007), and interannual variability to the HCS (Escribano et al. 2004). ENSO events such as those observed during 1997-98 in Chile provoked some oceanographic changes (Escribano et al. 2004). For instance, it led to the intrusion into coastal areas of warmer oceanic water, which is more saline, low in nutrients and more oxygenated, causing a decrease in the biomass of primary producers, and a positive sea surface temperature anomaly along the Chilean coast (Escribano et al. 2004). This event also directly affected benthic populations such as *Aulacomya atra*, reducing their landings (Laudien et al. 2007). In addition, some areas located off of central/southern Chile, which in normal conditions present a benthic hypoxia, were oxygenated near the bottom, and the carbon input decreased (Escribano et al. 2004).

The Humboldtian and Central Chile ecoregions are extremely arid (Atacama Desert), lack freshwater inputs from rivers (only the Loa River and Copiapó River), and are centres of mining activity (Valdés & Tapia 2019). The number of rivers increases towards southern latitudes, forming important estuaries in the Araucanian ecoregion from 35° to 39° S (e.g. Maule, Itata, Bío Bío, Imperial, Toltén, Lingue Mehuin and Valdivia; light blue points Figure 1B).

1.2.2. The Magellanic Province (from 41.5º to 56º S)

This province is divided into two ecoregions: the Chiloense and the Channels and Fjords (figure 1). It covers approximately 240,000 km^2 and is also known worldwide as the Chilean Patagonian Fjords (Pantoja el al. 2011). The Magellanic province is mainly composed of numerous islands, fjords, gulfs and basins (Pantoja et al. 2011, Quiñones et al. 2019). The area is considered one of the largest estuarine regions (Iriarte et al. 2010) and one of the most productive areas in the world (Betti et al. 2017), being relevant for the biological productivity and carbon cycles (González et al. 2010). In turn, the fjords have high concentrations of diverse anthropogenic activities such as aquaculture, industry, fisheries and tourism (Jordà Molina et al. 2019). In this province, the complex topography forces and defines the interplay between deeper oceanic, saline, nutrient-rich water and surface freshwater, which is poor in nutrients and originates from the coastal runoff, local rivers, and high rainfall (Iriarte et al. 2007, Pantoja et al. 2011, Quiñones et al. 2019), and it generates micro-environments (Aracena et al. 2011) and consequently a heterogeneous or mosaic environment with the capacity of maintaining a high biodiversity (Iriarte et al. 2010). Thus, the Magellanic province represents a transitional marine ecosystem (Iriarte et al. 2010).

The Inner Sea of Chiloe (ISCh; blue point Figure 1B), located in the north zone of the Chiloense ecoregion, represents an extensive part of the Chiloense ecoregion. This area is composed of an estuarine system on one side and a group of islands on the other, forming a large archipelago. The ISCh receives inputs of organic matter from river runoff, coastal erosion and evergreen forests, as well as from masses of water and kelp accumulation (Zapata-Hernández et al. 2016). In these complex ecosystems the atmospheric, geomorphologic and hydrodynamic interactions cause a high biological productivity (Iriarte et al. 2007). The ISCh is a highly productive area, where the phytoplankton blooms are seasonal and they grow in nitrogen-deficient waters due to the depletion of nutrients by the microalgae blooms of spring and summer (Soto & Norambuena 2004, Iriarte et al. 2007).

Towards southern latitudes of this province in the channels and fjords ecoregion, the salinity and solar radiation decrease (Iriarte et al. 2018), and the input of nutrients and silicic acid from rivers and glaciers also decrease, affecting the growth of diatoms in the area (Montecino & Pizarro 2008). Thus, the relationship between nutrients and primary productivity in the channels and fjords ecoregion differs from those observed in the Chiloense ecoregion. The Channels and Fjords ecoregion also has freshwater inputs from the five icefields, located between 46° to 48° S, which are considered an important freshwater reservoir to the world (Pantoja et al. 2011). The freshwater runoff also has an effect on the horizontal buoyancy, the water column stratification (e.g. pycnocline), and the regulation of primary producers; because this separates the algae from the main nutrient sources and limits the depth of the turbulent mixing (Iriarte et al. 2018).

1.3. Diversity of marine benthic invertebrates

An increase in species diversity from poles towards tropical latitudes is very generally observed (Gray 2001). This paradigm was re-evaluated by Gray (2001), and some authors have found some evidence to support it for fishes and invertebrates (e.g. Macpherson 2002).

However, there is much weaker evidence for this paradigm in benthic marine invertebrates in both the northern and southern hemispheres. For example, a high diversity of species is observed in the Canadian Arctic regions (e.g. Cusson et al. 2007), through the continental shelf of Europe (e.g. Renaud et al. 2009), and in both hemispheres (e.g. Piacenza et al. 2015).

The distribution patterns of benthic organisms seem to be more related to the effect of the interaction between biotic and abiotic environmental factors, for instance, environmental heterogeneity including depth and sediment (e.g. Ellingsen & Gray 2002, Piacenza et al. 2015), and the level of threats from human activities and climate change (e.g. Snelgrove 2001, Duarte et al. 2020). Although Macpherson (2002) showed that species richness of benthic and pelagic taxa responds to the latitudinal paradigm in both hemispheres, the distribution patterns of benthic taxa seemed to be more correlated to factors such as nitrate and chlorophyll, sea surface temperature, freshwater inputs, and upwelling processes, than to latitude itself. Thus, factors and associated environmental drivers (i.e. interaction between factors) and human pressures mainly influence benthic species distribution patterns.

Understanding where hotspots of benthic biodiversity occur is crucial in determining distribution patterns on both a regional and global scale (e.g. Stuart-Smith et al. 2013, Bundy et al. 2017). Myers et al. (2000) defined hotspots as areas of high concentration of endemic species, high biodiversity, and high vulnerability to species loss. In ecological terms, hotspots are also related to high species abundance (e.g. Bartolino et al. 2010), high density of individuals (e.g. Nelson & Boots 2008), high biomass of organisms (e.g. Grebmeier et al. 2015), high aggregation of multiple trophic levels (e.g. Santora et al. 2017), and high diversity of functional groups (e.g. Bundy et al. 2017). Defining hotspots can also be motivated by marine spatial planning, fisheries management (Santora et al. 2017), and the establishment of Marine Protected Areas (MPAs) networks (Bundy et al. 2017). Therefore, the appropriate definition of a hotspot depends on the study's interests. In addition, the spatio-temporal persistence of hotspots seems to be related to environmental dynamics involved in the region studied (e.g. upwelling systems; Santora et al. 2017). Environmental drivers (interaction between biotic or abiotic factors) can also be important, including levels of primary production, pelagic production, organic carbon content and bathymetry (e.g. Grebmeier et al. 2015), and nutrient enrichment, cooler superficial water and surface pycnocline (e.g. Santora et al. 2017). However, the maintenance of biodiversity hotspots, in both time and space, is threatened by anthropogenic pressures including fisheries (Bundy et al. 2017), climate change, and species introductions (Coll et al. 2010).

In Chile, patterns and hotspots of benthic diversity have been primarily evaluated in terms of species composition metrics such as species richness (i.e. number of species). These patterns have revealed that diversity of polychaetes and molluscs peaks between 39° to 41° S (e.g. Lancellotti & Vásquez 2000, Valdovinos et al. 2003, Hernández et al. 2005) and between 51° to 53° S in soft bottom sediments, and the diversity of peracarida increases poleward (Rivadeneira et al. 2011). Species richness of herbivores, on the other hand, peaks between 30 to 32° S, decreasing toward northern and southern latitudes in rocky shores (e.g. Rivadeneira et al. 2002). However, although species richness is the simplest and most frequently used measure of biodiversity (Johnston & Roberts 2009), it is highly influenced by sampling effort. Thus, the largest species richness will be observed in localities that are under intense research activity (Clarke et al. 2007). Sampling effort is a recognised limitation in studies of distribution patterns on a macroscale (e.g. Clarke & Lidgard 2000, Miloslavich et al. 2011).

Thus, different approaches have been used to compensate for the effect of varied sampling efforts on estimated species richness. For instance, Chao et al. (2014) fitted the accumulated number of species in relation to sample size (Colwell et al. 2012), and sample-coverage (Chao & Jost 2012). Through this approach, species richness may be rarefied (interpolated) and extrapolated according to a standardised sample size (Branco et al. 2018). Rare species are more difficult to detect than common species; thus, some measures of diversity are focused on identifying undiscovered taxa (Branco et al. 2018). Such measures include non-parametric estimators (Chao & Chiu 2016) such as Chao 1 (Colwell & Coddington 1994) for abundance data and Chao 2 for incidence data (Chao 1987). Alternatively, the first-order Jackknife (Heltshe & Forrester 1983) and second-order Jackknife (Burnham & Overton 1978) are based on the frequency of singletons (the number of species represented by one single individual) and doubletons (the number of species represented by two individuals; Magurran 2004, p. 87); the first works with abundance data, while the second works with incidence data. Another related measure, the abundance-based coverage estimator (ACE; Chao & Yang 1993), is based on the separation into species with >10 species abundance from those with <10 abundance (Magurran 2004, Branco et al. 2018). Its partner, the incidence-based coverage estimator (ICE; Chao & Lee 1992), is based on the separation into an infrequent species group (incidence frequency not higher than 10) and a frequent species group (incidence frequency higher than 10; Magurran 2004, Chao & Chiu 2016). All of these measures have their merits, however being based only on numbers of species they neglect information on the role of species in a community along an environmental gradient (McGill et al. 2006, Cadotte et al. 2011).

A current challenge, faced with the impacts of climate change on coastal ecosystems, is to determine how species will respond to single and multiple environmental drivers (Ramajo et al. 2019). New methods have been developed to evaluate the communities' response of plants and animals to environmental processes such as functional diversity (FD). FD takes species information about functional traits (Ricotta & Moretti 2011). One clear advantage of the functional trait approach is the possibility to make some inferences about ecosystem processes (Llanos et al. 2020). According to Törnroos and Bonsdorff (2012), the FD approach reduces the costs and increases the effectiveness of the analysis. Thus, it is not necessary to take a large sample or cover an extended area to get a picture of how the ecosystems vary in terms of functional features (Törnroos & Bonsdorff 2012). FD also allows us to differentiate between areas of higher and lower salinity, and higher and lower anthropogenic pressure (Törnroos & Bonsdorff 2012). Dimitriadis and Koutsoubas (2011) argued that understanding the relationship between the loss of species diversity and the changes in functional diversity might improve our knowledge about the consequences of anthropogenic pressures on marine ecosystems.

Functional traits are the basis of the functional ecology (Villéger et al. 2010), and they are defined as the biological attributes influencing the performance of the organisms (Violle et al. 2007). A simple division of functional traits differentiates them into response traits, related to the resistance and resilience of the species, and effects traits, related to ecosystem processes (Villéger et al. 2010). Thus, traits can say more about the relationship between species and the environment. For example, in benthic marine invertebrates, life-history traits (e.g. larval development mode and type of larvae) are response traits. These traits are important in the dispersion, connectivity and geographical extension of marine communities, being associated with oceanographical features (Thiel et al. 2007). They might change due to environmental drivers (i.e. the relationship between environmental factors). Thus, life-history traits say more about the plasticity of the species in a community (Allen et al. 2018). For instance, the identification of feeding strategies in larval stages is relevant in the determination of latitudinal patterns of diversity of benthic marine invertebrates in the southern hemisphere (Fernández et al. 2000, Pappalardo & Fernández 2014), and these patterns might be explained through their relationship with environmental factors such as temperature and biogeographical breaks associated with coastal upwelling (Pappalardo & Fernández 2014).

1.4. Anthropogenic drivers of benthic diversity in Chile

As well as the environmental factors impacting benthic diversity in Chile described above, a range of anthropogenic activities are potentially important. The United Nations estimates that the population of Chile in 2021 was 19.2 million, with a mean population density of 25.8 km^{-2} and a growth rate of 1.1%. Most of the population is concentrated on the coast and in the central zone at mid latitudes, between 30° to 40° S (Figure 2A). The capital city of Santiago is located (33°27′ S 70°40′ W) toward the Cordillera de Los Andes. In the Santiago Metropolitan region, the population is approximately 7.2 million (source: https://www.worldometers.info/world-population/chile-population/, United Nations data). The highest population density is located in the centre zone of Chile and in coastal areas (Figure 2A).

There are small harbours (caletas pesqueras artesanales in Spanish; Figure 2B) all along the coast of Chile, defined as a productive, economic, and social and cultural unity located in a specific geographical area, in which direct and indirect activities related with artisanal fisheries are developed (SUBPESCA 1991). The activities associated with small harbours are local and small-scale, due mainly to fishermen. Fishermen are defined as individuals working in the sea as part of a crew or being owners of a maximum of two boats which together do not exceed 50 gross tons (SUBPESCA 1991). These individuals can also develop activities of resource extraction through scuba diving, free diving, shore and algae collection in the corresponding artisan exclusive zone (AEZ) of Chile (5 nautical miles; source: www.subpesca.cl). Apart from activities directly related to fisheries, small harbours are centres of assembling boats, resource extraction, sale of products, as well as being part of the social and cultural environment (source: www.subpesca.cl). In contrast to the small harbours, there are trading ports (Figure 2B). Part of the activities developed in trading ports are carried out by the industrial fleet, which includes vessels above 50 gross tons (SUBPESCA 1991). Moreover, these ports present a high-activity product by tourist cruises. Thus, the main impact of these ports is related to the oil spills as well as the discharge of sewage from industrial and mercantile ships, and cruises.

On the other hand, the landings by ports are related to the extractive activities carried out by the industrial fisheries in vessels over 18 metres in length, with technological fisheries systems such as those related to bottom trawling, longline fishing, and seine fishing (source: www.subpesca.cl). Chile supports one of the main industrial fisheries in the world, which includes mainly pelagic resources and, on a minor scale, invertebrates and algae (Fernández et al. 2000). Over decades, the main aim of the activity was to capture native fish (e.g. *Strangomera bentincki*, *Engraulis ringens*, and *Trachurus murphyi*) for the production of oil to supply food for salmon farms. However, demersal and deep-water resources are also important. It includes fishes such as *Merluccius australis*, *Merluccius gayi*, *Micromesistius australis*, and *Dissostichus eleginoides*, and the crustaceans *Cervimunida Johni,* and *Pleuroncodes monodon* (source: www.sernapesca.cl;). The most productive areas in terms of total landings for pelagic and benthic species such as molluscs (e.g. *M. chilensis, A. atra,* and *Venus antiqua*), crustaceans (e.g. *Cancer edwardsii*), and echinoderms (e.g. *Loxechinus albus*) are located towards southern latitudes of Chile (source: www.sernapesca.cl; Figure 2B). This activity has a direct impact on the population of marine and coastal invertebrates, for example through the overfishing of sea urchins (e.g. *L. albus*, and *Arbacia dufresnii*), and mussels (Chilean abalone, *C. concholepas*).

Chile has approximately 162 mines, which are mainly located in the north and centre zones of Chile (Figure 2C). The mining activity is mostly focused on copper (Cu) and iron (Fe). Although mining is mostly developed inland and close to the mountain range (Los Andes; Ramirez et al. 2005, Fariña & Castilla 2001), there are around 800 mining tailings deposits along the coast, mostly located north of the capital city of Santiago (National Geological and Mining Survey, 2018). Mining tailings have direct effects on coastal and marine ecosystems, which can even be visible after 50 years (e.g. direct discharges to Caleta Palito from the El Salvador Cu mine; Correa et al. 1999), with some recovery in species diversity after 60 years (e.g. the coastline around Chañaral; Medina et al. 2005). The intense development of human activities in coastal northern Chile has not been accompanied by corresponding environmental regulation, increasing the number of polluted marine areas (Valdés & Tapia 2019). In terms of laws, mining does not have a proper environmental legislation with the aim of protecting the marine ecosystems from mining discharges, even when the effects on marine communities have been evidenced (e.g. Castilla 1983, Vásquez et al. 1999). For instance, monitoring programmes are not totally focused on the effect of mining on terrestrial and marine ecosystems along Chile (Valdés & Tapia 2019), as with aquaculture. Thus, to obtain direct measures in water and sediment is not possible in areas with high mining activity or being indirectly influenced (e.g. Valdés & Tapia 2019).

Mining tailings have direct effects on the excessive accumulation of allochthonous materials, such as particulate Fe (Lancellotti & Stotz 2004) and Cu in water and fine sediment of coastal areas (Correa et al. 1999, Ramirez et al. 2005, Vásquez et al. 1999). The excessive accumulation of these pollutants increases turbidity in the water column (Lancellotti & Stotz 2004). In biological terms, mining tailing has effects on biological diversity, decreasing the diversity of species of marine invertebrates, and marine algae (Castilla 1983; Ramirez et al. 2005, Fariña & Castilla 2001, Rodríguez et al. 2021), reducing the number of taxa and densities of meiofauna (Lee & Correa 2005), increasing the dominance of green algae species such as *Enteromorpha compressa* on rocky shores (Fariña & Castilla 2001), affecting the trophic structure of benthic communities, being mostly represented by deposit feeders (e.g. *Lumbrineris bifilaris* and *Diastylis tongoyensis*; Lancellotti & Stotz 2004), and the absence of carnivorous species (Medina et al. 2005), and decreasing the populations of sessile species in rocky intertidal communities (Fariña & Castilla 2001, Medina et al. 2005).

Aquaculture is a major industry in Chile. Salmon aquaculture is the most important in production; however, other species are also commercially important, with the blue mussel *M. chilensis* intensively cultivated in the southern zone of Chile (Figure 2C). Salmonids and blue mussels represented 79% and 20% respectively of the total national aquaculture harvest in 2014 (González-Poblete et al. 2018, SERNAPESCA 2014). The remaining 1% of the total harvest is represented by a range of species including the mussel *A. atra*, the oysters *Ostrea chilensis,* and *Crassostrea gigas*, the scallops *Argopecten purpuratus*, the gastropod abalone *Haliotis rufescens*, the algae (*Gracilaria chilensis*)*,* and the non–native turbot (*Scophthalmus maximus*).

Chile is the second-largest producer of salmon in the world after Norway (Niklitschek et al. 2013). Although the commercial activity started in 1987 (Niklitschek et al. 2013), since the late 1980s, this industry has increased in production exponentially (Quiñones et al. 2019). All salmon species are non-native species: Atlantic salmon (*S. salar*), Pacific salmon (*O. kisutch*), and Rainbow trout (*O. mykiss*). The aquaculture of salmon in their marine phase is mainly located in the fjords and channels of Southern Chile (Iriarte et al. 2010, Quiñones et al. 2019). As an intensive activity (i.e. external food supply), it was initially mainly focused on the inner sea of Chiloe from 41° S to the system of fjords and channels 46° S (Soto & Norambuena 2004, Niklitschek et al. 2013). However, from 2008, and due to the ISA virus crisis in 2007, the activity has been extended towards the Aysén Fjords System and is increasing rapidly; this region represents a more pristine area, with lower industrial development, lower population density and three biosphere reserves declared by UNESCO (Niklitschek et al. 2013, see Figure 2C).

The effects of aquaculture are related to the input and accumulation of dissolved and solid residues in the water column and sediments (Niklitschek et al. 2013). The retention of nutrients, such as nitrogen and phosphorus due to excretion (e.g. ammonia and urea), faeces, and non-consumed food, can exceed the carrying capacity of the ecosystems to incorporate these nutrients, resulting in anaerobic or anoxic processes (Soto & Norambuena 2004, Niklitschek et al. 2013, Quiñones et al. 2019). The habitat degradation, due to the excessive accumulation of OM, and the consequently oxygen dissolved depletion in the interface water-sediment under salmon farms are related to a low species diversity of benthic marine invertebrates in areas under high aquaculture pressure (e.g. Northern Patagonian Fjords of Chile; Villalobos et al. 2021).

To address some of these impacts, Protected Areas have been established in Chile. Protected areas are "clearly defined geographical space, recognised, dedicated and managed through legal or other effective means, to achieve the long term conservation of nature with associated ecosystem services and cultural values" (IUCN Definition 2008; source: https://www.iucn.org/theme/protected-areas/about). From the total area of Chile, including both its islands and continental territories, 20.9% is categorised as terrestrial protected areas (Figure 2D). Marine protected areas (MPAs), defined as "any area of the intertidal and subtidal terrain together with its overlaying water and associated flora, fauna, historical and cultural features, which has been reserved by law or other effective means to protect part of all of the enclosed environment" (IUCN Definition 2008; source: https://www.iucn.org/theme/protected-areas/about), are zones where the fisheries and other activities are spatially limited, and they are considered as spawning sites and nursery ground (Palumbi 2004). From the total area of Chile, including both its islands and continental territories, 41.3% is classified as marine protected areas (UNEP-WCMC 2020). However, according to the Atlas of Marine Protection, which based their classification on a strict categorisation of MPAs, only 5.8% of the total area of Continental Chile is covered by MPAs, and the fully marine protected areas (marine reserved) correspond only to 37.6km^2, a very small part of the total area of Chile (Figure 2D).

Another important tool for managing marine ecosystems in Chile is Territorial Use Rights for Fishers (TURFs), also known as Management and Exploitation Areas for Benthic Resources (MEABR). In this Thesis, I will use the term TURFs because it has a wider use at global level. TURFs are a form of co-management, where fishers are assigned to small-scale fisher unions in specific coastal areas (Castilla 1994) for the management of inshore benthic resources strongly exploited by small-scale fisheries (Castilla et al. 1998, Gelcich et al. 2008b). These defined areas range from ~50 to 300ha of seabed (Gelcich et al. 2008b). TURFs were developed as a reaction to the overfishing of important benthic species such as gastropods *C. concholepas* (Chilean abalone), *Fissurella* spp (key-hole limpet), and sea urchins *L. albus* (Gelcich et al. 2008a). TURFs, as a management tool, restrict the access to the total area, avoiding the extraction of benthic target-species (Castilla et al. 1998). TURFs have had a positive impact on the recovering of benthic target-species populations strongly overexploited in the past (Gelcich et al. 2008b), also increasing species abundances, body size, and recruitment of benthic invertebrates more generally, and impacting the trophic structure of inshore communities (Castilla et al. 1998, Gelcich et al. 2008b). These management tools have also positively changed the perception of fishers regarding the benefits of these protectiveness measures (Gelcich et al. 2008a). Thus, TURFs have improved Chilean marine ecosystem services such as support for biodiversity conservation, larvae production of species of economic importance, pelagic and benthic small fisheries, food provision, social engagement with marine ecosystems, and cultural and recreation (Gelcich et al. 2019). Even considering their benefits, the efficacy of the TURFs in Chile, as a bottom-up type of governance, cannot replace the need of PAs and they can be seen as a good complement for conservation purposes (Gelcich et al. 2008b). Moreover, ~40% of TURFs in Chile are inactive or abandoned (Gelcich et al. 2017). According to Gelcich et al. (2019), there is a gap in the Chilean literature regarding the relationship between TURFs and drivers of global change or environmental stressors with the aim to predict their effects on these areas and to adapt the policy in a suitable way.

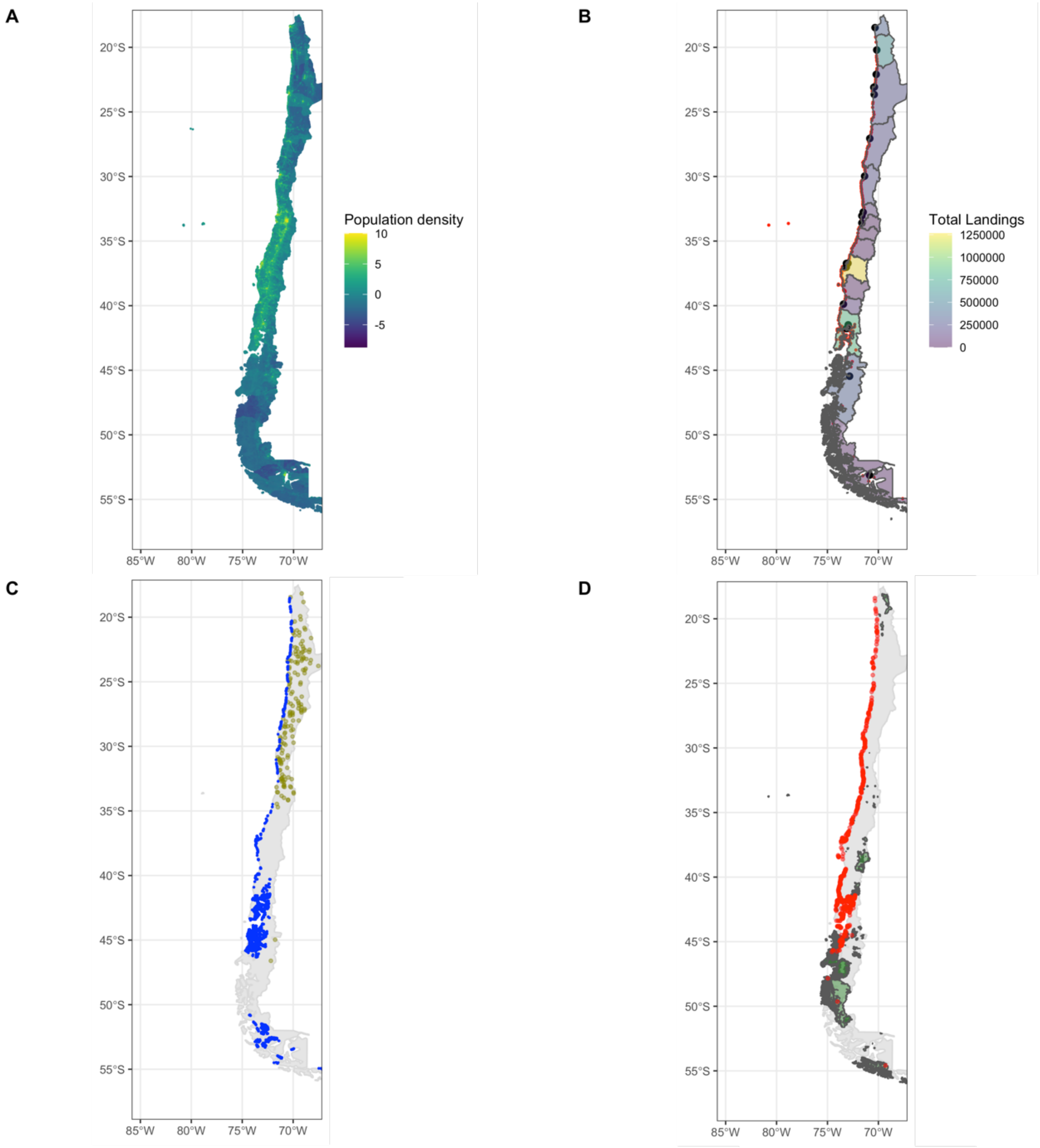

Figure 2. Main anthropogenic activities influencing the coastline and continental shelf of Chile and protectiveness measures. **A)** Chilean population density. **B)** Small harbours (red points), Trading ports (Black points), and total landings according to the administrative divisions. **C)** Mining (yellow point), and aquaculture (blue points). **D)** Protected areas (green areas), and TURFs (red points).

1.5. Structure of the Thesis

My thesis consists of the four following chapters.

Chapter 2: Development of an integrated biodiversity database for benthic marine invertebrates of Chile

The main aim of Chapter 2 was to construct an integrated and standardised biodiversity database for benthic marine invertebrates of Chile based on five sources of information with the main objective to be suitable for further macroecological analyses. The sources of information correspond to environmental surveys, a fourth to a research cruise and the last to the global database Ocean Biodiversity Information System (OBIS). Firstly, I describe each of the five datasets built from the information sources in terms of occurrences, stations, geographical distribution, sampling methodology, and taxa composition. Secondly, I describe some considerations regarding lack of information, differences in methodologies, and data standardisation. Finally, I assess the pros and cons of the database and how these datasets are complementary in terms of geographical distribution, occurrences, and taxonomic composition.

Chapter 3: Spatial patterns in the diversity of benthic marine invertebrates along the Chilean coastline and continental shelf

In Chapter 3, I aim to respond to one main question: What are the major spatial patterns in the diversity of benthic marine invertebrates throughout the Chilean coastline and continental shelf? I use the integrated biodiversity database constructed in Chapter 2. A range of diversity measures designed to deal with uneven sampling efforts, such as nonparametric metrics and taxonomic distinctness, were used to estimate species richness and taxonomic diversity. Thus:

- I compare observed and estimated species richness among the five Chilean ecoregions described previously.
- I describe spatial patterns of species richness (nonparametric richness) and taxonomic distinctness (taxonomic diversity) through the five Chilean ecoregions using the latitude gradient.
- I identify hotspots of species richness and taxonomic diversity and their congruence.

Chapter 4: Do spatial patterns in the functional diversity of benthic marine invertebrates along with the Chilean coastline and continental shelf match those in species richness and taxonomic diversity?

In Chapter 4, I aim to evaluate whether functional diversity patterns of benthic marine invertebrates match with the observed patterns for species richness and taxonomic diversity described in Chapter 3. I use eight quantitative and qualitative biological traits related to the ecology, morphology, and life history of 762 species of benthic marine invertebrates to estimate four functional diversity metrics. Thus:

- I respond to the research question by describing functional diversity patterns with latitude through the five Chilean ecoregions.
- I identify hotspots of functional diversity.
- I evaluate congruence among hotspots of functional diversity.
- I evaluate congruence among hotspots of functional diversity, species richness, and taxonomic diversity described in Chapter 3.
- I assess complementarity between functional diversity, species richness, and taxonomic diversity.

Chapter 5: How do key environmental drivers and human activities influence the spatial patterns of benthic marine invertebrates in Chile?

In Chapter 5, I aim to identify key environmental drivers (interaction between factors) and human activities influencing the spatial patterns of benthic marine invertebrates. I use a set of water and sediment variables (environmental factors) and some anthropogenic activities that directly or indirectly influence Chile's coastline and continental shelf. I use four measures of diversity in total: species richness, taxonomic diversity, and two functional diversity metrics to assess their relationship with environmental factors and anthropogenic activities. Thus:

- I evaluate the relationship between diversity metrics and environmental factors, identifying the most important.
- I describe the latitudinal patterns through the five Chilean ecoregions of the most important environmental factors.
- I evaluate the relationship between diversity metrics and anthropogenic activities, identifying the most important.

2. Development of an Integrated Biodiversity Database for Benthic Marine Invertebrates of Chile

2.1. Abstract

Local datasets have the potential of being merged into integrated databases with clear advantages to developing macroecological research. This chapter elaborates an integrated database of benthic marine invertebrates combining data from three Chilean surveys (survey datasets), one Chilean scientific cruise and the global database OBIS (research datasets). The resulting database presents 34,183 occurrences to 766 species from 10 phyla, covering a time from 1991 to 2017 and a geographical range between 18° to 57° S from 110km to the coast. The resulting integrated database was gridded into equal-area cells of 55 x 55 km for subsequent analyses. The survey's datasets contribute more to the species incidence. Research's datasets contribute more to species occurrences and show a higher species accumulation rate. The phyla with a higher number of species were Mollusca, Annelida, and Arthropoda. The occurrences mainly were at around 42° S. The number of species per grid cell was highly related to the number of stations per grid cell. The integrated database presents similar issues to global databases regarding frequency, imperfect detectability, and differences in species occurrences between coastal and continental areas and the methodologies used. However, it has advantages related to the complementarity of the datasets composing the integrated database in terms of coverage in geographic range, time and have associated some relevant environmental information.

2.2. Introduction

In the last few decades there has been an increasing interest in storing and protecting marine diversity data through their compilation in different local datasets. These local datasets have the potential to be merged into integrated and open access databases, producing global repositories which have brought clear advantages to develop regional and macroecological spatial and temporal research, between them the reduction of costs related with collecting data (Edgar et al. 2016), or problems associated with lack of ethics in some experiments (e.g. physiological thermal experiments; Webb et al. 2020). Thus, research based on different levels of spatial and temporal scales has played a key role in marine ecology (Edgar et al. 2016). These databases organise and store records in tables connecting information from different sources (Griffiths et al. 2003). In addition, integrated databases demand the willingness of researchers, government agencies, and citizens to share, record, maintain and allow open access to these databases.

Ideally, a suitable integrated biodiversity database should include records collected from comparable methodologies encompassing a wide geographical range (Renaud et al. 2009). There are some examples of successfully integrated databases. For instance, the European Macrobenthic fauna database (MacroBen) was created by the European network on Marine Biodiversity and Ecosystem Functioning (MarBEF). This database integrated 44 datasets with records of macrobenthic fauna from soft bottoms (Vanden Berghe et al. 2009). The spatial scope of the MacroBen database meant that questions, for example, about latitudinal diversity gradients (Renaud et al. 2009) could be addressed on much larger scales than had previously been possible. The Southern Ocean Mollusc Database (SOMBASE), which relates species and georeferenced information, was constructed from ecological and systematic papers, research reports and raw data (Griffiths et al. 2003). Questions addressed using this database have included analysis of gastropod and bivalve diversity throughout the Southern Ocean (Clarke et al. 2007). Thus, the efforts to construct these repositories have brought great benefits for the knowledge of marine biodiversity in a macroscale, which without their existence might have been impossible or may have taken longer.

Building on these regional initiatives, the Ocean Biodiversity Information System (OBIS 2022), originating during the Census of Marine Life (Grassle 2000), has grown to become the largest global open-access database of marine species occurrences (Thompson et al. 2021). OBIS integrates records from c.1,700 different datasets each with its own objectives and methodologies (Edgar et al. 2016). Currently, OBIS contains about 60 million occurrence records for more than 120,000 marine species (Webb & Vanhoorne 2020), and holds data from diverse OBIS nodes (e.g. FishBase), and other providers (e.g. local datasets; Webb et al. 2010). OBIS has been used widely; for example, in a global context, OBIS has allowed us to determine spatial bias and gaps of biodiversity, thus, it has been estimated that midwater biodiversity is extremely under-represented in comparison with surface water and the sea bed (Webb et al. 2010). OBIS has also allowed us to estimate the thermal affinity of marine species on a global scale, through the match of species occurrences and sea temperature records (e.g. Webb et al. 2020), as well as the assessment of the stability of the global biogeographic patterns of benthic marine species in a long-term scale, comparing between current and cenozoic biogeography (e.g. Kocsis et al. 2018). In addition, OBIS enabled matching species occurrences with other global environmental databases such as Bio-ORACLE (Tyberghein et al. 2012, Assis et al. 2018), as well as comparing them with the fossil register of marine species using the Paleobiology database, and to complement data with other more specific databases (e.g. GlobTherm databases; see Kocsis et al. 2018). These are only some of the potential uses and advantages of accounting with global open access repositories.

Thanks to initiatives such as OBIS, access to marine biodiversity data has greatly improved; however, these data present biases associated with the wide differences in spatial and geographical precision, temporal scale, methodological differences, as well as with the imperfect detectability (i.e. possibility of difference a true species absence; Edgar et al. 2016), and a higher number of occurrences in well-known taxa (e.g. vertebrates; Webb & Vanhoorne 2020). Thus, macroecological research based on integrated databases can face difficulties due to the lack of standardisation of sampling methods, species names, as well as in the organisation of records, and differences in sampling efforts and sampling intensity (e.g. Clarke et al. 2007, Renaud et al. 2009, Vanden Berghe et al. 2009) where some geographical areas are more sampled than others. The differences in sampling effort have an impact on recorded species richness, the simplest measure of diversity (Johnston & Roberts 2009). This means that the highest species richness is typically observed in localities under intense research activity (Clarke et al. 2007), a pattern which can remain even after methods have been applied to correct for sampling (Clarke et al. 2007). Thus, differences in sampling effort are a limitation in studies of distribution patterns on a macroscale using integrated datasets (Clarke & Lidgard 2000, Miloslavich et al 2011).

Chilean coastal waters span ~39° of latitude (18° 30'' to 57° 30'' S; Fernández et al. 2000), encompassing important variation in temperature, salinity, oxygen, and primary productivity. This portion of the western Pacific Ocean is impacted by two main current systems, the Humboldt Current System (HCS, towards the Equator; Thiel et al. 2007), and Cape Horn Current System (CHC, towards the Southern Pole; Silva et al. 2009). The HCS is particularly productive due to upwelling of cold and nutrient-rich waters (Camus 2001, Thiel et al. 2007), as well as being influenced by El Niño Southern Oscillation (ENSO) periods. On the other hand, the CHC system is influenced by inputs of organic matter, and freshwater (Silva et al. 2009, Quiroga et al. 2012, 2016), creating a transitional marine system (Iriarte et al. 2010) of estuaries, channels and fjords. Part of these coastal and heterogeneous marine ecosystems are the benthic marine invertebrates. These organisms provide a range of ecosystem services (Rife 2018). For example, they support higher trophic levels in marine food webs (Gray & Elliott 2009), as well as directly providing food to humans (Rife 2018), through the benthic fisheries. Invertebrates are also central to ecosystem functions including bioturbation, biogeochemical cycles, waste material recycling and take of harmful substances (Cooper et al. 2008). In particular, bioturbators contribute to biogeochemical cycles, increasing the depth of the oxygenated layer in the sediment, thus increasing oxygen exchange at the water-sediment interface (Gray & Elliott 2009). Moreover, benthic invertebrates may be used as bioindicators because of their variety of responses to environmental pressures (Muniz et al. 2005).

Fernandez et al. (2000) argued that the reduced number of marine studies at mesoscale in Chile is related to the lack of appropriate databases, the concentration of research in a few sites, and the low sampling intensity. Even though some efforts to construct an integrated database have been attempted recently (e.g. Marin et al. 2014, 2020, unpublished), as yet there is no single database integrating georeferenced information related to Chilean benthic invertebrates. However, some existing surveys of benthic organisms, including information on sediments and water column characteristics, do cover a large proportion of Chile's marine waters. For instance, The National Fisheries Service (known in Spanish as SERNAPESCA), and the Fisheries Development Institute of Chile (known in Spanish as IFOP) carry out monitoring with the aim of assessing the effect of aquaculture on benthos, sediments and water column. Both of these surveys use the same sampling methodologies (SUBPESCA 2009, Exempt Resolution N° 3612/2009). The Department of Maritime Territory and Merchant Marine of Chile (known in Spanish as DIRECTEMAR) coordinates a marine monitoring programme to evaluate more broadly the effects of human activities (e.g. industrial and household wastes, and aquaculture) over the coastal areas close to large urban centres. The Marine Investigation Cruises in Remote Areas (known in Spanish as CIMAR) aim to evaluate the effect of human activities such as aquaculture, tourism, and fisheries on the system of fjords in southern Chile, as well as to improve knowledge of the more pristine zones (Silva & Palma 2006). In addition to these dedicated surveys, additional data exists for Chilean waters within OBIS.

The main objective of this chapter is therefore to combine data from the four Chilean surveys together with OBIS to create an integrated database of benthic marine invertebrate species for Chile. The aim is to create a new standardised database suitable for further macroecological analyses. In this chapter I first describe the datasets composing the database in terms of species occurrences (defined as the number of specific geographical locations at which a species has been recorded as present) and species incidence (defined as the number of distinct sampling events at a specific geographical location in which a species has been recorded as present) in research datasets (CIMAR + OBIS) and survey datasets (SERNAPESCA + IFOP + DIRECTEMAR). I also describe the geographical distribution of species occurrences and species richness, the number of stations sampled, and differences in sampling methodology and taxonomic composition.

2.3. Materials and Methods

2.3.1. Database collation

A database of Chilean benthic invertebrates identified to a taxonomic resolution of "species" was constructed from five sources of information. Three of them correspond to environmental monitoring along the Chilean coast (survey datasets), a fourth corresponds to an annual cruise throughout the Patagonian Fjords, and the last is the global Ocean Biodiversity Information System (research datasets; OBIS, 2022).

i. . SERNAPESCA

Since 2001, the Chilean National Fisheries Service (known in Spanish as SERNAPESCA) has collated information generated by environmental consultants. The information gathered by SERNAPESCA covers benthic macrofauna (benthic invertebrates retained in a 1mm sieve; SUBPESCA 2009, Exempt Resolution N° 3612/2009), sediments and water columns directly influenced by aquaculture of molluscs and salmon along the Chilean continental shelf. Therefore, the samples (i.e. the material collected by station) are obtained within the area covered by the aquaculture farm. Since 2014, SERNAPESCA has monitored the sampling to guarantee the quality of the data. As a result, only data from 2014 to 2017 were included in the dataset (Table 1; Figure 4).

The SERNAPESCA dataset presented a total of 18,630 occurrences (i.e. species presence at a specific geographical location) from 5,842 stations defined as a unique code obtained joining the year, and the longitude and latitude which determine the geographical location where each occurrence was obtained; Table 1). The methods of sampling and analysis are described in a reference document known as Exempt Resolution N° 3612/2009 (SUBPESCA 2009); this resolution establishes the sampling of soft sediments at a depth of up to 60 metres using 0.1m^2 Van Veen grabs (Table 1). This survey encompasses 27° to 54° S latitude, with the major concentration of the sampling being located in the southern zone of Chile where the aquaculture is strongly developed (Figure 3). A total of 217 species were identified in this dataset, corresponding to the phylum Mollusca (84 species, 39%), Arthropoda (63 species, 29%), Annelida (46 species, 21%), Echinodermata (18 species, 8.3%), Cnidaria (3 species, 1%), Brachiopoda (2 species, 0.9%), and Nemertea (1 species, 0.5%; Table 2).

ii. IFOP

Since 2012, the Fisheries Development Institute of Chile (known in Spanish as IFOP) has carried out annual monitoring of the environmental status of benthos, sediments, and the water column under the influence of aquaculture in Chile. The information gathered by IFOP covers benthic macrofauna (benthic invertebrates retained in a 1mm sieve; SUBPESCA 2009, Exempt Resolution N° 3612/2009), sediments and water columns influenced by aquaculture of molluscs and salmon along the Chilean continental shelf. In comparison with SERNAPESCA, IFOP locates the stations outside the farms (e.g. between two different farms, or in the centre point among a group of farms). The methodology used by IFOP is described in the Exempt Resolution N° 3612/2009 (SUBPESCA 2009), this resolution establishes the sampling of soft sediments at a depth of up to 60 metres using 0.1m^2 Van Veen grabs (Table 1). The range of latitude encompassed by this survey is 27° to 52° S, with the major concentration of the sampling being located within the southern zone of Chile where the aquaculture activity is strongly developed (Figure 3). The information is available on https://www.ifop.cl, where the data were extracted to construct a unified dataset.

From 2012 to 2017, IFOP dataset presented 10,975 occurrences (i.e. species presence at a specific geographical location) from 1,393 stations (Defined as a unique code obtained joining the year, and the longitude and latitude which determine the geographical location where each occurrence was obtained; Table 1). A total of 182 species were identified in this dataset, corresponding to the phylum Mollusca (79 species, 43%), Arthropoda (49 species, 30%), Annelida (48 species, 26%), and Echinodermata (6 species, 3%; Table 2).

iii. DIRECTEMAR

Since 1988, the Department of Maritime Territory and Merchant Marine of Chile (known in Spanish as DIRECTEMAR) has carried out the Observation Programme of the Littoral Environment (known in Spanish as POAL). This programme studies the effect of human activities on benthos, sediment and the water column in Chile near to the coastline. Information is only available for 2013, 2014 and 2015 (Table 1) from different spreadsheets on the DIRECTEMAR webpage https://www.directemar.cl. The dataset includes only soft-bottom organisms from shallow waters to 49 metres of depth. The samples (i.e. the material collected by station) were obtained using a core with an area of $0.056m^2$. The type of organism considered was identified as benthic fauna, but the specific size was not given. The range of latitude covered by this survey is 18° to 55° S (Figure 3).

From 2013 to 2015, DIRECTEMAR dataset presented 1,670 occurrences (i.e. species presence at a specific geographical location) from 524 stations (Defined as a unique code obtained joining the year, and the longitude and latitude which determine the geographical location where each occurrence was obtained; Table 1). A total of 115 species were identified in this dataset, corresponding to the phylum Mollusca (69 species, 60%), Arthropoda (24 species, 21%), Annelida (18 species, 16%), and Echinodermata and Cnidaria (2 species, 2%, respectively; Table 2).

iv. CIMAR

Since 1995, Cruises of Marine Investigation in Remote Areas (known in Spanish as CIMAR) prepared by the National Oceanographic Committee (known in Spanish as CONA) have been carried out with the aim of studying the Austral Zone of Chile (Silva & Palma 2006). The range of latitude encompassed by the CIMAR survey was 41° to 56° S (Figure 3). Sources of information from CIMAR were diverse. They included the website of Hydrographic and Oceanographic Service of the Chilean Navy (known in Spanish as Shoa) http://www.shoa.cl, scientific papers and technical reports as well as directly, by request, from the National Centre of Hydrographic and Oceanographic information of Chile (known in Spanish as CENDHOC). A list of technical and scientific reports is provided in Supporting information (Appendix S1).

CIMAR has been widely used in the biodiversity research of Chile (e.g. 82 scientific publications were published based on CIMAR records until 2006; Silva & Palma 2006), and the taxonomic identification is done or validated by taxonomists experts. CIMAR does not have a specific format, database, or a unique repository. All data are found in different Excel sheets containing more than one table, or in scientific reports, and the presentation of the raw data depends exclusively on the main researcher. This makes it difficult to access the information. Therefore, there was no access to new information of benthic invertebrates up to 2014.

The information obtained from CIMAR did not present the stations as a variable to all the species occurrences (i.e. species presence at a specific geographical location), therefore a code for station was obtained joining the year of sampling, and the longitude and latitude, therefore each occurrence was related to a station. From 1995 to 2014, the CIMAR dataset presented 1,969 occurrences from 293 stations (Defines as a unique code obtained joining the year and the longitude and latitude which determine the geographical location where each occurrence was obtained; Table 1). The main aim of the CIMAR changed each year, and as a consequence the dataset included marine invertebrates, from soft and hard bottom, and obtained using different sample devices. For example, box corer (87 stations, 30% of the total number of stations), Agassiz trawl (173 stations, 59% of the total number of stations), and diving (4 stations, 1.4% of the total number of stations); the type of device used was not identified in 29 stations (10% of the total number of stations). The dataset includes organisms > 0.01mm to > 0.5mm (Table 1). However, at around 50% of the stations the sieve used was not identified. The range of depth of the stations was between 2.5 and 933 metres; however, not all the occurrences presented data for depth. A total of 323 species were identified in this dataset, corresponding to the phylum Mollusca and Annelida (both of them with 110 species, 68% of the total number of species), Arthropoda (50 species, 16%), Echinodermata (49 species, 15%), Brachiopoda (2 species, 0.6%), and Bryozoa and Cnidaria (1 species, 0.3%, respectively; Table 2).

v. OBIS

Data for Chile were extracted from the global Ocean Biodiversity Information System OBIS (OBIS, 2022). OBIS was created as part of Census of Marine Life (Grassle, 2000) to provide standardised and georeferenced information on the diversity, abundance and distribution of marine organisms. OBIS contains occurrence records from more than 1,700 different datasets, each of them with its own objectives and methodologies (Edgar et al. 2016). Standard information for each record includes species name, decimal longitude, decimal latitude, and source of information, with many records including additional information on a range of additional variables such as sampling station, date of sampling, depth, number of individuals, biomass (grams of individuals of a species per square metre), species density (number of individuals of a species per square metre), the dredge or device used to obtain the sample, and the mesh size used.

I obtained all occurrence records in OBIS for Chile using the `checklist()` function in the `robis` package (Provoost & Bosch 2018) in R 3.5.1 (R Core Team 2018), and specifying as a geometry search term the boundary of the Chilean Exclusive Economic Zone (EEZ) using `mregions` package (Chamberlain 2022). The species were standardised and identified as benthic using species attributes available in the World Register of Marine Species (WoRMS; https://www.marinespcies.org; WoRMS Editorial Board 2022), accessed using the package `worrms` (Chamberlain 2020) and an additional function available from https://github.com/tomjwebb/WoRMS-functional-groups (Webb 2020). Only records identified as adult stages were added to the dataset. The benthic species corresponded to meiofauna (63 to 500um), macrofauna (500um to 5cm), and megafauna (> 5cm). All species names were matched to WoRMS using the taxon matching tool available on http://www.marinespecies.org to standardise taxonomic nomenclature. The validated name from WoRMS, and their respective phylum, class and valid species ID (AphiaID) were added to the database following this standardisation. Full occurrence records for this set of benthic species were then obtained using the `occurrence()` function in the `robis` package. The full code used to generate the OBIS Chilean benthos dataset is provided in Supporting information (Appendix S2).

OBIS presents a lack of structure due to the variety of datasets composing the database, as well as the non-possibility of distinguishing a true species absence (i.e. imperfect detectability; Edgar et al. 2016). Miloslavich et al. (2011) argued for the importance of improving OBIS Latin America through the increasing number of shared data from taxonomic experts. Thus, there were some attempts to fill gaps in biodiversity information in Latin America. For example, the creation of a regional OBIS (Chile, Argentina and Brazil) with georeferenced records belonging from the Census of Marine Life and focused mainly in unexplored areas (Miloslavich et al. 2011) was established in 2002. However, since 2015, information about Chilean benthic marine invertebrates has not been updated, which means that the aim of promoting and implementing a unique database where records are organised and integrated has been only partially achieved in Chile.

Therefore, in the OBIS dataset, information on Chilean benthic invertebrates is available from 1846 to 2014 (Figure 4). Not all the occurrences obtained from OBIS presented the stations as a variable, therefore a code was obtained joining the year of sampling, and the longitude and latitude, and this new variable called station was associated with each species occurrence (i.e. species presence). As a result, from 1846 to 2014, the OBIS dataset presented 3,559 occurrences from 1,086 stations (Table 1). The range of latitude covered by the stations was 18° to 59° S (Figure 3). The range of depth of the stations was between 2.5 and 933 metres (Table 1); however, not all the occurrences presented data related to depth. I did not dig into individual dataset metadata to obtain the type of device used to the invertebrates obtention, nevertheless, OBIS was used as a unique dataset, obtained from a variety of sampling methods with the aim to complement the information from the three surveys dataset and CIMAR, previously described. The occurrences provided for OBIS could be relevant due to the lack of data for the northern latitudes of Chile (Figure 3).

A total of 1,129 species were identified in the OBIS dataset, corresponding to the phylum Mollusca (191 species, 17%), Foraminifera (177 species, 16%), Annelida (159 species, 14%), Echinodermata (157 species, 14%), Arthropoda (146 species, 13%), Porifera (108 species, 10%), Cnidaria (101 species, 9%), Bryozoa (74 species, 7%), Nematoda (7 species, 0.6%), Nemertea and Sipuncula (4 species, 0.4%, respectively), and Hemichordata (1 species, 0.1%; Table 2).

Table 1. Summary details of datasets used to construct the benthic invertebrate database (Compiled by author).

Dataset	**Geographic coverage (South Latitude)**	**Temporal cover**	**No. of occurrences ***	**No. of stations ****	**Depth range (metres)**	**Sampling device used**	**Area device (m^2)**	**Sieve size (mm)**	**Type of organism**
SERNAPESCA	27° - 54°	2014 - 2017	18,630	5,842	0 - 60	Van Veen grab	0.1	1	Benthic macrofauna > 1mm
IFOP	27° - 52°	2012 - 2017	10,975	1,393	0 - 60	Van Veen grab	0.1	1	Benthic macrofauna > 1mm
DIRECTEMAR	18° - 55°	2013 - 2015	1,670	524	0 - 49	Core	0.056	Not specified	Benthic macrofauna (Size not specified)
CIMAR	41° - 56°	1995 - 2014	1,969	290	2.5 - 933	Agassiz net / Cores / Diving / Not specified	Not specified	0.01 to 0,5	Benthic invertebrates/ (Size not specified)
OBIS	18° - 59°	1846 - 2014	3,558	1,086	0 – 5,929	Not specified	Not specified	Not specified	Benthic fauna (Size not specified)

* Occurrence: Species presence at a specific geographical location.

** Station: Defined as a unique code obtained joining the year, and the longitude and latitude which determine the geographical location where each occurrence was obtained.

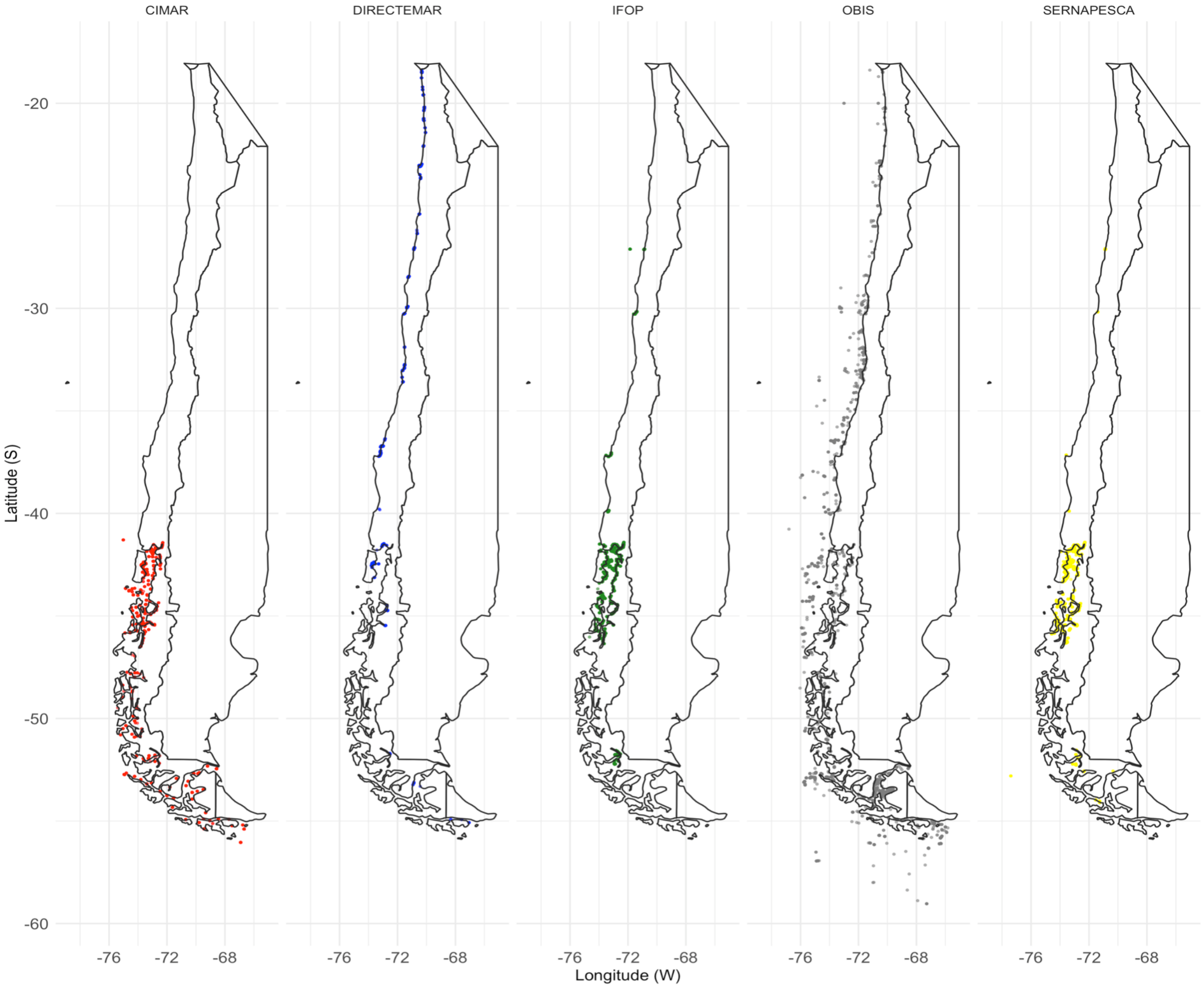

Figure 3. Distribution of the occurrences of the five datasets CIMAR, DIRECTEMAR, IFOP, OBIS, and SERNAPESCA along the Chilean latitudinal gradient.

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Table 2. Number of species per phylum across the five datasets.

Phylum	SERNAPESCA	IFOP	DIRECTEMAR	CIMAR	OBIS
Mollusca	84	79	69	110	191
Arthropoda	63	49	24	50	146
Annelida	46	48	18	110	159
Echinodermata	18	6	2	49	157
Cnidaria	3		2	1	101
Brachiopoda	2			2	
Nemertea	1				4
Bryozoa				1	74
Foraminifera					177
Porifera					108
Nematoda					7
Sipuncula					4
Hemichordata					1
Total	217	218	115	323	1129

2.3.2. Data processing

The five datasets were combined to produce a single composite database of Chilean benthic invertebrate occurrences (i.e. species presence at a specific geographical location). The database only accounts for species level. Juveniles of individual species and parasitic species were excluded from the database. WoRMS (Horton et al. 2022) was used to standardise the taxonomic information across the datasets, using the online Taxon Match tool available at http://www.marinespecies.org/aphia.php?p=match. Because not all constituent datasets included information on biomass or abundance, the final dataset recorded occurrences only of these species, which will also be more robust to variation in sampling methodology. SERNAPESCA, IFOP, DIRECTEMAR, and CIMAR have different aims, they are focused on different areas, and they have not contributed invertebrate data to the OBIS global dataset, as a consequence the main database did not present duplicated information.

Due to not all datasets specifying depth of each occurrence, only the occurrences within a distance of 110km from the coast, using the function `lookup_xy()` in the `obistools` package (Provoost & Bosch, 2022). This will be key to relating biodiversity with sediment and water covariates, and the impact of coastal human activities on biodiversity in the following chapters.

Because not all datasets included information on sampling stations (e.g. CIMAR and OBIS), I used the same methodology described above on CIMAR and OBIS datasets, to standardise the variable 'station' to the whole database. I joined the year of sampling, and the longitude and latitude of each occurrence. This variable was connected to each occurrence of a species. More details about the variables are given in the metadata (Table S1).

The combined dataset included 36,718 occurrences to 1,412 benthic species for the 13 phyla present in Table 2, and collected between 1,846 and 2,017, although most occurrences were made after 2012 (Figure 4). As a result, for future analyses, I decided to focus on the occurrences between 1991 to 2017 because of the possibility of accounting for sediment and water variables available for this period of time. Even this period presented a lack of occurrences in 1993, and a low number of occurrences (<50), for example, in 1992, 1998 to 2000, and 2005 to 2011 (Figures 4B, C).

The resulting integrated dataset was gridded into equal-area cells of 55 x 55 km for subsequent analyses. Spatial data were re-projected from decimal latitude and longitude (WGS84) onto an Albers Equal Area Conic projection (ESRI projection 102033), due to the geographic position and elongated shape of Chile. This spatial data manipulation was performed using the R packages `sp` (Pebesma & Bivand 2005; Bivand et al. 2013), and `raster` (Hijmans 2021).

2.3.3. Diversity dataset 1991-2017

The species occurrences in the research (OBIS and CIMAR) datasets were compared with the species occurrences in the survey datasets (SERNAPESCA, IFOP, and DIRECTEMAR) with the aim to observe how they contribute to the diversity of species in terms of incidence (i.e. defined as the number of distinct sampling events at a specific geographical location in which a species has been recorded as present). To compare the five datasets and their contribution to the database, the species accumulation curves (SAC) were used to observe the rate of accumulation of species with respect to a sampling effort measure (Colwell et al. 2012), in this case the number of stations. The analysis was performed using the function `specaccum()` in the `vegan` package (Oksanen et al. 2020). A frequency matrix species by stations (i.e. number of occurrences of each individual species by stations) was used as an argument in the function, and 999 permutations. A Kruskal Wallis test was carried out to observe significant differences between the average species richness in the five sources. A

Wilcoxon rank sum test was performed to observe which pairwise groups show statistically significant differences.

For the complete dataset, the species richness at grid cells level was obtained counting the number of individual species per cell equal to 55 x 55. The number of species by grid cell was also obtained by taxa. The same methodology was used for the number of stations at grid cell level. The Pearson correlation was obtained between the number of species and the number of stations.

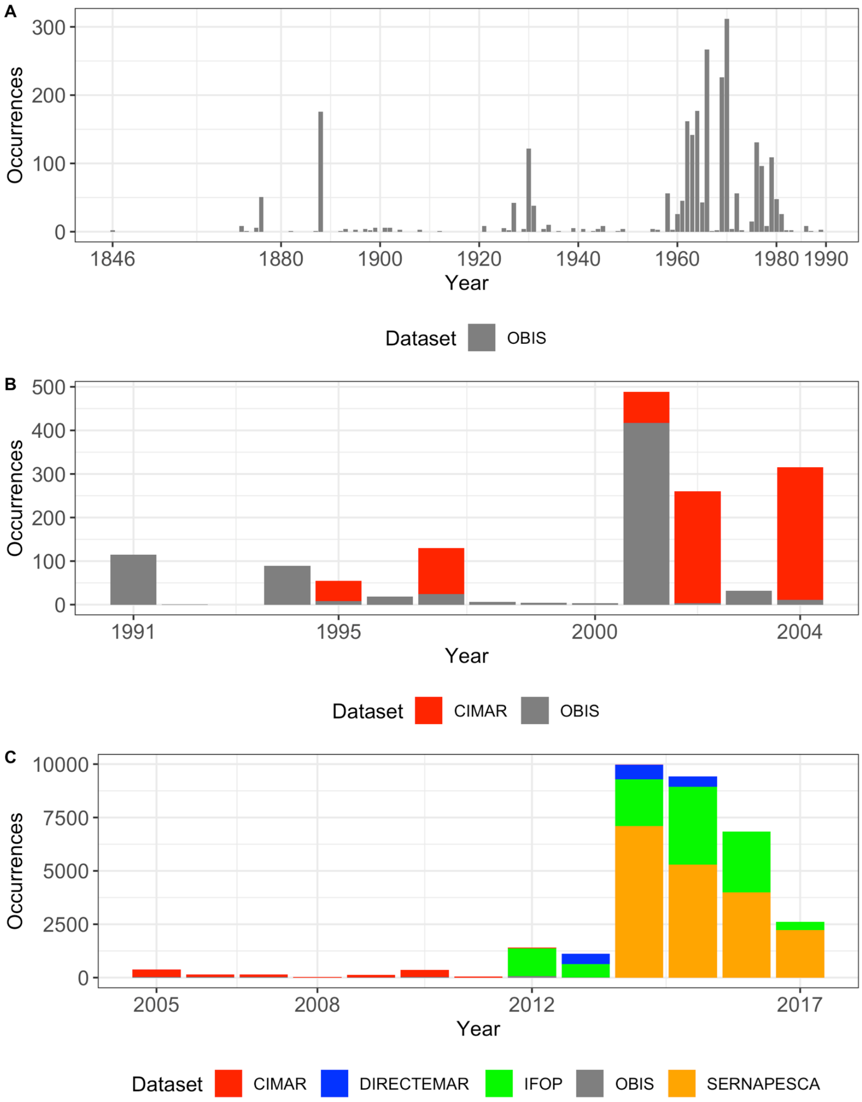


Figure 4. Occurrences through the time for the three periods: **A)** 1846 - 1990, **B)** 1991 - 2004, and **C)** 2005 - 2017.

2.4. Results

2.4.1. Dataset 1991 to 2017

The latitude covered ranged between 18° to 57° S, with occurrences only within 110km of distance from the coast (Figure 5). SERNAPESCA, IFOP, and CIMAR datasets mainly occurred in southern zones (Figure 5), OBIS and DIRECTEMAR occurred throughout the latitudinal gradient, and both datasets contribute with occurrences to the northern zone (Figure 5). The dataset presented 34,183 occurrences to 766 benthic marine invertebrates' species from 10 phyla (Table 3).

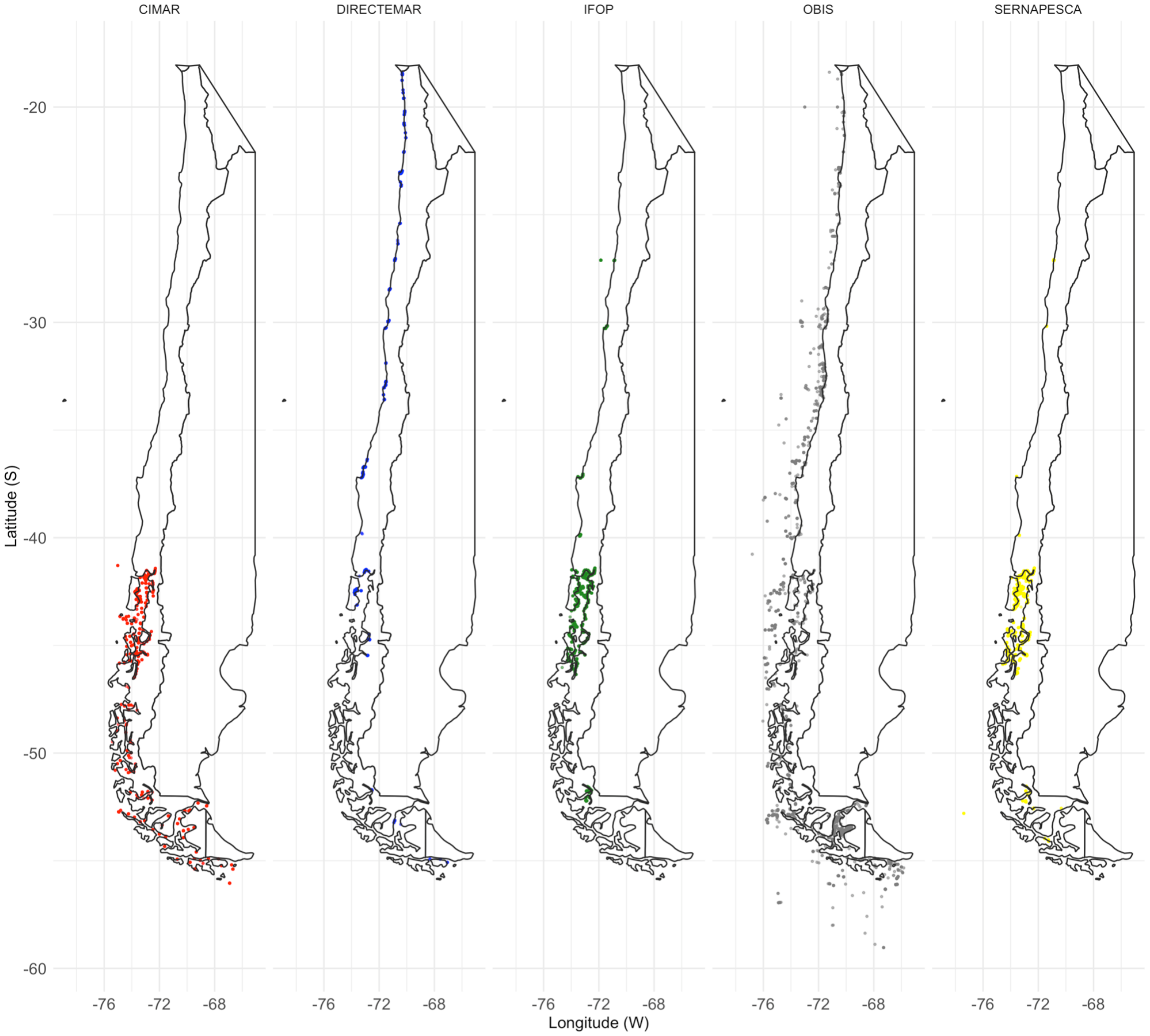


Figure 5. Distribution of the occurrences of the five datasets: CIMAR, DIRECTEMAR, IFOP, OBIS, and SERNAPESCA along the Chilean latitudinal gradient for the period 1991 to 2017.

Table 3. Number of species per phylum.

Phylum	Number of species	%
Mollusca	214	28
Annelida	168	22
Arthropoda	127	17
Foraminifera	87	11
Echinodermata	66	9
Porifera	40	5
Cnidaria	38	5
Bryozoa	20	3
Brachiopoda	2	0.3
Nemertea	1	0.1

Surveys and Research datasets shared 141 species. A total of 167 species only occurred in the survey's datasets, while 455 species occurred only in the research's dataset (Figure 6A). From the 766 species, 235 presented only one occurrence (i.e. singletons), equivalent to 31%. The survey's dataset contributes more with the incidence of the species (defined as the number of distinct sampling events at a specific geographical location in which a species has been recorded as present; grey square Figure 6A); the research datasets contribute with species occurrences (i.e. Species presence at a specific geographical location; yellow square Figure 6A).

The CIMAR dataset, followed by the OBIS dataset, showed the highest rate of species accumulation with the increase of the number of stations. Neither dataset reached an asymptote (Figure 6B). The IFOP dataset reached an asymptote at around 150 species (Figure 6B). DIRECTEMAR and SERNAPESCA datasets reached an asymptote at around 100 species (Figure 6B). There were significant differences in the average species richness between datasets (Kruskal Wallis chi-squared = 664, df = 4, $p < 0.0001$). The pairwise comparison showed that there were significant differences between all the tested pairs (Wilcoxon rank sum test, $p < 0.0001$) with the exception of DIRECTEMAR and SERNAPESCA (Wilcoxon rank sum test, $p = 0.08$).

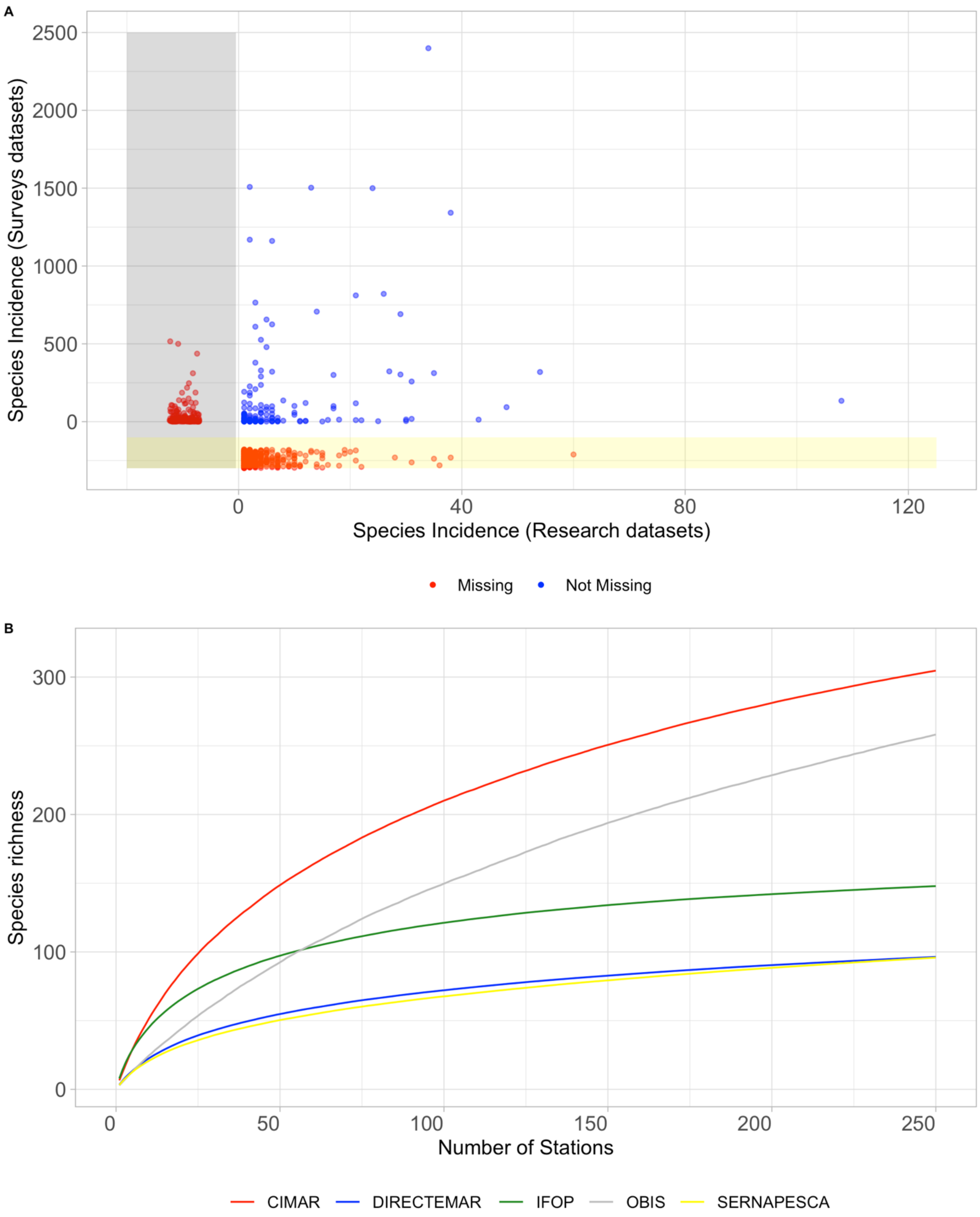


Figure 6. A) Relationship between species' incidence (defined as the number of distinct sampling events at a specific geographical location in which a species has been recorded as present) in research datasets (OBIS and CIMAR), and surveys datasets SERNAPESCA, IFOP, and DIRECTEMAR) for the period 1991 to 2017. Blue points indicate species occurring in both datasets. Red points inside the yellow band are species occurring only in the survey datasets, whereas red points in the grey band are species occurring only in research datasets. **B)** Species accumulation curve to each dataset with respect to the number of stations.

The species occurred in 168 grid cells (55 x 55km; Figure 7A). The highest number of species per grid cell was 195 and it was located at around 42° S (Figure 7A). The maximum number of stations per grid cell was observed in the same latitude (Figure 7B). The grid cells were mainly located in the coastal areas (Figure 7A, B). The correlation between the number of species by grid cell and the number of stations by grid cell was strong, significant and positive (Figure 8; Pearson = 0.7, $p < 0.0001$).

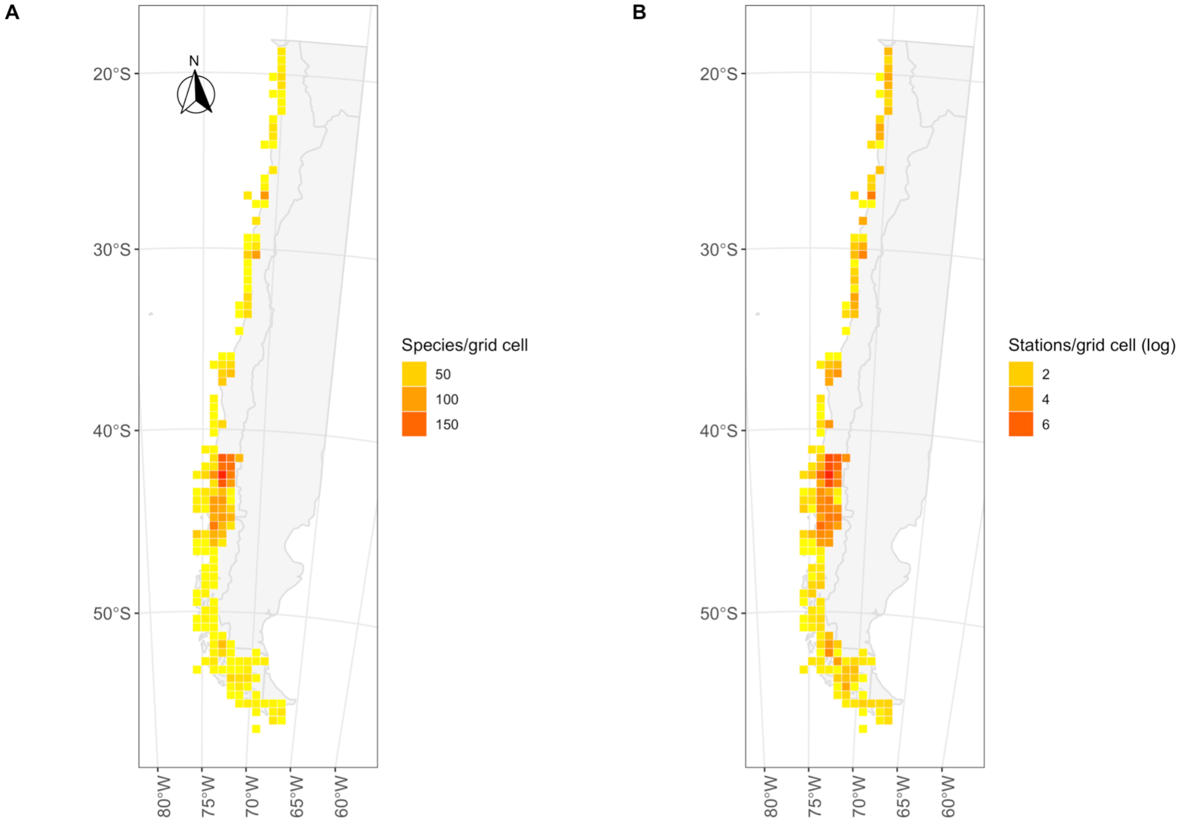


Figure 7. A) Number of species per grid cell (55 x 55 km) along the Chilean latitudinal gradient, for the period 1991 to 2017. **B)** Number of stations per grid cell (55 x 55 km) along the Chilean latitudinal gradient, for the three periods 1991 to 2017.

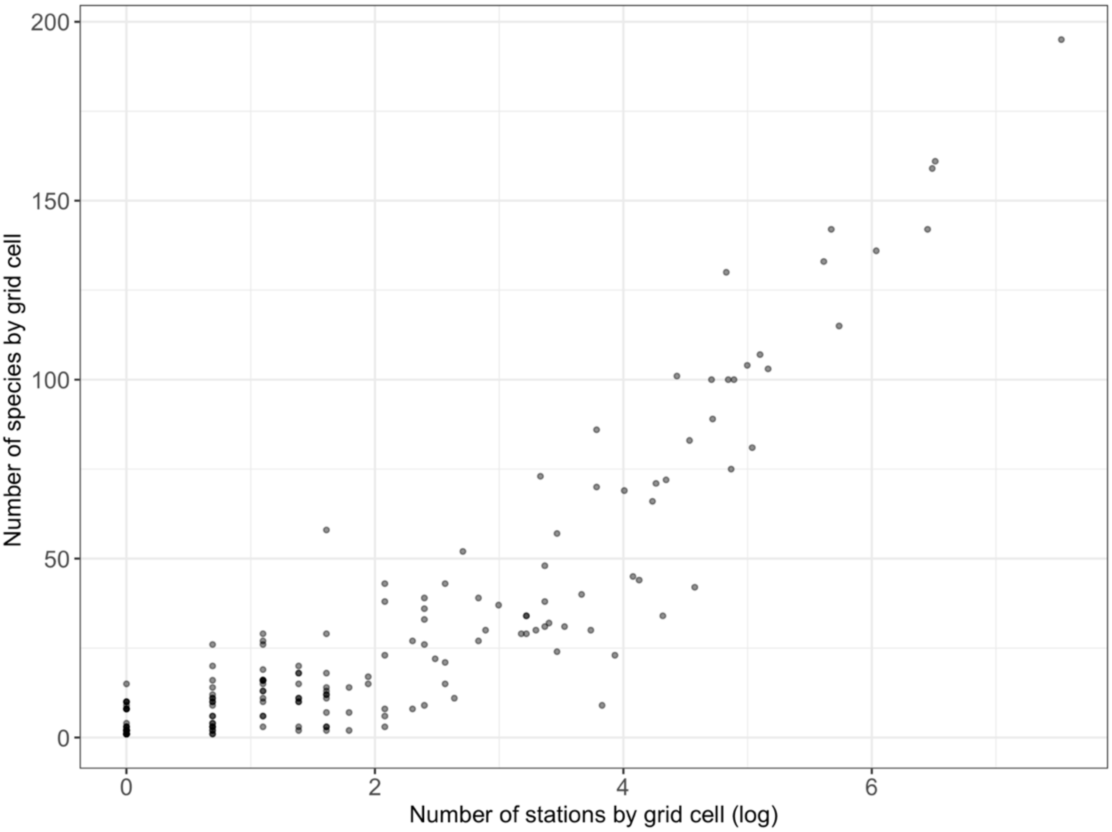


Figure 8. Relationship between the number of stations per grid cell (55 x 55 km) and the number of species per grid cell (55 x 55 km) for the dataset with observation between 1991 to 2017.

The phyla with a major number of species were Mollusca (214 species, 28%), Annelida (168 species, 22%), and Arthropoda (127 species, 17%; Table 3). Said phyla presented occurrences along the entire latitudinal gradient (Figures 9A-C). The phylum Foraminifera was present between 23° to 46° S (Figure 9D). The phyla Echinodermata, Brachiopoda and Nemertea were mainly found in southern latitudes from 42° to 57° S (Figures 9E, 10D, E). The phyla Porifera, Cnidaria and Bryozoa presented lower occurrences (Figures 10A-C). The higher number of species per grid cell for the phyla Mollusca, Annelida, and Arthropoda was mainly observed toward the southern latitudinal gradient at around 43° S (> 60 species/grid cells; Figures 9A-C). Same pattern was observed for the phyla Foraminifera and Echinodermata: however, both phyla presented a lesser number of species per grid cell (> 20 species/grid cells; Figures 9D, E). The rest of the phyla presented a lower number of species per grid cell (Figure 10).

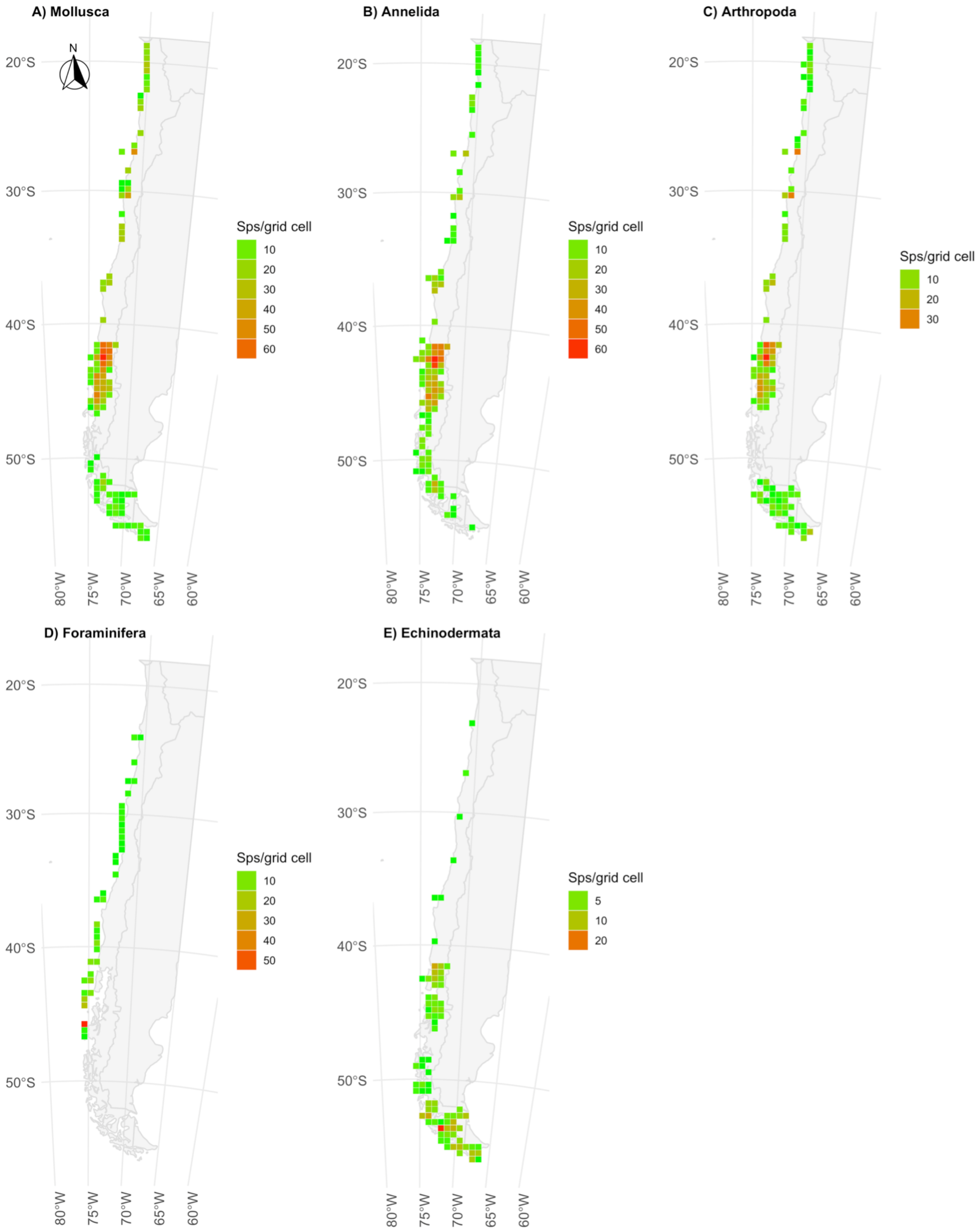


Figure 9. Number of species by grid cells according to the phyla **A)** Mollusca, **B)** Annelida, **C)** Arthropoda, **D)** Foraminifera, and **E)** Echinodermata.

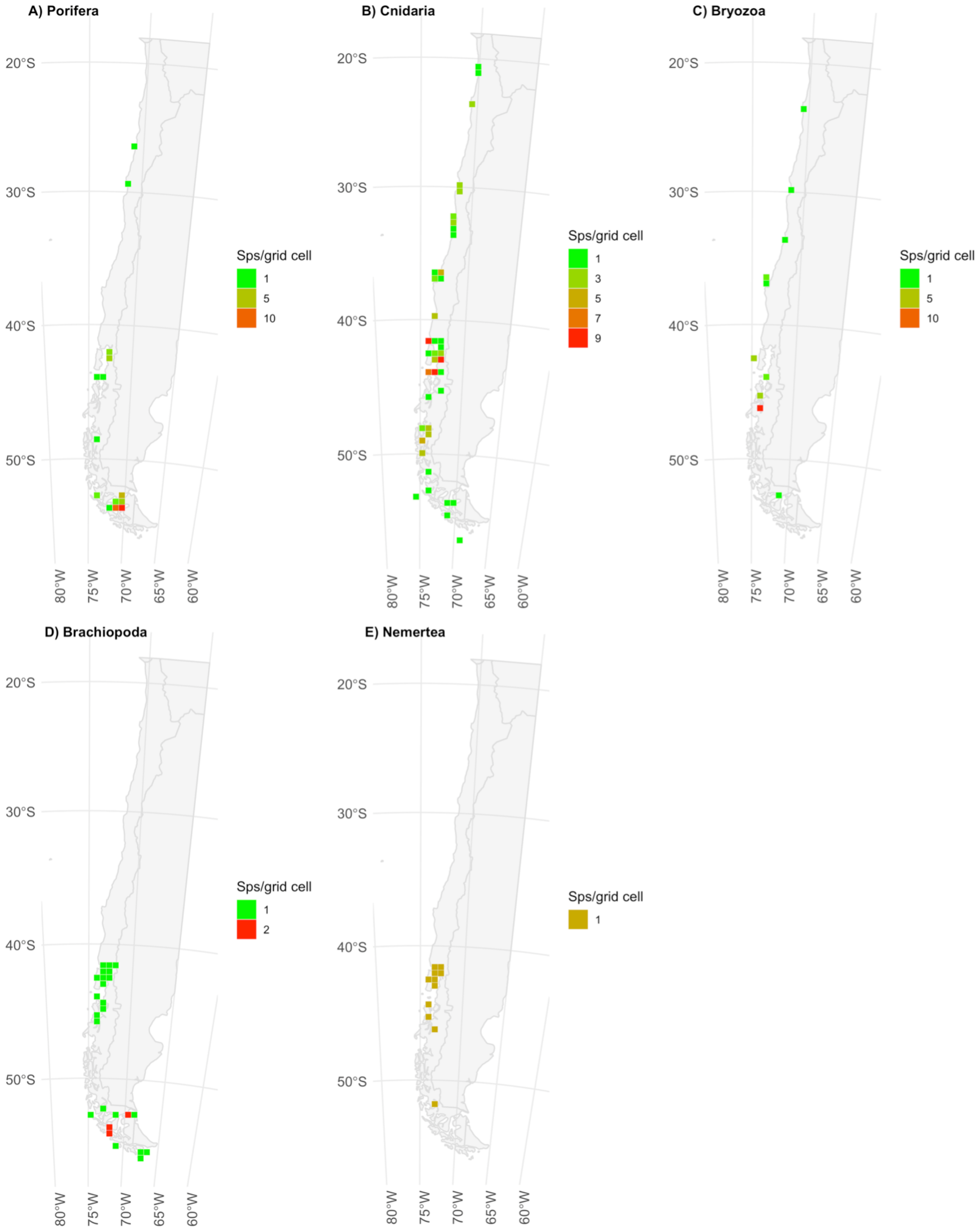


Figure 10. Number of species by grid cells according to the phyla **A)** Porifera, **B)** Cnidaria, **C)** Bryozoa, **D)** Brachiopoda, **E)** Nemertea.

2.5. Discussion

The aim of this chapter was to introduce several datasets containing useful information on the spatial distribution of benthic marine invertebrates in Chile and to describe how they were aggregated to construct a final database. I recognise that this database is not perfect. However, all databases are biassed in respect to the records that they include and exclude (Renaud et al. 2009). In fact, the frequency of data based on human observations present biases associated with the space and time that humans inhabit (Dornelas et al. 2018). Here, I consider the pros and cons of this aggregated database. To recognize the pros and cons of using diverse types is one of the considerations when datasets are being used in biodiversity conservation (Cardinale et al. 2018).

Firstly, I observed a low number of annual occurrences (< 50) through long periods of time, with no occurrences recorded for some years (e.g. lack of occurrences in 1993, and a low number of occurrences in 1992, 1998 to 2000, and 2005 to 2011; Figure 4). I also observed that the number of occurrences has increased since 2014, mainly due to the IFOP and SERNAPESCA surveys. The global estimations of marine biodiversity show an increase in species richness since 2000 (Appeltans et al. 2012). Thus, the main database is a clear example of the global tendency in which marine species have been described over time. On the other hand, the scarce availability of biodiversity time series for Chile has previously been revealed by the BioTIME project, with only short (<2y) series available for marine invertebrates in the northern Chilean coast (Dornelas et al. 2018). This limits the scope to perform temporal analyses of Chilean marine biodiversity, although the aggregated dataset does provide opportunities to analyse recent trends between 1991 to 2017. This period also has the best coverage of environmental covariate data (Chapter 5).

I also recognise differences in the methodologies among the datasets, which use a variety of sampling gears differing in selectivity, size, and volume sampled. The number of records obtained with identical gear (e.g. Van Veen grab) was limited to only two datasets (SERNAPESCA and IFOP), and their occurrences were mostly restricted to the southern latitudes (Figure 5). Renaud et al. (2009) argued that integrated databases should be constructed by records sampled using the same or comparative methodologies. Therefore, comparative analyses based on records obtained using different sampling methodologies might be more influenced by these differences than by variations in diversity (Dornelas et al. 2018). However, the Chilean reality is still far behind the European efforts to construct a unique integrated, georeferenced and standardised database such as MacroBen (e.g. Webb et al. 2009) or BioTIME (e.g. Dornelas et al. 2018), or to reach the density of occurrence records of marine species in the UK (e.g. Tyler et al. 2012). Having a higher amount of records would allow us to choose only stations sampled by the same methodology, encompassing all the latitudinal gradients including affected and pristine zones, and coastal and offshore areas, thereby reducing biases in the results. However, plans and decisions in conservation, for example hotspots identification, cannot wait for perfect databases; thereby, it is relevant to explore how the currently available range of data performs (Norman & White 2016). Thompson et al. (2021) argued that by combining structured and unstructured datasets (e.g. database constructed by Cooper & Barry 2017, and OBIS) it is possible to obtain a more complete landscape of the benthic marine biodiversity in time and space. These authors identified hotspots of benthic taxa diversity across the UK's exclusive economic zone using a combined database constructed with records obtained using different methodologies. The combined database therefore provides a pragmatic solution to examining the distribution of benthic diversity in Chile, making best use of available data.

Key to this is the fact that the datasets composing the final database are complementary in geographic coverage (Figures 5 and 7). For example, CIMAR, SERNAPESCA, and IFOP datasets contain more occurrences in southern latitudes, with CIMAR mainly focused on the more pristine areas of the fjord system, while IFOP and SERNAPESCA target the environmental assessment of aquaculture in the same region. The DIRECTEMAR dataset is important due to the focus on coastal areas and the proximity of their stations to highly populated areas, particularly in Northern Chile. OBIS includes records from all regions, collected for a range of purposes.

Research and survey datasets are also complementary in terms of species occurrences and species incidence. Research datasets such as OBIS and CIMAR contributed more species occurrences, and the rate at which species accumulate with an increasing number of stations was higher than for the survey datasets (Figure 6). In OBIS, the low number of occurrences per individual species is recognised. For example, Webb & Vanhoorne (2020) observed that across all marine animals, the median number of occurrences per species is 7, and 18% of the species in OBIS present only one occurrence. Moreover, these authors recognised few records for benthic invertebrates in comparison with fish, mammals, birds, and reptiles in OBIS. Thus, OBIS database seems to present issues related with the frequency with which the species occurrences are recorded, the lack of structure because it is composed by a variety of datasets, and the imperfect detectability of species (Edgar et al. 2016), and the lower number of records and information of more unknown taxa such as benthic marine invertebrates (Webb & Vanhoorne 2020). Consequently, these issues have brought some difficulties to perform deeper analyses. For example, it is still not possible to evaluate temporal changes of marine biodiversity (Edgar et al. 2016).

Survey datasets such as SERNAPESCA, IFOP and DIRECTEMAR contributed more to species incidence (defined as the number of distinct sampling events at a specific geographical location in which a species has been recorded as present; Figure 6A). However, despite the lower number of species occurring in SERNAPESCA and IFOP, the higher species incidence in comparison with research datasets (Figure 6A), might reduce the bias associated with the identification due to a major familiarisation and expertise to identify the most frequent species, as well as the identified species are sampled by standardised sampling methodologies.

Some taxa were better represented than others in terms of occurrences and geographical distribution (Figures 9 and 10). For example, taxa such as Porifera, Cnidaria, Bryozoa, Brachiopoda, and Nemertea, presented a lower number of species, and they were restricted to limited areas (Figure 10). On the contrary Mollusca, Annelida, and Arthropoda presented the highest number of species and they were widely distributed along the latitudinal gradient (Figure 9). The observed patterns for these phyla are consistent with those described by Appeltans et al. (2012) in a global context and based on the species recorded in the World Register of Marine Species (WoRMS). These authors estimated a lower number of known species in Porifera, Bryozoa, Brachiopoda, and Nemertea in comparison with Mollusca, Arthropoda, and Annelida, which are better represented in terms of the number of species. In addition, Pisces, Mollusca and Crustacea present the highest number of species in coastal areas of the South Pacific Ocean according to estimations derived from OBIS records (UNESCO IOC & UNEP 2016). In a local context, Mollusca, Arthropoda, and Annelida have been well described in terms of the number of species in Chile. For instance, Mollusca, Polychaeta, and Crustacea presented the highest number of species observed by Lancellotti and Vásquez (2000) in their biogeographical study of Chilean marine invertebrates. Miloslavich et al. (2011) observed that some taxonomic groups such as Amphipoda, Gastropoda, and Polychaeta present the highest number of described species along the Humboldt Current system. However, many species from other groups such as Anthozoa, have been cited only once, or they have been poorly studied (Häussermann 2006). Therefore, the inclusion of more records probably would not result in a higher increase in representation of taxa with fewer occurrences.

Of the 766 species in the combined database, 31% were singletons, i.e. species with only one recorded occurrence. Lancellotti and Vásquez (2000) recorded 1,601 species of benthic invertebrates from intertidal to 100m in the Chilean continental shelf. These authors observed 38.2% of singletons. According to them a high percentage of singletons could reveal a lack of knowledge in the diversity of benthic marine invertebrates. In a global context, the entire OBIS database presents only 9.1% (18,869 from a total of 206,849 recorded species) of species having one occurrence (Webb & Vanhoorne 2020). Thus, in terms of singletons, the large difference between the regional database and the global OBIS may support the fact of the lack of knowledge in the diversity of the Chilean benthic marine invertebrates. Taxon-level rarity in the database likely conflates true rarity with differences in the extent of study between taxa; however, in the absence of clear information on this, I decided to include all groups due to their relevance for the next chapters. Webb et al. (2009) did not observe a significant difference in the frequency distribution of species occurrence after the exclusion of singletons from the European MacroBen database. I also argue that macrobenthic species act as a whole assemblage where different taxa can perform similar and complementary functions in the ecosystem, as well as influencing or responding to the environment. Therefore, I consider that it is not relevant to perform analyses by taxa, more than has already been presented in this chapter. Smaller benthic organisms perform complex biological traits. For example, Nemertea has relevant feeding behaviours influenced by environmental stress (e.g. Thiel & Kruse 2001, Caplins et al. 2012). On the other hand, Foraminifera species can be used as bioindicators of environmental disturbance due to dissolved oxygen depletion (Brower 2014, Risgaard-Petersen et al. 2006). These features would be relevant for future steps in this research. Thus, the focus will be on the assemblages of benthic marine invertebrates. In addition, there are some ecological interactions in complex environments; for example, the competition for space and resources in the intertidal, where it is necessary to consider different phylogenetic groups to obtain good interpretations (Underwood 2005). It is relevant when the aim in the fourth chapter is to study the communities of benthic invertebrates in terms of functional diversity. Moreover, at larger spatial scales, such as those studied by macroecology, the community complexity tends to be higher, and the comparisons might consider the interactions among individuals from many different species (Webb 2012).

Some latitudes were better sampled than others (e.g. the zone at around 42° S), and consequently these grid cells presented a higher number of stations than those located toward northern and southern latitudes (Figure 7B). This spatial bias in sampling has previously been recognised. For instance, the interest in this zone around 42° S started with the expedition by Lund University (1948-49; Häussermann 2006). Marin et al. (2014, unpublished) also observed the strong sampling effort to evaluate the impacts of the large number of salmon and mussel farms in those latitudes on the benthos, sediments, and water column. These authors accounted for approximately 250 sampled localities only in the Chiloe Archipelago (~ 42° S). From the 1980s, the aquaculture of salmonids (e.g. *Oncorhynchus mykiss, Salmo salar, Oncorhynchus kisutch*) and mussels (e.g. *Mytilus chilensis*) has been strongly developed south of 42° S and, as a consequence, the environmental monitoring of the activity has led to the collection of many samples through programmes carried out by SERNAPESCA and IFOP. Moreover, Camus (2001), in a revision of 27 marine biogeographic reports for Chile, described the problems of the sampling bias throughout the latitudinal gradient, where historically zones of easier access that are close to the populated areas are better sampled than those of difficult access. In the combined database, species richness was strongly and positively correlated with the number of sampled stations (Figure 8). This is not only specific to Chile; for instance, Clarke et al. (2007) argued that the variability in sampling effort among localities is the main source of bias in broad-scale studies. Thus, the description of distribution patterns of species is difficult (Clarke et al. 2007) and removing the influence of sampling bias is challenging even in very large databases (e.g. Renaud et al. 2009, Dornelas et al. 2018). Even well-sampled regions like Europe still present many areas where more than 30% of species are undercover or unreported (UNESCO IOC & UNEP 2016). Therefore, diversity measures designed to control for this effect to some extent are required. Fortunately, a suite of such measures now exists, including nonparametric measures such as the second-order Jackknife, Chao 2, Incidence based on coverage (ICE), and taxonomic distinctness (see Chapter 3).

The stations and therefore the grid cells were mainly distributed along the coastal areas, followed by the continental shelf until 110km from the baseline. This might be due to access to coastal areas being easier compared to those located offshore or far from populated cities. This is not only a local and regional scale issue. In a global context, the major part of the OBIS records derive from the continental shelf (0 - 200m; Webb et al. 2010, UNESCO IOC & UNEP 2016), c. 10 million records according to updated analysis (UNESCO IOC & UNEP 2016). In addition, the continental shelf presents the highest number of sampling days (c. 530,000) and number of species (c. 89,500; UNESCO IOC & UNEP 2016). This contrasts with what was observed in the deeper ocean (> 1000m of depth), where the number of sampling events, records and distinct species decrease dramatically (Webb et al. 2010, UNESCO IOC & UNEP 2016). In addition, globally, coastal areas (0 - 100m) have the highest concentration of species distribution records, which increased from 1980 (UNESCO IOC & UNEP 2016). However, the Chilean coast is one of the areas presenting gaps in OBIS (UNESCO IOC & UNEP 2016). Moreover, the diversity of some areas of the ocean, such as the mid and deep waters are underestimated and underrepresented (Webb et al. 2010). This has been attributed, among other causes, to the use of old and outdated techniques of sampling, which are not designed to capture a better representation of all taxa such as gelatinous fauna (Webb et al. 2010). Thus, even increasing the sampling effort, the number of species in some phyla does not increase (Webb et al. 2010). In addition, Montiel et al. (2011) concluded that using different sampling methods is possible to represent better the benthic assemblages of polychaetes in southern latitudes of Chile regarding species number and range of size. These could reinforce the use of different sampling methods to obtain better description of marine taxonomic and functional diversity. On a regional scale, Clarke et al. (2007) observed that Antarctic zones without sampling are areas of difficult access due to the dense ice. Expeditions in offshore and polar areas are required to assure the health, safety and the security of the researchers' team (Dornelas et al. 2018). In part, areas of difficult access in the southern system of fjords were covered by the CIMAR dataset. On the other hand, Gray (2002) argued that littoral or coastal areas are also better sampled due to the importance of monitoring the health of these systems; this is coincident with the aim of survey datasets such as DIRECTEMAR, SERNAPESCA, and IFOP. In Chile, the focus on coastal areas of easy access in the sampling of marine invertebrates, as well as in the latitude 42° S, has been widely recognised (e.g. Fernandez et al. 2000, Camus 2001, Häussermann 2006), and it has affected the description of new species in taxonomic groups less studied, as well as in the description of biogeographical breaks. For example, Häussermann (2006) recognised that areas being important in terms of diversity of Anthozoa in the Southern Fjords of Chile are little explored due to the difficult access. Camus (2001) described the bias associated with the differences in sampling efforts through a revision of 27 Chilean marine biogeographical classification. In fact, the recognised zoogeographical break at 42° S for marine invertebrates might be more artificial than real, and it might be related to local efforts in research focused in only specific areas (Lancellotti & Vásquez 2000).

To summarise, the integrated database presents similar issues to some global databases such as OBIS and BioTIME. For instance, the frequency with which the occurrences of the species are recorded. This has an effect on the difference in the number of occurrences per year. Other issues include the imperfect detectability of the species, the difference of records among taxa, the fact that Mollusca and Arthropoda are better represented than the others, and that more species records occur in coastal areas and in the continental shelf. I decided to account for only the records occurring up to 110km from the baseline. Some of these issues will be covered in the next chapters using diversity measures dealing with the differences in sampling effort or being independent of the sampling effort, such as nonparametric richness estimators and taxonomic distinctness (Chapter 3). The integrated database was constructed using complementary geographical datasets, thus, I could cover a wide range of latitude from 18° to 57° S, having associated some relevant environmental information, which will be used to evaluate key environmental drivers influencing diversity patterns (Chapter 5). However, the data were obtained using different methodologies, which might be seen as a clear disadvantage. Nevertheless, it is an advantage, as benthic marine invertebrate assemblages might be better represented if taxa are included that could not be obtained using the same sampling methodology. Moreover, when the functional diversity and the functional structure of the benthic assemblages will be evaluated (Chapter 4).

2.6. Supporting information

Appendix S1: Scientific papers and technical reports provided by CIMAR.

Appendix S2: Full code used to generate the OBIS Chilean benthos dataset.

Table S1. Metadata of attributes included in the main database (1846 to 2017) and in the final dataset (1991 to 2017), including the measurement units, the type of variable and a brief description of each attribute.

3. Spatial patterns in the diversity of benthic marine invertebrates along the Chilean coastline and continental shelf

3.1. Abstract

Biodiversity provides a fundamental part of goods and services necessary to support human society. Biodiversity estimations patterns of species and their influence on ecosystem functions are relevant for conservation strategies. Species richness, the simplest and most used biodiversity measure, is sensitive to the effects of uneven sampling effort. I describe the diversity patterns of benthic marine invertebrates throughout the Chilean coastline and continental shelf using an integrated database (Chapter 2) and a range of diversity measures designed to be robust to differences in sampling intensity (the nonparametric measures: Jackknife 2 (Jackk 2), Incidence Coverage-based estimator (ICE), and taxonomic distinctness). I identify diversity hotspots and their congruence. The Chiloense presents the highest species accumulation rate, Jackk 2 and ICE peak, and hotspots of both measures. These observed patterns are driven partially by spatial variation in sampling effort. Taxonomic distinctness peaked ~43° S, and hotspots are mainly observed from 52° to 56° S. Taxonomic distinctness is not significantly correlated with sampling effort and moderately correlated with the number of species by grid cell. The Chiloense and the Channels and Fjords are the most important ecoregions regarding species richness and taxonomic diversity of benthic marine invertebrates; these Sub Antarctic ecosystems are a source of high marine biodiversity and essential ecosystem functions and services necessary to preserve and protect. The low congruence between hotspots of Jackk 2 and ICE with taxonomic distinctness indicates that this measure captures a different dimension of overall diversity.

3.2. Introduction

Coastal and marine ecosystems are highly biodiverse. Biodiversity, defined as the variety of life, genes, species and functional traits (Cardinale et al. 2012), provides a fundamental part of goods and services necessary to support human society (Gamfeldt et al. 2008) and is the main determinant of community-ecosystem dynamics and their functioning (Tilman et al. 2014). Ecosystem functions are related to those ecological processes controlling the fluxes of energy, nutrients and organic matter in the environment. Marine ecosystem functions include the primary production by algae and phytoplankton, the nutrient cycling through the capture and trophic transfer of biologically essential nutrients, and the decomposition and recycling of dead marine animals and algae (Cardinale et al. 2012). These functions, in turn, lead to ecosystem services (UNEP 2006, Cardinale et al. 2012), including fisheries supported by marine biological food-web production, the retention, transformation, and detoxification of contaminants, cultural and scientific development, climate regulation and the maintenance of air and water quality, as well as the support for tourism, industries, and coastal settlements (UNEP 2006).

Benthic organisms play key roles in marine and coastal ecosystem functioning, through metabolism and catabolism, in dynamic processes such as bioturbation, food-webs, oxygen and nutrient cycles, waste material recycling, and catching harmful substances (Cooper et al. 2008). Understanding the faunal patterns and their spatial variability at different spatial scales within a latitudinal gradient is relevant before comparing species richness at larger spatial scales (Ellingsen & Gray 2002). The estimation of biodiversity patterns of species and their influence on ecosystem functions is also relevant for the management and establishment of conservation strategies (Renaud et al. 2009). Thus, obtaining knowledge of benthic marine invertebrate biodiversity and their distribution patterns is a key step towards understanding the complete structure and function of marine and coastal ecosystems, especially where the diversity of species and their patterns are still little known as the eco-geographical gradient of Chile.

Observed species richness is the simplest and most widely used biodiversity measure (Johnston & Roberts 2009). However, species richness is particularly sensitive to the effects of uneven sampling effort (Clarke et al. 2007). The highest species richness is typically observed in localities under intense research activity, a pattern that remains even after applying simple corrections for sampling intensity (Clarke et al. 2007). As a result, various metrics have been designed to be independent of sampling effort and sample size. These methods include using rarefaction and extrapolation curves and the nonparametric richness estimators based on estimating species richness in terms of equal sample size (Chao & Chiu 2016). Due to rare species being more difficult to detect than common species (Chao & Chiu 2016), some measures of diversity have been focused on identifying undiscovered taxa (Branco et al. 2018). These nonparametric richness estimators, for example, Chao 2, the second-order Jackknife, and the incidence-based coverage estimator (ICE), are based on the infrequent taxa such as singletons (the number of species represented by one single individual), doubletons (the number of species represented by two individuals; Magurran 2004, p. 87).

Species richness only explains one aspect of the biological variability within and between communities, and accounting for the differences between species might be necessary to explain the variance in the ecosystem functioning (Srivastava et al. 2012). A simple way to do this is to use taxonomic identity. Clarke and Warwick (1998) described taxonomic distinctness as a measure of the average taxonomic relatedness of all species within a community. Thus, taxonomic distinctness is the average distance between all the species pairs in a community sample, where interspecies distance is the path length between species across taxonomic levels, used to approximate a phylogenetic tree (Clarke & Warwick 1999). Taxonomic distinctness has been used to proxy for phylogenetic (i.e., evolutionary) diversity (e.g. Rivadeneira et al. 2011). According to Srivastava et al. (2012), evolutionary diversity might explain more about the key mechanisms determining ecosystem functioning than the species richness. The use of these metrics may result in identifying different patterns of diversity of marine invertebrates in space or over ecogeographic gradients, compared to analyses using species richness alone.

In general terms, biodiversity hotspots have been defined as areas with large concentrations of endemic species, significant biodiversity, and susceptibility to species loss (Myers et al. 2000). Hotspots are essential to establishing spatial planning and fisheries management (Santora et al. 2017) and marine protected area networks (Bundy et al. 2017). Historically, a common strategy in biodiversity conservation is to define hotspots according to the object of study, for instance as areas presenting the highest number of species (Norman & White 2019), the highest α, β, and γ diversity (e.g. Thompson et al. 2021), largest biomass (e.g. Grebmeier et al. 2015), the highest diversity of trophic levels (Santora et al. 2017), or functional groups (e.g. Bundy et al. 2017). However, before the hotspots are ready for their use as a conservation tool, it is important to consider the quality of the data used for its estimation and how to measure diversity. For example, the influence of sampling biases (i.e. data collection), data stored (i.e. data collation), and data analysis (Norman & White 2019), as well as the different ways of measuring diversity.

Chile offers an interesting latitudinal gradient that spans ~39° (18° 30'' to 57° 30'' S; Fernández et al. 2000) and encompasses a particularly broad range of marine ecosystems within its 200 nautical mile Exclusive Economic Zone (EEZ). Under the Marine Ecoregions of the World (MEOW) classification (Spalding et al. 2007), Chilean waters span two provinces: Warm Temperate Southwestern Pacific and Magellanic; and five ecoregions: Humboldtian, Central Chile, Araucanian, Chiloense, and Channels and Fjords of Southern Chile. These diverse marine ecosystems have not been comprehensively studied in terms of species diversity of benthic invertebrates at a regional level.

In this research, I will address one main question: What are the major spatial patterns in the diversity of benthic marine invertebrates throughout the Chilean coastline and continental shelf? To do this, a compilation of data from three Chilean environmental surveys and one research cruise were combined with species occurrence records from the Ocean Biodiversity Information System (OBIS 2022) for the Chilean coastline and continental shelf. Using this integrated database, I first compare observed and estimated species richness among the five ecoregions described by the MEOW (Spalding et al. 2007). Secondly, I describe species diversity distribution through the five ecoregions along the Chilean coastline and continental shelf using a range of diversity measures designed to be robust to differences in sampling intensity. Finally, I identify hotspots of diversity according to each method and compare whether hotspots identified using different diversity measures are congruent.

3.3. Materials and Methods

3.3.1. Database collation

I used a georeferenced and standardised database of marine benthic species, fully described in Chapter 2. The database contains 34,184 species occurrences acquired between 1991 to 2017, within 110km from the coast. Seven hundred sixty-six benthic marine invertebrate's species belong to the phyla Mollusca, Annelida, Arthropoda, Foraminifera, Echinodermata, Porifera, Cnidaria, Bryozoa, Brachiopoda, and Nemertea were included. The database contains information from five sources. Three corresponded to surveys (environmental monitoring) of human activities associated with coastal areas and aquaculture: SERNAPESCA (Chilean National Fisheries Service), IFOP (Fisheries Development Institute of Chile), and DIRECTEMAR (Department of Maritime Territory and Merchant Marine of Chile). Each of these surveys employs a distinct, well-documented sampling methodology. The remaining two sources include research data from CIMAR (Cruises of Marine Investigation in Remote Areas) and marine biodiversity data from multiple sources available from OBIS (Ocean Biodiversity Information System; OBIS 2022). CIMAR is focused on researching the fjords system located in southern Chile (south of 42° S); the main aims and the methodology of these cruises change each year. OBIS is the largest open and free-access database providing standardised and georeferenced information of marine species (OBIS 2022). OBIS contains occurrence records from more than 1,700 different datasets, each with its objectives and methodologies (Edgar et al. 2016). After extracting relevant data from the five primary sources, I used the World Register of Marine Species (WoRMS, Horton et al. 2022) taxon match tool (http://www.marinespecies.org/aphia.php?p=match) to standardise all species names.

I recognise that the database has biases that could affect the estimations. These biases were fully described in Chapter 2. For example, the benthic marine invertebrates were collected with different sampling devices, such as grabs (e.g. Van Veen), cores, aggasis net, and diving. Moreover, information regarding the device is often unknown for occurrences in CIMAR and OBIS. In addition, CIMAR, OBIS, and DIRECTEMAR datasets did not identify if species corresponded to benthic meiofauna, macrofauna or macroinvertebrates. I, therefore, denominate all organisms in the database as benthic marine invertebrates with no further subdivision into groups. In addition, the database presents only species occurrence, where each detected species was noted as being present (i.e. species presence). The absence of one species in the database could represent a true absence (the species occurred in one or more than one dataset) or a false absence (the species was not detected for any of the datasets; Gotelli & Colwell 2001). Despite the differences among the five sources contained in the database, they have the major advantage of being complementary in terms of geographical distribution, covering the entire latitudinal gradient of Chile between 18° to 57° S, which is important given that describing the spatial distribution of benthic marine invertebrates across this gradient is an aim.

Data were gridded into equal-area cells of 55 x 55 km. Latitude and longitude were projected as Albers Equal Area Conic (ESRI projection 102033) because of Chile's geographic position and elongated shape, and each location was assigned to one of the five ecoregions proposed by MEOW (Spalding et al. 2007). This classification divided the global continental shelf into 62 provinces and 232 ecoregions. These divisions were based on Chilean research developed by Fernandez et al. (2000), Ojeda et al. (2000) and Camus (2001). The ecoregions correspond to areas with relatively homogeneous species composition (Spalding et al. 2007). The continental area of Chile is divided into two provinces and five ecoregions. The Warm temperate Southeastern Pacific Province ranges between 18° to 41° S. This province includes the Humboldtian, Central Chile and the Araucanian ecoregions. The second, the Magellanic province, ranges from 41° to 56° S, is divided into the Chiloense and the Channels and Fjords of South Chile.

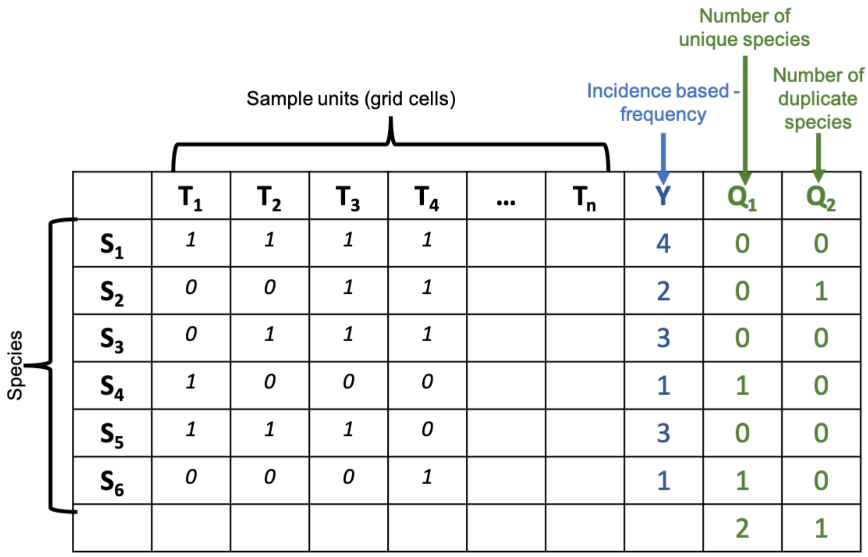
3.3.2. Measures of diversity

For each 55 x 55 km grid cell, I recorded the observed species richness as simply the total number of distinct species occurring in that cell across all data sources. These results are presented in Chapter 2. As shown in Chapter 2, the observed species richness by grid cell was influenced by the sampling effort (i.e. the number of stations per grid cell equal to 55 x 55 km; station represents the location where the sample was obtained). Four metrics of species diversity were estimated to address differences in sampling effort along the Chilean latitudinal gradient. First, Sample-based Rarefaction/Extrapolation curves were used to compare species accumulation rates and estimated total species richness between ecoregions. Second, I used two nonparametric metrics: the second-order Jackknife estimator for incidence frequency data (Jackk 2) and the Incidence based coverage estimator (ICE) at the grid level. Finally, at the grid grid level, I incorporated species identity to map taxonomic distinctness (Δ^{+}). These three methods are detailed below.

Comparison between observed species richness (S obs) and estimated species richness (S est) among ecoregions using Sample-based Rarefaction/Extrapolation curves (R/E; Colwell et al. 2012). Observed and estimated species richness were defined by increasing the number of sample units (grid cell equal to 55 x 55 km) by ecoregion until a standard (150 grid cells). A matrix of species (S) as row and sampling units as columns (T = grid cells; Figure 11) was constructed. The occurrence of one individual species in each grid cell was noted as 1, and the absence as 0. All the occurrences of one species were added to obtain the incidence per row denoted as the incidence-based frequency (Y; Figure 11). As a result, the rarefaction curves were obtained.

The analysis to create the extrapolation curves considers the number of unique species (Q_1, those found in only one sample unit), and the number of duplicate species (Q_2, those found in exactly two samples), to estimate the number of undetected species (Chao & Chiu 2016) using the nonparametric measure Chao 2 (Chao 1987). Once the asymptote is achieved, the accumulation curve is flat, and it is assumed that additional grid cells will not add more species (Gotelli & Colwell 2001).

The R/E for occurrence data is based on the product-Bernoulli model, where Y (incidence-based frequency) of T (sample unit = grid cell) follows a binomial distribution (i.e. probability that one species would be detected in a sampling unit; Chao & Chiu 2016). The sample-based R/E curves analysis was performed using the function `iNEXT()` in the package `iNEXT` (Chao et al. 2014, Hsieh et al. 2020) in R (R Core Team 2019). The function constructs the associated 95% confidence interval around the R/E curves. I used the “incidence raw” as a data type argument in the function.



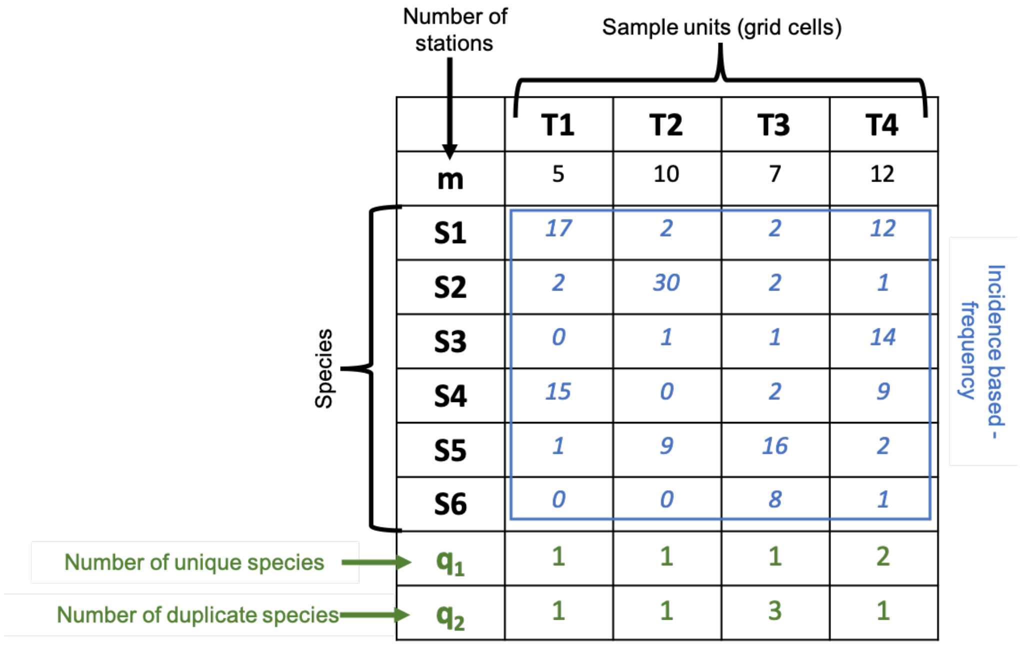
	T_1	T_2	T_3	T_4	...	T_n	Y	Q_1	Q_2
S_1	1	1	1	1			4	0	0
S_2	0	0	1	1			2	0	1
S_3	0	1	1	1			3	0	0
S_4	1	0	0	0			1	1	0
S_5	1	1	1	0			3	0	0
S_6	0	0	0	1			1	1	0
								2	1

Figure 11. Example of the matrix species as rows (S) by sample units as columns (T, grid cells equals to 55 x 55 km) and the variables considered to find the number of undetected species. The occurrence (i.e. incidence) of one individual species is noted as 1, and the absence as 0. Y corresponds to the sum of each row to obtain the incidence-based frequency. The number of unique species is Q_1 (those species found in only one sample unit), the number of duplicate species is Q_2 (those species found in exactly two sample units).

Estimated species richness by grid cell using the second-order Jackknife estimator (Burnham & Overton 1978), a nonparametric richness estimator for occurrence data. The second-order Jackknife (Jackk 2) is denoted as:

$$S_{Jackk2} = S_{obs} + \left[\frac{q_1\ (2m - 3)}{m} - \frac{q_2\,(m - 2)^2}{m(m - 1)}\right]$$

Where S_{obs} is the number of observed species, q_1 is the number of unique species (those found only once), q_2 is the number of duplicated species (those found exactly twice), and m is the number of stations by grid cell (Gotelli & Colwell 2001). To obtain the Jackk 2 by grid cell, a matrix as shown in figure 12 was constructed, with species as row (S) and grid cells as columns (T). This time the incidence frequency of one species in a grid cell was noted. The first row corresponds to the number of stations by grid cells (m) in this matrix. Jackk 2 was obtained using the function `ChaoSpecies()` in the `SpadeR` package (Chao et al. 2016) in R. I used the "incidence frequency" as a data type argument in the function and a 95% of confidence interval. Jackk 2 was not obtained for grid cells with only one station or in grid cells with all the species with an incidence based-frequency equal to 1.



	T1	T2	T3	T4
m	5	10	7	12
S1	17	2	2	12
S2	2	30	2	1
S3	0	1	1	14
S4	15	0	2	9
S5	1	9	16	2
S6	0	0	8	1
q_1	1	1	1	2
q_2	1	1	3	1

Figure 12. Example of the matrix species as rows (S) by sample units as columns (T, grid cells equals to 55 x 55 km) and the variables considered to estimate the second-order Jackknife. The incidence-based frequency is considered as the number of times that one individual species was found in a grid cell. q_1 is the number of species found only one time (incidence based-frequency equal 1), q_2 is the number of species found twice (incidence based-frequency equal 2), and m is the number of stations by grid cell.

Most nonparametric estimators are biassed because they underestimate the actual diversity; however, Jackk 2 and Chao 2 minimise bias when small samples (i.e. Colwell & Caddington 1994).

Estimated species richness by grid cell using the Incidence Coverage-based estimator ICE (Chao & Lee 1992). ICE is a nonparametric measure that compares species richness among data from diverse sources (Basualdo 2011). ICE was estimated using the incidence frequency of one species in a grid cell and a cut-off point dividing the species into an infrequent species group (incidence frequency < cut-off) and a frequent species group (incidence frequency > cut-off). A cut-off equal to 10 is recommended by Chao and Chiu (2016). The ICE is denoted as:

$$ICE = S_{freq} + \frac{S_{infreq}}{C_{infreq}} + \frac{Q_1}{C_{infreq}} {y^2}_{infreq}$$

Where S_{freq} is the number of species in the frequent group (incidence frequency > 10), S_{infreq} is the number of species in the infrequent group (incidence frequency < 10; e.g. frequent and infrequent groups defined based on threshold values of species incidence), Q_1 is equal to those species found in only one sample unit. C_{infreq} is the estimated sample coverage in the infrequent groups, whose formula is:

$$C_{infreq} = 1 - Q_1 / \sum_{i=1}^{k} iQ_i$$

The square of the coefficient of variation of the species is y^2_{infreq}, which estimates the probabilities of species detection in the infrequent group.

A matrix of species (in rows) by grid cells (in columns) was built. In the matrix, the observed incidence frequency of each species pooled by grid cells was recorded (Chao et al. 2016). ICE was obtained using the function `ChaoSpecies()` in the `SpadeR` package (Chao et al. 2016) in R. ICE was not obtained for grid cells with only one station.

Taxonomic diversity by grid cell using taxonomic distinctness (Δ^+ or Dplus; Clarke & Warwick 1998). This measure is based on the Linnaean taxonomic classification (i.e. phylum, class, order, family, and genus) and estimates the mean taxonomic distance between species in a community (Griffin et al. 2013). For example, species in the same group are separated by a taxonomic distance of 1, species in different genera but the same family by a distance of 2, and so on. Taxonomic distinctness is unbiased with respect to sample size (Clarke & Warwick 1999). High values indicate that species in the assemblage are, on average, less closely related to each other and therefore more diverse in terms of taxonomy (Rivadeneira et al. 2011). Taxonomic distinctness is estimated as:

$$\Delta^+ = [\sum\sum_{i<j} w_{ij}]/[s(s-1)/2]$$

Where w_{ij} is the length of the branch between all the possible pairs of species (i and j), and s is the number of species (Warwick & Clarke 1998). Taxonomic distinctness per grid cell was obtained considering the ecoregions as a unit (or community). First, a matrix by ecoregion, with taxonomic distances among species pairs was constructed using the function `taxa2dist()` in the `vegan` package (Oksanen et al. 2020). A table of taxonomic classification (i.e. phylum, class, order, family, genus) of each species was used as an argument in the function. Branch lengths were generated using the default process in the function `taxa2dist()`, where the successive classification levels are divided into equal steps. Secondly, taxonomic distinctness was estimated using as arguments the matrix of taxonomic distances and a presence/absence community matrix with species as columns and grid cells as rows in the function `taxondive()` in the vegan package. Taxonomic distinctness was not obtained for grid cells with only one station or grid cells where all species had an incidence frequency of 1.

3.3.3. Analysing spatial patterns in richness and taxonomic diversity

The species richness measures Jackk 2 and ICE, and taxonomic diversity Δ^+ were analysed as a smoothed function of the latitude and the longitude of each grid cell using Generalised Additive Models (GAMs), of the form taxonomic diversity index ~ s(latitude) + s(longitude), to describe spatial patterns of diversity in benthic marine invertebrates and their levels of significance. Latitude and longitude were included as separate smooth terms, with latitude as the primary variable of interest (because it represents the primary eco-geographical gradient) and longitude included to account for additional spatial structure in the data. Smooths were fitted using restricted maximum likelihood (REML). GAMs were chosen because they are flexible, with smooth functions allowing the response curve to be fitted for the predictor variable without assuming a distinct functional form (Lawler et al. 2006). GAMs were fitted using the package `mgcv` (Wood 2003, 2004, 2011, 2017, Wood et al. 2016) in R. The F test statistic, and its significance, as well as the R-squared, and the effective degrees of freedom (edf - an indication of the extent of nonlinearity of the fitted smooth) were all extracted from the model.

Gridded maps were produced to represent the spatial patterns of Jackk 2, ICE and Δ^+. The maps were produced using `sp` (Pebesma & Bivand 2005, Bivand et al. 2013), `maps` (Becker et al. 2021), and `ggplot2` (Wickham 2016) packages.

Pearson coefficients of correlation were obtained to describe the influence of sampling effort and species richness on Jackk 2, ICE and Δ^+. As in Chapter 2, sampling effort was measured as the number of stations (i.e. unique sampling locations in space and time) by 55 km grid cell, and species richness was simply the number of species recorded across all samples in a grid cell.

3.3.4. Hotspots of richness and taxonomic diversity, and their congruence

Hotspots were determined in terms of Jackk 2, ICE, and Δ^+. In addition, an overall ranking for each grid cell using a combination of these measures was derived. Hotspots of taxonomic diversity corresponded to the 10% most diverse grid cells in terms of Jackk 2, the 10% most diverse grid cells in terms of ICE, and the 10% most diverse grid cells with respect to Δ^+. The combined ranking was simply the sum of the ranks of each grid cell according to each diversity measure (1 = least diverse). The 10% of the grid cells with the highest score were defined as hotspots as they were diverse across all three measures using the summed rank.

Finally, I identified congruence between the three measures of diversity using a Venn diagram. The diagram was built with the function `ggvenn()` in the package `ggvenn` (Yan 2021).

3.4. Results

3.4.1. Comparison between observed and estimated species richness among ecoregions

The Chiloense ecoregion had the highest observed and estimated species richness (red line, Figure 13). The Channels and Fjords ecoregion presented a low accumulation rate in the observed species richness (purple line, Figure 13); however, as the number of grid cells increased, its value of estimated species richness increased more rapidly, exceeding the values for Central Chile and Araucanian ecoregions (grey and green line respectively, Figure 13). The Humboldtian ecoregion had the lowest observed and estimated species richness (blue line, Figure 13).

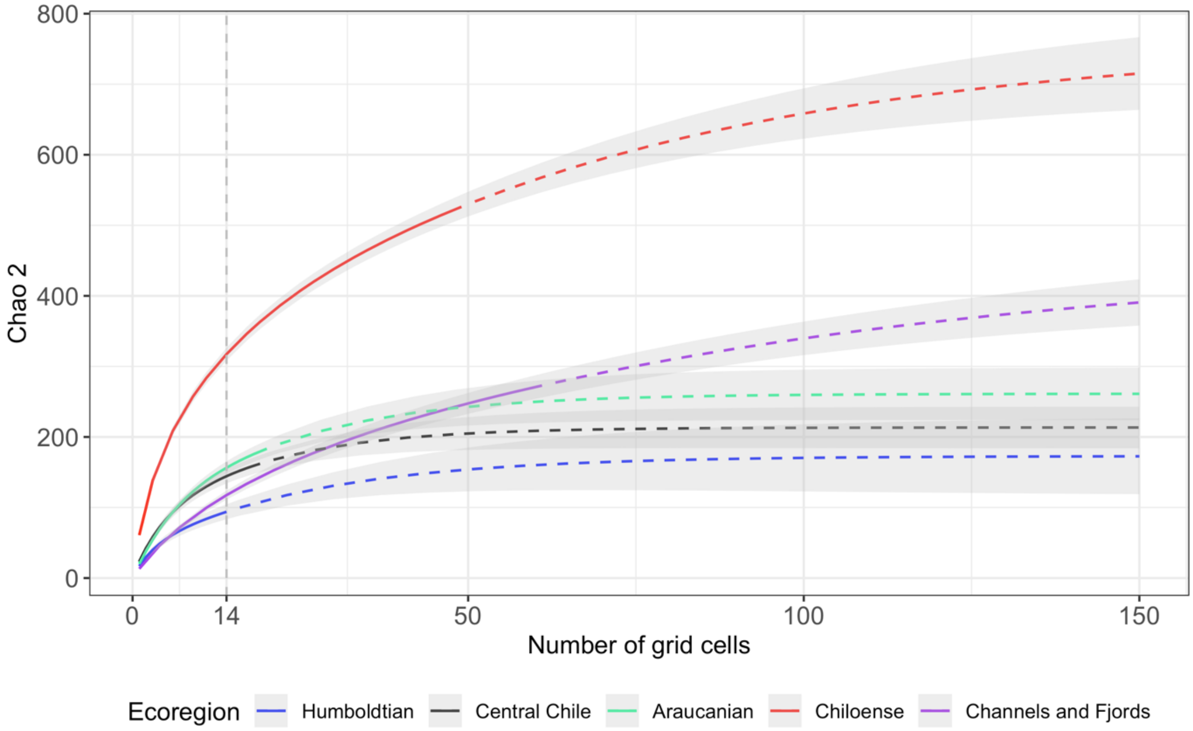


Figure 13. Sample-based interpolation (rarefaction; solid lines: it represents the observed species richness) and extrapolation (dashed lines: it represents the estimated species richness) curves with 95% confidence interval showing the species richness (Chao 2) accumulation of benthic marine invertebrates according to the number of grid cells by ecoregions.

3.4.2. Spatial patterns in richness and taxonomic diversity

Across the full latitudinal gradient, Jackk 2 ranged between 14 and 316, peaking at around 43° S (Figure 14A; GAM: $F = 5$, $edf = 5$, $p = 0.0002$, $R^2 = 0.5$). ICE ranged between 17 and 297, peaking at 43° S (Figure 14B; GAM: $F = 5.4$, $edf = 4$, $p = 0.003$, $R^2 = 0.3$). Δ^+ ranged between 66 and 93, increasing poleward and with a peak at around 43° S (Figure 14C; GAM: $F = 4$, $edf = 3$, $p = 0.006$, $R^2 = 0.4$). These peaks were all located in the Chiloense ecoregion (Figure 14).

All measures also varied somewhat with longitude. Jackk 2 was highest between 71° and 73° W (Figure S1A; GAM: $F = 6$, $edf = 4$, $p = 0.0003$, $R^2 = 0.5$), ICE decreased toward western longitudes (Figure S1B; GAM: $F = 4$, $edf = 2$, $p = 0.04$, $R^2 = 0.3$), and Δ^+ decreased at around 72° W (Figure S1C; GAM: $F = 11$, $edf = 4$, $p < 0.0001$, $R^2 = 0.4$).

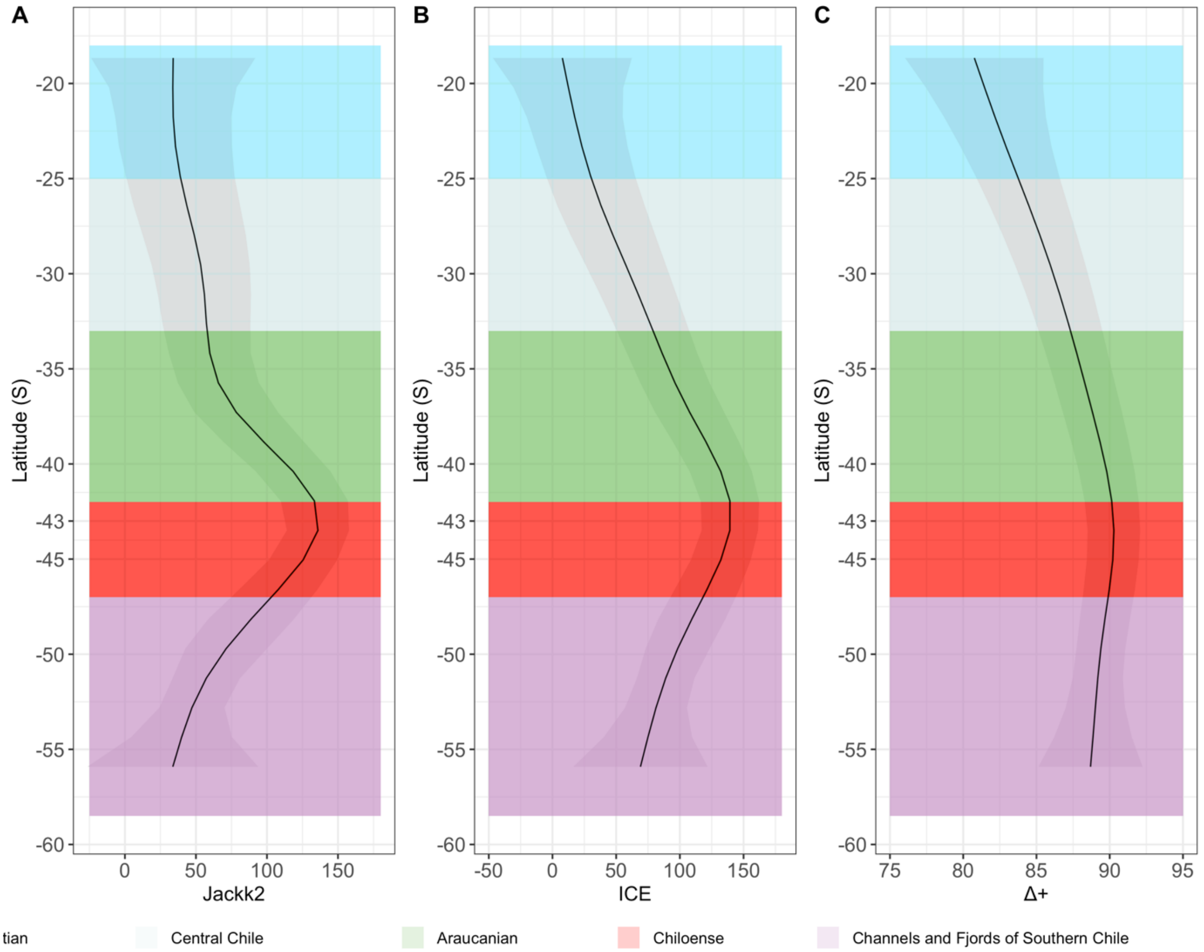


Figure 14. The relationship between latitude and **A)** Jackk 2 - Second order Jackknife, **B)** ICE - Incidence Coverage-based Estimator, **C)** Δ^+ - Taxonomic distinctness. Black line represents the fitted Generalised Additive Model (GAM), with the confidence interval in grey.

Jackk 2 was positively and significantly correlated with the sampling effort ($r = 0.7$, $p < 0.0001$), and with the number of species per grid cell ($r = 0.9$, $p < 0.0001$). ICE was also positively and significantly correlated with sampling effort ($r = 0.5$, $p < 0.0001$), and with the number of species per grid cell ($r = 0.7$, $p < 0.0001$). Δ^+ was positively but not significantly correlated with sampling effort ($r = 0.2$, $p = 0.06$), and positively and significantly correlated with the number of species by grid cell ($r = 0.4$, $p = 0.0005$). Furthermore, the diversity measures were correlated with each other: Jackk 2 was positively and significantly correlated with ICE ($r = 0.8$, $p < 0.0001$), and with Δ^+ ($r = 0.4$, $p < 0.0001$). ICE was positively and significantly correlated with Δ^+ ($r = 0.5$, $p < 0.0001$).

3.4.3. Hotspots of richness and taxonomic diversity, and their congruence

The Jackk 2, ICE, and Δ^+ hotspots were mainly located in southern latitudes (Figure 15A-C). The ten Jackk 2 hotspots were observed inside the Chiloense ecoregion between 41.5° and 46° S (black circles, Figure 15A). Eight ICE hotspots were located between 41.5° and 46° S (black circles, Figure 15B). One ICE hotspot was located at around 33° S in the Araucanian ecoregion, and another at around 56° S in the Channels and Fjords ecoregion (black circles, Figure 15B). Nine Δ^+ hotspots were observed in the Channels and Fjords ecoregion between 52° and 56° S, and one in the Chiloense ecoregion at around 44° S (black circles, Figure 15C).

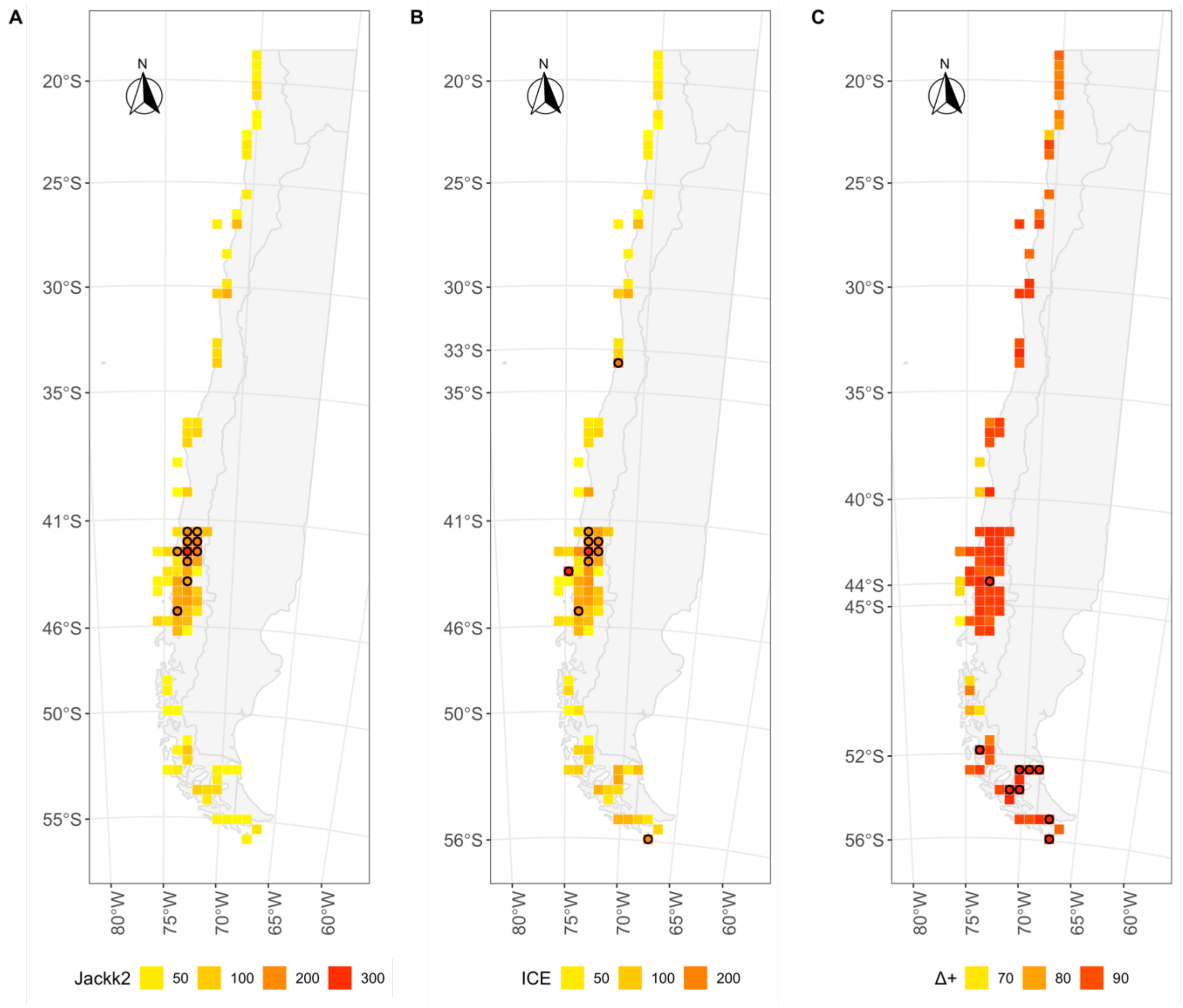


Figure 15. Gridded map showing the spatial distribution of each diversity metric. Hotspots (defined as the 10% most diverse grid cells for each metric) are indicated by black circles. **A)** Jackk 2 - Second order Jackknife, **B)** ICE - Incidence based on coverage estimator, and **C)** Δ^+ - Taxonomic distinctness.

Congruence between hotspots was relatively high, but not complete. Seven hotspots showed congruence between Jackk 2 and ICE. One hotspot showed congruence between Jackk 2 and Δ^+, and one hotspot showed congruence between ICE and Δ^+ (Figure 16). The ten hotspots derived from the combined ranking across Jackk 2, ICE, and Δ^+ were all located in the Chiloense ecoregion (black circles; Figure 17).

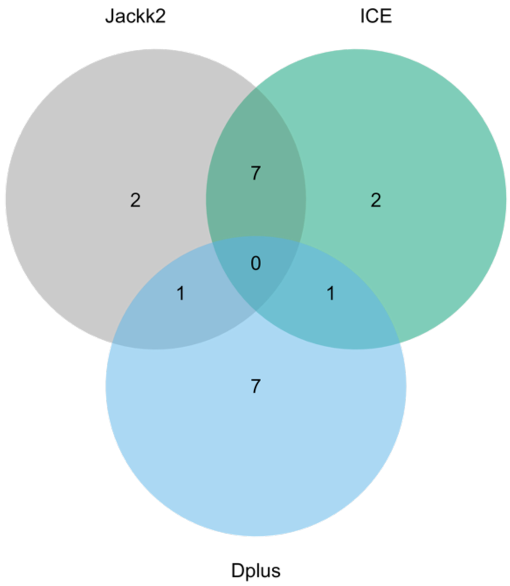


Figure 16. Congruence between hotspots of Jackk 2 - Second order Jackknife, ICE - Incidence Based on Coverage Estimator, and Dplus - Taxonomic Distinctness.

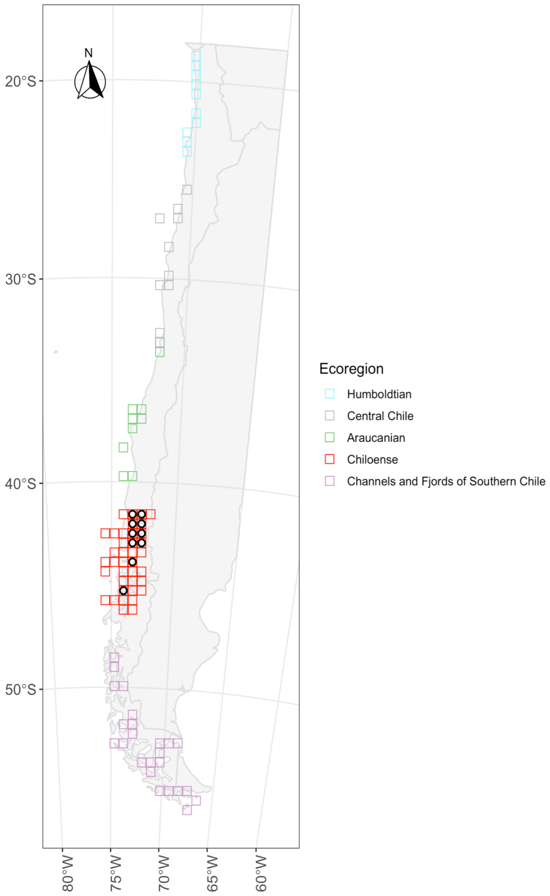


Figure 17. Spatial distribution of the hotspots throughout the Chilean latitudinal gradient. Here hotspots were defined as the 10% of the grid cells with the highest final score after ranking diversity metrics: Jackk 2, ICE, and Δ^+. All sampled grid cells are shown, coloured by ecoregions, and hotspots identified by the combined ranking of diversity metrics are indicated by black circles.

3.5. Discussion

The analysis of a new and comprehensive compilation of data on the distribution of marine benthic invertebrates in Chile has revealed clear variation in diversity between ecoregions and over the latitudinal gradient. However, it is recognised that nonparametric estimations and data biases are far from being perfect (e.g. Gutt et al. 2004). As Gutt et al. (2004) argued, after using similar nonparametric diversity measures to estimate the number of species inhabiting the Antarctic shelf, these results may inspire the development of new and more advanced studies about diversity encompassing the total eco-geographical gradient of Chilean continental latitude. I agree with these authors that it is impossible to wait until all the species are fully described.

According to the richness measures, the Chiloense ecoregion was consistently the most diverse, with the highest observed and estimated species richness values and the highest rate of species accumulation (Figure 13). The second-order Jackknife estimator (Jackk 2) and the Incidence Coverage-based estimator (ICE) also peak at 43° S (Figure 14). The majority of Jackk 2, ICE and combined diversity hotspots were located between 41.5° to 46° S in the Chiloense ecoregion (Figure 15A, B, 7). These findings revealed the importance of the Chiloense ecoregion for the diversity of benthic marine invertebrates in Chile. Moreover, diversity is known to be high in the Chiloense ecoregion in numerous taxonomic groups, including Echinodermata and Demospongiae (Lancellotti & Vásquez 2000), Anthozoa (Häussermann 2006), Polychaetes (Cañete et al. 1999, Hernández et al. 2005), and Cephalopods (Ibáñez et al. 2009).

On the other hand, Lancellotti and Vásquez (2000) argued that the peak in diversity around 41° S in the Chiloense ecoregion might be driven more by the strong sampling effort in the area. The Chiloense ecoregion has been widely studied since 1948 (Lund University expedition; Häussermann 2006) due to its oceanographic and biogeographic importance and increasing interest in the consequences of intense human activity, especially aquaculture of salmon and mussels in this zone. The performed analysis attempted to control for differences in sampling effort; however, through the Pearson correlations, it was possible to observe that both measures of richness (Jackk 2 and ICE) still showed some correlation with the number of stations by grid cell. Therefore, it is not possible to entirely rule out the possibility that the patterns I observe are driven at least partially by spatial variation in sampling effort.

However, there are good environmental reasons to expect areas around 41° to 43° S to have genuinely high diversity. For instance, the species inhabiting these latitudes must tolerate changes of salinity related to the increase of channels, estuaries, fjords, and precipitation from 39° S. Recent research has evidenced the high biodiversity of the Magellanic Province (Chiloense + Channels and Fjords ecoregions). For example, Villalobos et al. (2021) argued that due to complex variability among environments within fjords located in this province, the communities of benthic invertebrates are formed for an overlap of species with different environmental tolerances to the interaction between freshwater and oceanic waters and to the decline of salinity towards the mouth of the fjords. Moreover, the high presence of ecosystem engineering such as cold-water corals (e.g. *Desmophyllum dianthus*), mussels (e.g. *Aulacomya atra*), brachiopods (e.g. *Magellania venosa*), sponges (e.g. *Scopalina sp.*), and polychaetes (e.g. *Chaetopterus variopedatus*) increases the substrate availability, providing habitats to different taxa in shallow and deep water (Zapata-Hernández et al. 2016, Villalobos et al. 2021). From an ecological point of view, Camus (2001) independently identified a marine floral and faunal boundary at 41° S after a revision of 27 biogeographical studies. In addition, two theories have tried to explain the importance of the region around this latitude. The first theory argues that a high diversity of marine invertebrates is related to high endemism of species (Fernández et al. 2000), because the heterogeneity of the coastal morphology (Häussermann 2006), and the divergence between Humboldt Current and Cape Horn Current, create a high diversity of biotopes (Hernández et al. 2005). The high degree of endemism of benthic marine invertebrates gives the title of biodiversity hotspots to the area, as was proposed by Myers et al. (2000) in part of their definition of a hotspot. The second theory proposed that high species diversity is related to a transitional zone at 41° to 43° S (Camus 2001). Transitional zones were defined as areas where species from zones of higher diversity could advance towards northern coastal areas due to the similarity in environmental features (Montiel et al. 2005). Therefore, even though this ecoregion might be a hotspot only for some particular taxa and not for benthic invertebrates in general, the oceanographical and environmental importance should not be ignored.

The Channels and Fjords ecoregion exhibited a lower accumulation rate of observed species richness than the Humboldtian, Central Chile, and Araucanian ecoregions; however, it had a higher value of estimated species richness (Figure 13). Consistently high values of taxonomic distinctness were observed poleward from around 43° S (Figure 14C). In addition, hotspots of taxonomic distinctness were mainly observed further south than the richness-based hotspots, from 52° to 56° S, specifically in the area corresponding to the Strait of Magellan and south of Tierra del Fuego (Figure 15C). In addition, taxonomic distinctness was not significantly correlated with the number of stations by grid cell (i.e. sampling effort) and only showed a moderate positive correlation with the number of species by grid cell. Thus, taxonomic distinctness was not strongly affected by the sampling effort, as Clarke & Warwick (1998) already showed. Rivadeneira et al. (2011) have previously observed an increase of taxonomic distinctness poleward in peracarida, with a peak at around 54° S. By using taxonomic distinctness as a proxy for phylogenetic diversity, Rivadeneira et al. (2011) related this pattern to the accumulation of older clades, and a higher rate of speciation toward southern latitudes of the Pacific Ocean. These authors also proposed that Southern Chile might be the source of evolutionary novelties. According to Clarke et al. (2004), the Antarctic region is considered an "evolutionary incubator" or the point of origin for many taxa. Also, on a long scale, Ellingsen et al. (2005) observed a positive relationship between the taxonomic distinctness of annelids and crustaceans with latitude (from 55° to 71° N). Taxonomic distinctness showed a different pattern with species richness in the Norwegian continental shelf (Ellingsen et al. 2005). The authors argued that environmental factors could be more related to the taxonomic distinctness pattern than anthropogenic pressure.

In the Channels and Fjords ecoregion, the high accumulation rate of estimated species richness obtained using the nonparametric Chao 2 (Figure 13) is related to the higher number of unique and duplicate species (i.e. rare species); this suggests that there are a large number of undiscovered species in this ecoregion. Studied carried out south 52° in assemblages of Polychaeta and Molluscs, using nonparametric measures such as ICE, Chao 2 and Jackknife 1 to estimate the expected richness, estimated values of approximately 223 polychaetes (Montiel et al. 2011) and 350-360 molluscs species respectively (Aldea et al. 2020). It indicates that the expected species richness (estimated species richness of around 400 species; Figure 13) across all taxonomic groups in the Channels and Fjords ecoregion is most likely underestimating the actual species diversity. According to Gutt et al. (2004), the low values obtained using estimators based on species presences such as Jackknife 2, Chao 2, and ICE may partially explain their sensitivity when rare species are abundant.

The importance of the Channels and Fjords ecoregion for a wide variety of taxa is recognized. The Magellanic or Sub Antarctic ecosystems are highly complex and show a diversity of habitats and biodiversity (Gambi & Mariani 1999, Montiel et al. 2011). For example, hotspots of diversity of species have been observed between 51° and 53° S for polychaetes (Hernández et al. 2005), at 54° S for Prosobranchia (Cape Horn; Valdovinos et al.

2003), and peracarida (Rivadeneira et al. 2011). Moreover, the latitudinal band between 52° and 56° S is one of the three zones of higher species richness (including marine mammals, reptiles, fishes, and invertebrates) along with the Humboldt current system (Miloslavich et al. 2011). It also matches with peaks of seaweed diversity between 50° to 55° S (Santelices & Marquet 1998, Fernández et al. 2000), and the number of species of marine mammals increasing toward 55° S (Fernández et al. 2000).

All these results show that the Magellanic biogeographic province described by Spalding et al. (2007), composed of the Chiloense and Channels and Fjords ecoregions, is the most important in terms of richness and taxonomic diversity of benthic marine invertebrates. Therefore, these Sub Antarctic ecosystems are a source of high marine biodiversity and essential ecosystem functions and services necessary to preserve and protect. Thus, the findings largely confirm previously documented distributional patterns for Chilean benthic marine invertebrates, with diversity hotspots increasing toward the south of 42° S (Fernandez et al. 2000, Valdovinos et al. 2003). It also validates the use of new sources of benthic invertebrate's data different to those already used in the past by other scientific research. It reveals the importance of preserving, maintaining, and sharing diversity data further than those only collected by the academy.

All diversity metrics were lower in northern ecoregions. Only one ICE hotspot was observed in the Araucanian ecoregion, and no hotspots were observed in the Humboldtian and Central Chile ecoregions. These results might be affected by a lower sampling effort towards northern latitudes. However, the lower diversity of marine invertebrates in these areas has previously been recognised (Carrasco 1997, Carrasco & Moreno 2006). For instance, Hernández et al. (2005) described a low species density of polychaetes in the latitudinal band between 18° and 20° S, corresponding to the Humboldtian ecoregion, and attributed this to the low diversity of microhabitats and low speciation rate. The latitudes between 18° and 33° S are associated with strong upwelling centres of cold and nutrient-rich water (Thiel et al. 2007), being one of the most productive centres on earth (Miloslavich et al. 2011). However, there are contrary opinions concerning the primary productivity as a driver of benthic invertebrate diversity in upwelling systems. Productivity has been identified as a minor driver of benthic invertebrate communities in some coastal upwelling systems of New Zealand and Mexico (e.g. Menge et al. 2003, Paz-Ríos et al. 2020, respectively) and as the main driver in upwelling systems associated with estuarine areas (e.g. Brazil; Wouters et al. 2018). Moreover, according to Thiel et al. (2007), in their extensive revision of the Humboldt current of Chile, the effects of this system of current on benthic marine invertebrates is still unknown, and it remains. Thus, defining which factors and drivers influence the diversity levels found in northern latitudes would be key to understanding coastal and shelf ecosystems in this extended zone of the Humboldt Current system.

Some mechanisms and theories may describe the decrease of species diversity with productivity towards the Northern latitudes of Chile. For instance, in highly productive systems, the diversity of epifauna and infauna monotonically decreases with mechanisms such as disturbance (i.e. local environmental differences) and environmental stress (e.g. oxygen dissolved depletion and nutrients; Witman et al. 2008). The species-energy theory described by Wright (1983) may explain how energy (e.g. productivity) might regulate the population of benthic invertebrates in northern latitudes. Thus, understanding which roles play the environmental stress (e.g. the oxygen minimum zones and eutrophication) and some forms of energy (e.g. primary productivity, temperature) in the low diversity levels of species richness of benthic marine invertebrates is key to maintaining ecosystem functions and processes of northern benthic assemblages to face environmental changes. Moreover, it is relevant to understand how these ecosystems are functionally diverse and how these benthic assemblages can contribute to the ecosystem functioning of upwelling systems.

Both richness measures, Jackk 2 and ICE, were highly and strongly correlated, but they were weak correlated with taxonomic distinctness. It was reflected in the degree of congruence in hotspots identified by the different measures: Jackk 2 and ICE shared seven hotspots in common, while only one ICE hotspot was congruent with taxonomic distinctness. The congruence in areas identified as highly diverse will be in part influenced by choice of the diversity metrics with higher congruence expected between measures influenced by species richness (Pavoine et al. 2013, Pardo et al. 2017). However, a low overall congruence between diversity hotspots and weak overall correlations among measures biodiversity based on species diversity were observed in avian diversity by Orme et al. (2005) on a global scale. These authors suggested that low congruence among hotspots represents different ecological, evolutionary and anthropogenic mechanisms responsible for the origin and conservation of distinct aspects of diversity. At the same time, it could be used as a relevant conservation tool (Orme et al. 2005). The low congruence between species richness and taxonomic distinctness indicates that this last metric captures a different dimension of overall diversity than the richness-based metrics but that a single richness metric is probably sufficient to represent that dimension. Thus, it is essential to define hotspots using different aspects of diversity to further the community composition approaches.

The use of three different diversity metrics (Jackk 2, ICE, taxonomic distinctness) defined similar spatial patterns of diversity of benthic marine invertebrates throughout the latitudinal gradient of Chile. The diversity of species peaks at around 43° S, and hotspots were located between 41.5° to 46° S in the Chiloense ecoregion, and it is lower toward northern latitudes. The taxonomic distinctness peaks at 43° S, presenting higher values polewards,; it also new hotspot area of taxonomic diversity, specifically in the Channels and Fjords ecoregion. These new hotspots are added to those already known in the Chiloense ecoregion. Thus, the Magellanic province seems to be the most important area of species and taxonomic diversity of benthic marine invertebrates. The findings also reveal that single diversity metrics, such as those based on species richness, are insufficient to capture the full extent of biodiversity. Moreover, identifying which environmental factors are driving the diversity patterns of benthic marine invertebrates along the latitudinal gradient of Chile would be essential to support areas where species richness and taxonomic diversity peak.

3.6. Supporting information

Figure S1. The relationship between longitude and A) Jackk 2 - Jackknife 2, B) ICE - Incidence based on coverage estimator, C) Δ^+ - Taxonomic distinctness. Blackline represents the fitted Generalised Additive Model (GAM), and the grey bits the interval confidence.

4. Do spatial patterns in the functional diversity of benthic marine invertebrates along the Chilean coastline and continental shelf match those in species richness and taxonomic diversity?

4.1. Abstract

The Chilean continental shelf spans 39° of latitude, with a wide variety of marine habitats, and thus constitutes an ideal environment in which to examine ecogeographic gradients in the functional diversity (FD) of benthic invertebrates. Using eight biological traits, I assess patterns of Functional richness (FRic), Functional evenness (FEve), Functional divergence (FDiv), and Functional Redundancy (FRed) throughout this latitudinal gradient. I evaluate if these patterns match the species richness and taxonomic diversity patterns observed in Chapter 3. Hotspots of FD and their congruence were also observed. I also estimate complementarity between species richness, taxonomic diversity and FD. FD presents different patterns according to the measure; FRic peaks at 30° and 43° S, presenting a similar pattern with species richness. FEve peaks towards the extreme latitudes of the gradient. FEve and FRed do not present any pattern with latitude. Hotspots of FD were located between 20° to 33° S and south of 50° S, revealing new hotspots areas to those already known for species richness. Thus, limited congruence among FD hotspots and species richness and taxonomic diversity was observed. It reinforces the value of adopting a functional approach to macroecological and biogeographical analyses to understand new aspects of diversity that only species richness does not capture.

4.2. Introduction

One of the challenges for ecology and evolutionary biology is understanding the global patterns of biodiversity, mostly focused on taxonomic species (Berke et al. 2014). However, nowadays, the new trend is defining the functional structure and functional diversity of assemblages along eco-geographical gradients (e.g. Ellingsen & Gray 2002, Törnroos et al. 2015, Wouters et al. 2018). Even when the number of studies focusing on the functional trait approach is becoming more abundant, studies evaluating patterns of functional diversity in a latitudinal gradient or at a large scale are still scarce in marine ecosystems (Törnroos & Bonsdorff 2012, Garaffo et al. 2020), and this is more notorious throughout South America (e.g. Llanos et al. 2020, Gusmao et al. 2016, Wouters et al. 2018).

As another important aspect of biodiversity, the functional structure of a community can influence the ecosystems and be influenced by them (Ricotta & Moretti 2011). The functional traits of species are a fundamental part of the functional structure; they are defined as the biological attributes influencing the performance of the organisms (Violle et al. 2007). The functional traits form the basis of functional ecology (Villéger et al. 2010), and they are essential to estimate functional diversity. Basically, traits can be differentiated into effect traits, related to ecosystem processes, and response traits, related to the resistance and resilience of the species (Villéger et al. 2010, Beauchard et al. 2017). Any combination of traits can form a functional trait space, where species are positioned according to their traits' coordinates (Mouillot et al. 2013, Carmona et al. 2016). Thus, the distribution of species and their abundances in the functional space define the functional structure (Mouillot et al. 2013). By collating information on the traits of species, it is possible to quantify the functional structure through the Functional Diversity (FD) of a community (Villéger et al. 2010).

FD has three main components: Functional richness (FRic), Functional evenness (FEve), and Functional divergence (FDiv; Villéger et al. 2008, Mouchet et al. 2010). To understand these components, we can consider two traits and a community of nine species with their respective frequencies (the relative frequency of each species replaced abundance or biomass). We could plot these species in the functional space (Figure 18, based on Villéger et al. 2008). If we connect the species which represent the most extreme points (i.e. vertices), the volume generated by the figure represents the FRic (Figure 18A). Thus, FRic is defined as the volume of functional space filled by the species present in a community (Mouillot et al. 2013). A tree can be formed in the functional trait space if we link each species (Figure 18B); the FEve measures the uniformity of the species along this tree, weighted by their frequencies (Villéger et al. 2008). Assuming that the functional space has a centre of functional traits range, we could define how close or distant are the most frequent species from this point (Figure 18C); thereby, FDiv estimates how the species frequencies are distributed from the centre point in the functional trait space, and how this distribution is compared with the mean distance to the centre (red circle, Figure 18C; Villéger et al. 2008). As was seen before, the frequency of species is only included in the estimations of FEve and FDiv (Mouchet et al. 2010). In addition, Functional redundancy (FRed) was estimated to measure how similar, in terms of traits, an individual is from the whole community (Ricotta et al. 2016). For instance, if we have a group of species distributed close to each other in the functional trait space, they might contribute in an equivalent way (Figure 18D); if we remove one of these species, this will have a negligible effect on the ecosystem.

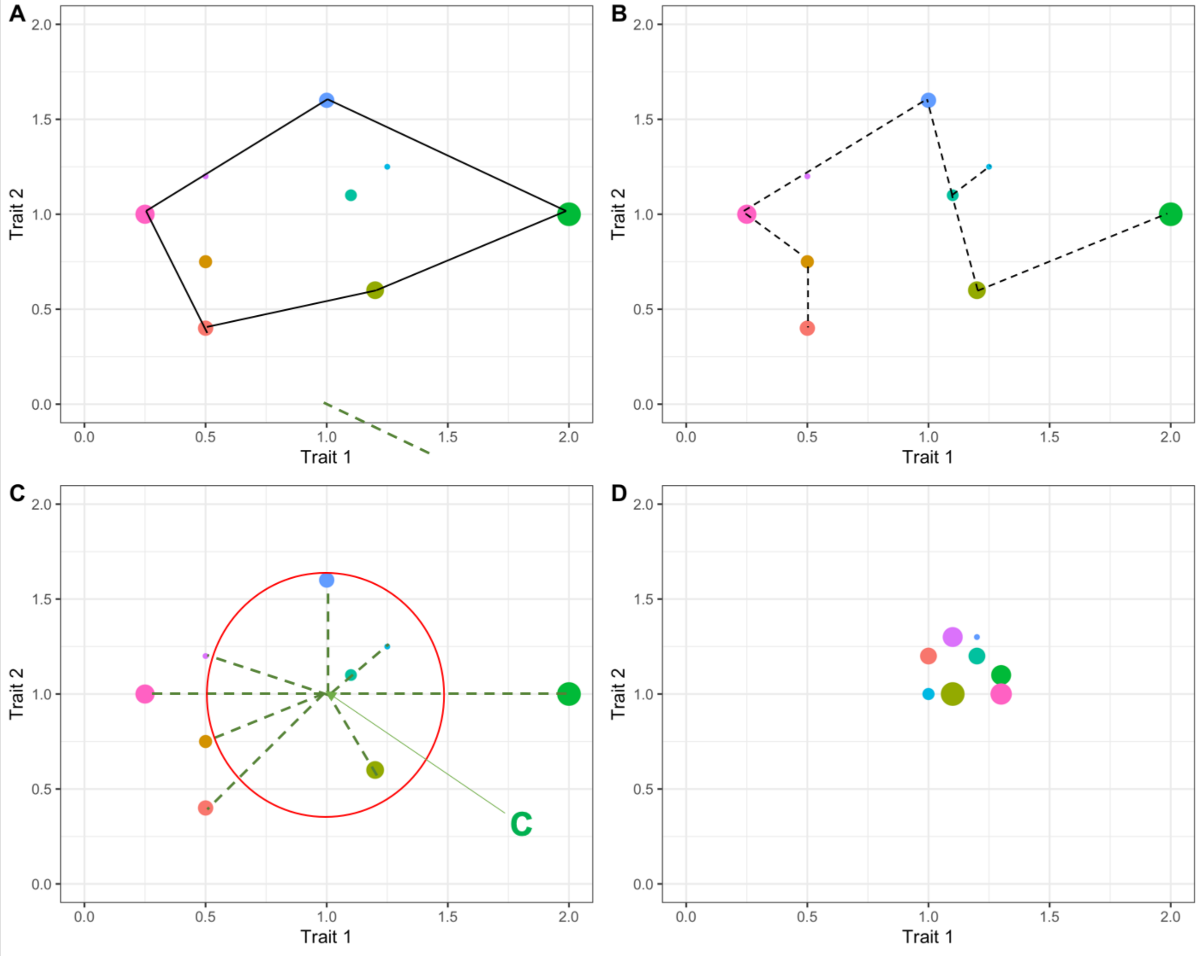


Figure 18. Diagram showing an example of each functional diversity measure. The axis represents two functional traits forming a functional space where nine species and their respective frequencies, represented by the size of the points, are positioned. **A)** FRic (functional richness) is represented by the polygon formed linking the points and corresponds to the volume of the traits space occupied by the species. **B)** FEve (Functional evenness) estimates the uniformity of the species along the tree formed linking each species with its closer one (dashed lines), weighted by the species frequencies. **C)** FDiv (Functional divergence) estimates how the species frequency is distributed

from the centre point within the functional space (green dashed lines from the centre C), and how this distribution is compared with the mean distance to the centre point (red circle). These three diagrams were adapted from Villéger et al. 2008. **D)** FRed (Functional redundancy) is a measure of the similarity of traits in terms of traits in a community. Having a group of species closer to each other in the functional space, the removal of one species could have a little effect on the ecosystem.

A high FRic indicates that the volume of functional traits space occupied by the species in a community is large (Villéger et al. 2008). Thus, species with more extreme traits built a larger volume of functional trait space (Villéger et al. 2008). High FEve might indicate a better distribution of the species in the functional space, better use of available resources, and more productive communities (Mason et al. 2005). High FDiv might indicate communities with low competition for resources (Mason et al. 2005). High FRed is related to a higher resilience or recovery from perturbations and the resistance to changes in species diversity or species loss (Micheli & Halpern 2005, Biggs et al. 2020). Furthermore, as a result, the community structure or the ecosystem function tend to be more stable (Biggs et al. 2020). Because the three components of FD may have different responses to the same perturbation (Schleuter et al. 2010, Legras et al. 2018), considering FD in this multifaceted way could be useful for observing the real impact of perturbations on biotic communities (Villéger et al. 2010), including their consequences for the ecosystem functioning (Mouillot et al. 2013). Ultimately, this may help design conservation measures that fully consider the preservation of traits and taxonomic biodiversity (Villéger et al. 2010).

While FD has now been widely studied in a range of systems, simultaneous evaluation of spatial patterns in FD together with other dimensions of biodiversity (e.g. taxonomic, phylogenetic) remains scarce (Hultgren et al. 2021). Such studies are essential because complementarity between diversity measures will influence conservation prioritisation and the effectiveness of management intervention to address the effects of environmental perturbations on the functioning of ecosystems (Micheli & Halpern 2005). FEve and FDiv are independent of species richness (Mason et al. 2005, Villéger et al. 2008), but species richness is expected to be related to FRic (Mason et al. 2008). Identifying diversity hotspots for conservation planning is another motivation for understanding the relationships between different dimensions of diversity (Pardo et al. 2017). Not many studies identify whether areas of high species diversity are also functional hotspots (Törnroos et al. 2015). Thus, estimating congruence between hotspots of different dimensions of diversity may be the first step to defining more complete conservation policies. It is known that the congruence in areas identified as highly diverse will be in part influenced by choice of the diversity metrics (Pardo et al. 2017), with higher congruence expected between measures influenced by species richness

(Pavoine et al. 2013, Pardo et al. 2017). Pardo et al. (2017) emphasised the choice of the right diversity metrics to define spatial congruence between hotspots.

Benthic marine ecosystems such as those observed through the 39° of latitude encompassing the Chilean coast and continental shelf, and the communities of benthic marine inhabiting these ecosystems might be interesting from a functional diversity perspective. Chilean marine ecosystems are influenced by a system of current (Humboldt and Cape of Horn currents), seasonal and permanent coastal upwelling centres, El Niño Southern Oscillation (ENSO) periods, and geographical changes, which include a system of estuaries, channels and fjords toward southern latitudes, among others. Coastal and offshore ecosystems are also affected by anthropogenic activities such as benthic fisheries, aquaculture and mining.

Marine benthic invertebrates correspond mainly to sessile or reduced mobility species (Poulin et al. 2001). These organisms are also considered bioindicators of environmental health in freshwater and marine ecosystems, and they can be used in a multiple functional trait framework (Beauchard et al. 2017). Thus, firstly, I use a combination of quantitative and qualitative biological traits to estimate FD using FRic, FEve, FDiv and FRed metrics in benthic marine invertebrate communities. Bremner et al. (2003) defined biological traits such as those features reflecting life history, morphology and behaviour of species. These features can highlight differences between taxa (Bremner et al. 2003). Moreover, the use of biological traits needs understanding of the species life history in marine environments (Beauchard et al. 2017). Thus, the biological traits were chosen considering the environmental features of the Chilean marine ecosystems. For example, motility in invertebrates is related to the dispersion, escape, and migration of adult individuals; and it could be considered response of the organisms to the environment and the effect of anthropogenic activities. The ecosystem engineering traits modalities are related to the effect of organisms whose activity causes physical changes in abiotic and biotic materials, controlling directly or indirectly the availability of resources for other organisms (Jones et al. 1994), and their presence or absence in an environment may have consequences in the nutrient cycling, and rate of exchange of oxygen between sediment and water. The life-history traits, such as early development (direct and indirect) and development mode (benthic and pelagic), are associated with the natural capacity of dispersion of larval stages. Secondly, I assess the spatial patterns of functional diversity through the latitudinal gradient, evaluating if these patterns match the already observed richness and taxonomic diversity patterns in Chapter 3 (e.g. species richness and taxonomic diversity peak in the Chiloense ecoregion). Then, hotspots of FD were identified, and the congruence between richness, taxonomic and diversity hotspots was also examined. Finally, I estimate complementarity between species richness, taxonomic diversity and FD to determine the influence of richness on FD metrics and describe the ecological cause of such a level of correlation or the non-correlation between metrics.

4.3. Materials and Methods

4.3.1. Benthic community data collation

For full details of the integrated database, see Chapter 2. In brief, the database was generated by aggregating data from multiple sources. For this chapter, a total of 34,179 occurrence records for 762 species of benthic marine invertebrates were accounted, from a broad range of taxa including Mollusca, Annelida, Arthropoda, Foraminifera, Echinodermata, Porifera, Cnidaria, Bryozoa, Brachiopoda, and Nemertea. Each species occurrence was georeferenced, and the dataset was gridded into equal-area cells of 55 x 55 km. Latitude and longitude were projected as Albers Equal Area Conic (ESRI projection 102033) because of Chile's geographic position and elongated shape.

The classification proposed by Spalding et al. (2007) was used to understand the Chilean latitudinal gradient better. These authors divided the global continental shelf into 62 provinces and 232 ecoregions. The ecoregions correspond to areas with relatively homogeneous species composition (Spalding et al. 2007). Two provinces and five ecoregions represent the continental area of Chile. The Warm temperate Southeastern Pacific Province, shared with Peru, ranges between 18º to 41.5º S and includes the Humboldtian, Central Chile and the Araucanian ecoregions. The Magellanic province, which ranges from 41.5º to 56º S, is divided into the Chiloense and the Channels and Fjords of South Chile ecoregions. The limits of each province and their ecoregions in Chile were based on Chilean research developed by Fernandez et al. (2000), Ojeda et al. (2000) and Camus (2001).

4.3.2. Biological trait data

A total of 11 biological traits were selected to describe the behaviour (e.g. adult motility, feeding methods) and life history (e.g. reproductive mode, lifespan) of the 762 species of benthic marine invertebrates in the dataset. The traits were divided into a total of 46 modalities (i.e., values which each trait could take; Table 4), and they were selected according to their relevance as effect or response traits. Response traits are those related to the expression of the species fitness, and effect traits are associated with the consequences from this expression in the environment (Beauchard et al. 2017). The selected traits are described in Table 4.

Information for each biological trait was obtained mostly from primary sources such as books and scientific papers, as well as supported by open databases, for instance: WoRMS (http://www.marinespecies.org), Biotic (http://www.marlin.ac.uk/biotic/), and Polytraits (http://polytraits.lifewatchgreece.eu). The full list of references for the construction of the biological traits database is provided in Supplementary material (Appendix S3).

Biological trait information was collected at the lowest possible taxonomic level, with priority given to data at the species and genus level, although the family level was also used. Data were available for most species for maximum body size (99%), feeding method (99%), larval development (98%), larval mode of development (95%), adult motility (91%), and reproductive mode (91%). For the traits, sexual differentiation and ecosystem engineering data were available for at least 70% of species (Table 4; 89 and 71%, respectively) (Appendix S5: Trait database). The three remaining biological traits (Lifespan, Generation length, and sociability) were missing data for more than 60% of species and were excluded from further analysis.

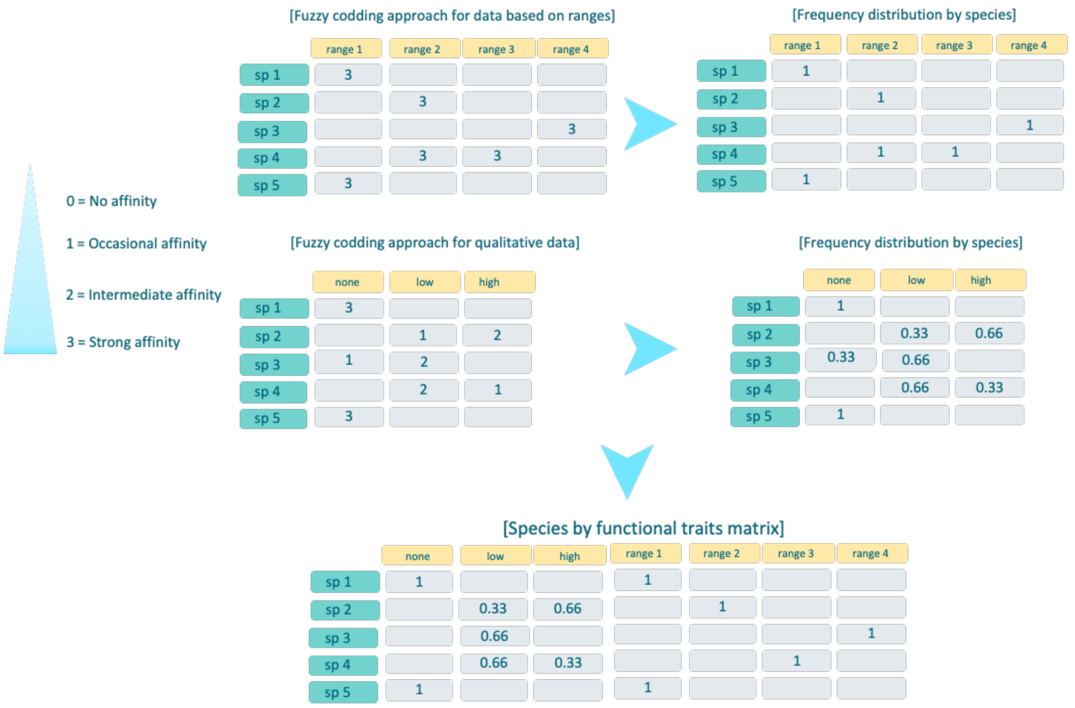
Each biological trait and its modalities were described in metadata according to the trait (response or effect), code, and unit (Appendix S4). For quantitative biological traits such as maximum body size and lifespan, when data for one species was found in any source of information, the original data (e.g. 1 mm or 2 years) was stored into the trait database together with the relevant reference. Thus, I had more than one value for some biological traits in some species derived from different sources. Then, the ranges of maximum body size (mm) and lifespan (years) were built to record each data in these cases (e.g. Table 4).

In constructing the species by biological traits matrix, combining quantitative and qualitative biological traits, a frequency table by biological trait based on the fuzzy coding approach (Chevenet et al. 1994) was produced. This approach works by assigning scores depending on the species affinity to each trait modality, based on its description from the different sources. Thus, the scores used were: 0 = no affinity, 1 = occasional affinity, 2 = intermediate affinity, and 3 = strong affinity. For example, *Cirratulus cirratus* is known as a deposit feeder; thus, this modality will present the higher affinity "3"; at the same time, this species can also show a moderate affinity for the suspension-feeding, then the affinity score will be 2 for this modality, and 0 for those modalities where the species do not show affinity (predator, filter feeder, and scavenger). The affinity scores were standardised as frequency distribution by species (Chevenet et al. 1994, Beauchard et al. 2017; see Appendix S5). Thus, per species, the sum of the modalities of one biological trait was equal to 1. It had the aim to give the same weight to each species and each biological trait in the analyses (van der Linden et al. 2012) and show full affinity for a modality. An example of the methodology used for different types of biological traits and their transformation into frequency distribution is given in Figure 19.

Table 4. Biological traits and modalities used to estimate functional diversity of Chilean benthic marine invertebrates (Compiled by author).

Biological Trait	Modalities	Type of trait	Biological trait and modality description	Data availability (%)
MBS: Maximum body size (mm)	≤ 2.5 2.6 to 5 5.1 to 10 10.1 to 20 20.1 to 50 50.1 to 80 80.1 to 100 ≥ 101	Response and effect	Related to the maximum length (mm) of the organisms. MBS is a descriptor of the expression of diverse functions (e.g. physiological, reproductive, and ecological), and species performances (Beauchard et al 2017).	99
EE: Ecosystem engineering	Biodiffuser Upward conveyor Downward conveyor Regenerator Blind ended ventilation Open ended ventilation Reef forming	Effect	Its modalities are categorised according to the type of bioturbation. *Biodiffuser of diffusive mixing:* Local sediment biomixing (Kristensen et al 2012). *Conveyor belt transport:* Head - down feeders, translocate sediment from the anoxic sub-surface to the surface as faecal material (Kristensen et al. 2012, Welsh 2003). *Downward conveyor:* Head - up feeders, transport particles from surface to the depth through feeding or as faecal material (Kristensen et al. 2012). *Regenerator:* Active excavator organisms. They transfer sediment from depth to the surface (Faulwetter et al. 2014). *Blind ended ventilation:* Organisms living in a burrow with only one opening. Their respiration and feeding activity imply a bidirectional or unidirectional ventilation of water, the bioirrigation through radial diffusion (i.e. wall - water interface), and the transport of solutes to the overlying water body (Kristensen et al. 2012). *Open ended ventilation:* Organisms living in U-shaped burrows, with at least two openings. The ventilation is through the openings in the burrow, and the biodiffusion could be radial (i.e. through wall - water interface) or by advective forcing (i.e. across the wall-water interface; Kristensen et al. 2012). *Reef forming:* Organisms creating, and modifying structures which can be inhabited for other organisms (Faulwetter et al. 2014).	71
LH: Adult motility	None Low Crawler Burrower High	Response and effect	Capability of motility to escape, migrate, and for dispersion (Beauchard et al. 2017). *None motility:* Organisms living attached to the bottom (Bremner et al. 2003). *Low motility*: Semi-motile organisms with the capability to move across or through the sediment. *Crawler:* Organisms with the capability to move along the substrate using legs, and appendages. *Burrower:* Organisms inhabiting or moving into burrows. *High motility or free living:* Non - attached organisms.	91
FM: Feeding method	Predator Suspension feeder Filter feeder Deposit feeder Scavenger	Response and effect	Related to food acquisition, demographic control through predation, and biogeochemical cycles (Beauchard et al. 2017). *Predator:* Organism killing others for food. *Suspension feeder:* Organism feeding on particulate organic matter, including plankton suspended in the water column. *Filter feeder:* creates water currents for food retention. *Deposit feeder:* Organism which feeds on fragmented particulate organic matter from the substratum. *Scavenger:* Organism that actively feeds on dead animals (Faulwetter et al. 2014).	99

Biological Trait	Modalities	Type of trait	Biological trait and modality description	Data availability (%)
ED: Early development	Direct development Indirect development	Response	Embryological point of view (Poulin et al. 2001) *Direct development:* There are no intermediate larval stage(s) or postembryonic metamorphoses. Embryonic development culminates in the hatching or birth of a fully formed miniature adult. *Indirect development:* One or more successive, free-living larval stages between embryo and adult, with a more-or-less abrupt transition/metamorphosis, between the last larval stage and the adult. They can present benthic and/or pelagic larvae.	98
DM: Development mode	Benthic Pelagic	Response	*Benthic:* Development on or near the bottom of a water body (Faulwetter et al. 2014). It can consider larvae and juveniles stages in the case of direct development. *Pelagic:* Development in the water column (Faulwetter et al. 2014). These larvae can be planktonic (i.e. lecithotrophic or non-feeding larvae), or planktotrophic (feeding larvae). It can also consider larvae and juveniles stages in the case of direct development.	95
RT: Reproductive mode	Asexual Sexual	Response	*Asexual reproduction:* The egg fertilization by the sperms does not occur. Asexual reproduction occurs by fragmentation, fission or parthenogenesis. *Sexual reproduction:* Broadcast spawning takes place when animals release their eggs and sperm into the water, the fertilization is externally (Bremner et al. 2003).	91
SD: Sexual differentiation	Gonochoristic Synchronous hermaphrodite Sequential hermaphrodite Hermaphrodite	Response	*Gonochorism:* Sexes are separated (dioecism). *Synchronous hermaphrodite:* Both male and female tissues mature together and simultaneously. *Sequential hermaphrodite:* Individuals sequentially alternate between male and female stage. *Hermaphrodite:* An individual produces male and female gametes during its lifetime.	89
LS: Lifespan	< 1 year 1 to 2 years 3 to 5 years 6 to 10 11 to 30 years > 31 years	Response	It indicates the persistence, recovering and stability of a population over time (Costello et al. 2015).	33
RF: Generation per year	One per year More than one per year	Response and effect	It is associated with the reproductive frequency, the capacity of recovery and dispersion (Törnroos & Bonsdorff, 2012). Species with more than one brood per year are associated with k - strategies.	27
SC: Sociability	Solitary Colonial Gregarious	Response	Species living as unique individuals or interacting with others forming colonies or communities.	29



0 = No affinity

1 = Occasional affinity

2 = Intermediate affinity

3 = Strong affinity

[Fuzzy codding approach for data based on ranges]

	range 1	range 2	range 3	range 4
sp 1	3			
sp 2		3		
sp 3				3
sp 4		3	3	
sp 5	3			

[Frequency distribution by species]

	range 1	range 2	range 3	range 4
sp 1	1			
sp 2		1		
sp 3				1
sp 4		1	1	
sp 5	1			

[Fuzzy codding approach for qualitative data]

	none	low	high
sp 1	3		
sp 2		1	2
sp 3	1	2	
sp 4		2	1
sp 5	3		

[Frequency distribution by species]

	none	low	high
sp 1	1		
sp 2		0.33	0.66
sp 3	0.33	0.66	
sp 4		0.66	0.33
sp 5	1		

[Species by functional traits matrix]

	none	low	high	range 1	range 2	range 3	range 4
sp 1	1			1			
sp 2		0.33	0.66		1		
sp 3		0.66					1
sp 4		0.66	0.33			1	
sp 5	1			1			

Figure 19. Scores used to define the species affinity to a biological trait modality. Example of the fuzzy coding approach used for quantitative and qualitative data, and their transformation into a matrix of a frequency distribution by species.

4.3.3. Functional diversity indices

As was described previously, FD can be divided into three independent but complementary components: (1) Functional richness (FRic), (2) Functional evenness (FEve), and (3) Functional divergence (FDiv; Mason et al. 2005, Villéger et al. 2008). Each component represents an estimation of how the species in a community fill the functional trait space and how these species and their abundances (here relative frequencies) are distributed in the functional trait space (Villéger et al. 2008, Schleuter et al. 2010).

A matrix of species by grid cells (matrix 1) was combined with the matrix of species by biological traits (matrix 2) to estimate the indices of FRic, FEve, FDiv, and FRed. FRic does not consider the frequency in its estimation (Mason et al. 2005, Villéger et al. 2008); thus, for the calculation matrix 1 was converted to presence and absence data, where 1 is a presence and 0 is absence. FRic, FEve, and FDiv, were obtained using the function `dbFD()` in the package `FD` (Laliberté & Legendre 2010, Laliberté et al. 2014) in R (R Core Team 2020). FEve and FDiv are naturally and strictly constrained between 0 to 1 (Villéger et al. 2008). FRic was constrained between 0 to 1 using the argument `stand.FRic = TRUE` in the function `dbFD()`. From the species by biological traits matrix, the function constructs a matrix of Euclidean distance (species by species). FRed was estimated using the function `rao.diversity()` in the package `SYNCSA` (Debastiani & Pilar, 2012). FRed is also constrained between 0 to 1. Each index value obtained was assigned to the respective grid cell. Gridded maps were produced to represent the spatial patterns of the four functional diversity indices using `sp` (Pebesma & Bivand 2005, Bivand et al. 2013), `maps` (Becker et al. 2021), and `ggplot2` (Wickham 2016) packages in R.

4.3.4. Latitudinal patterns in functional diversity

The four FD indices were analysed as a smoothed function of the latitude and the longitude of each grid cell using Generalised Additive Models (GAMs), of the form FD index ~ s(latitude) + s(longitude). Latitude and longitude were both included as separate smooth terms, with latitude the primary variable of interest (because it represents an eco-geographical gradient) and longitude included to account for additional spatial structure in the data. Smooths were fitted using restricted maximum likelihood (REML). GAMs were chosen because they are flexible, with smooth functions allowing the response curve to fit the predictor variable without assuming a distinct functional form (Lawler et al. 2006). GAMs were fitted using the package `mgcv` (Wood 2003, 2004, 2011, 2017, Wood et al. 2016) in R. The F test statistic, and its significance, as well as the R-squared, and the effective degrees of freedom (edf - an indication of the extent of nonlinearity of the fitted smooth) were all extracted from the model.

4.3.5. Hotspots of functional diversity and complementarity with richness and taxonomic diversity

Hotspots in terms of the four FD metrics were determined. The hotspots corresponded to the 10% most diverse grid cells based on each diversity measure (FRic, FEve, FDiv, and FRed). To estimate complementarity between these measures and other measures of diversity, Pearson coefficients of correlation between species richness (ICE - Incidence Coverage-based estimator) and taxonomic diversity (Δ^+- Taxonomic distinctness) and the FD measures (FRic, FDiv, FEve, and FRed) were calculated. Venn diagrams were used to observe congruence between hotspots of FD, species richness, and taxonomic diversity. The diagrams were built with the function `ggvenn` in the package `ggvenn` (Yan 2021).

4.4. Results

4.4.1. Latitudinal patterns in functional diversity

FRic ranged between 0.1 to 0.7, with two peaks observed at around 30° S and 43° S, corresponding to the Central Chile and Chiloense ecoregions (Figure 20A; GAM: $F = 4$, $edf = 6$, $p = 0.003$, $R^2 = 0.4$). FEve ranged between 0.3 to 0.8, with higher values towards northern latitudes (Humboldtian ecoregion) and southern latitudes (Channels and Fjords ecoregion); however, this pattern was not significant (Figure 20B; GAM: $F = 2$, $edf = 2$, $p = 0.1$, $R^2 = 0.2$). FDiv ranged between 0.5 to 0.9. FDiv did not show any pattern with the latitude (Figure 20C; GAM: $F = 0.1$, $edf = 1$, $p = 0.8$, $R^2 = 0.1$). FRed ranged between 0.5 to 0.8. Although FRed slightly increased at around 35° S in the Araucanian ecoregion, however this pattern was not significant (Figure 20D; GAM: $F = 1$, $edf = 3$, $p = 0.6$, $R^2 = 0.4$).

Higher FRic was observed at around 66°, and 73° W (Figure S2A; GAM: $F = 6$, $edf = 4$, $p = 0.0002$, $R^2 = 0.4$). FEve did not show a significant pattern with the longitude (Figure S2B; GAM: $F = 3$, $edf = 2$, $p = 0.09$, $R^2 = 0.2$). FDiv showed peaks at around 69° and 75° W; however, this pattern was not significant (Figure S2C; GAM: $F = 4$, $edf = 4$, $p = 0.007$, $R^2 = 0.1$). FRed slightly increased towards western from 73° W (Figure S2D; GAM: $F = 7$, $edf = 5$, $p < 0.0001$, $R^2 = 0.4$).

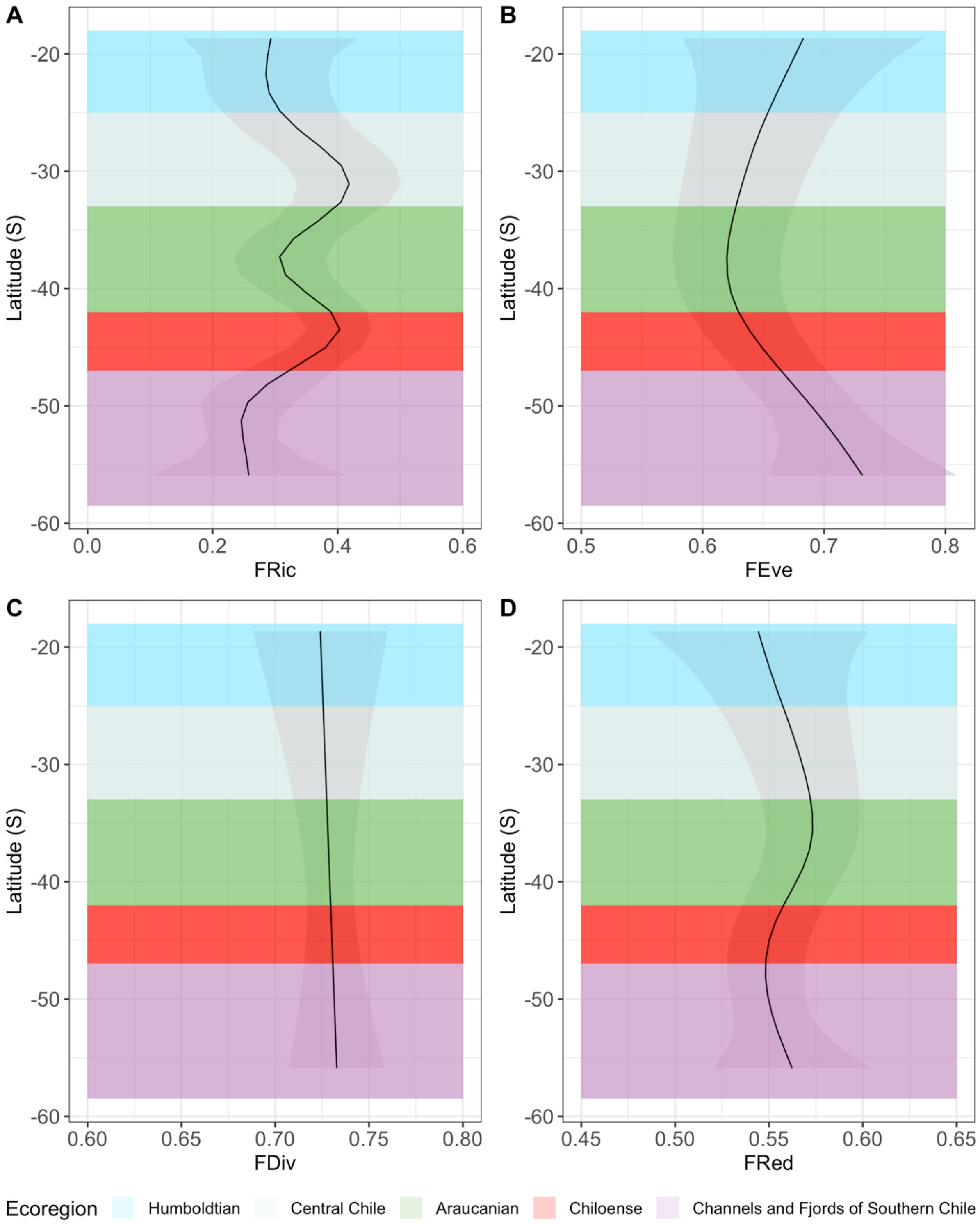


Figure 20. The relationship between latitude and **A)** FRic - Functional richness, **B)** FEve - Functional evenness, **C)** FDiv - Functional divergence, and **D)** FRed - Functional redundancy. Blackline represents the fitted Generalised Additive Model (GAM), with the confidence interval in grey.

4.4.2. Hotspots of functional diversity and complementarity with richness and taxonomic diversity

Hotspots of FRic were observed at around 30°, and 33° S (Central Chile ecoregion), and in the latitudinal band between 41.5° - 46° S (Chiloense ecoregion; Figure 21A). Only 7 of the 10 FRic hotspots presented values > 0.5. FEve hotspots were distributed at around 22° (Humboldtian ecoregion), 26° (Central Chile ecoregion), and 43° S (Chiloense ecoregion); however, the highest number of FEve hotspots were found towards southern latitudes, from 48° S (Channels and Fjords ecoregion; Figure 21B). FDiv hotspots were observed in northern latitudes, at around 20° and 22° S (Humboldtian ecoregion) and 26° S (Central Chile ecoregion). In southern latitudes, FDiv hotspots were found at around 40° S (Araucanian ecoregion), in the latitudinal band between 42° and 44° S (Chiloense ecoregion), and at around 54° S (Channels and Fjords ecoregion; Figure 21C). FRed hotspots were observed mainly towards southern latitudes, at around 34° - 40° S (Araucanian ecoregion), 43° - 46° S (Chiloense ecoregion), 50° and 55° S (Channels and Fjords ecoregion; Figure 21D).

FRic was positively but not significantly correlated with FEve (Figure 22A; Pearson = 0.1, $p = 0.3$). FRic was negatively and significantly correlated with FDiv (Figure 22B; Pearson = -0.2, $p = 0.03$), and with FRed (Figure 22C; Pearson = -0.6, $p < 0.0001$). FEve was negatively but not significantly correlated with FDiv (Figure 22D; Pearson = -0.2, $p = 0.09$), and negatively and significantly correlated with FRed (Figure 22E; Pearson = -0.7, $p < 0.0001$). FDiv was positively and significantly correlated with FRed (Figure 22F, Pearson = 0.3, $p = 0.001$).

In terms of complementarity between FD measures and richness and taxonomic diversity metrics, FRic was significantly and positively correlated to ICE (Figure 23A; Pearson = 0.5, $p < 0.0001$) and to Δ+ (Figure 23B; Pearson = 0.7, $p < 0.0001$). FRic achieved an asymptote with increasing ICE, and Δ+. FEve was negatively but not significantly correlated to ICE (Figure 23C; Pearson = -0.2, $p = 0.1$), and positively and significantly correlated to Δ+ (Figure 23D; Pearson = 0.4, $p < 0.0001$). FDiv was uncorrelated to ICE (Figure 23E; Pearson = -0.01, $p = 0.9$), and negatively correlated to Δ+ (Figure 23F; Pearson = -0.2, $p = 0.05$). FRed was negatively but not significantly correlated to ICE (Figure 23G; Pearson = -0.1, $p = 0.0$), and negatively and significantly correlated to Δ+(Figure 23H; Pearson = -0.7, $p < 0.0001$).

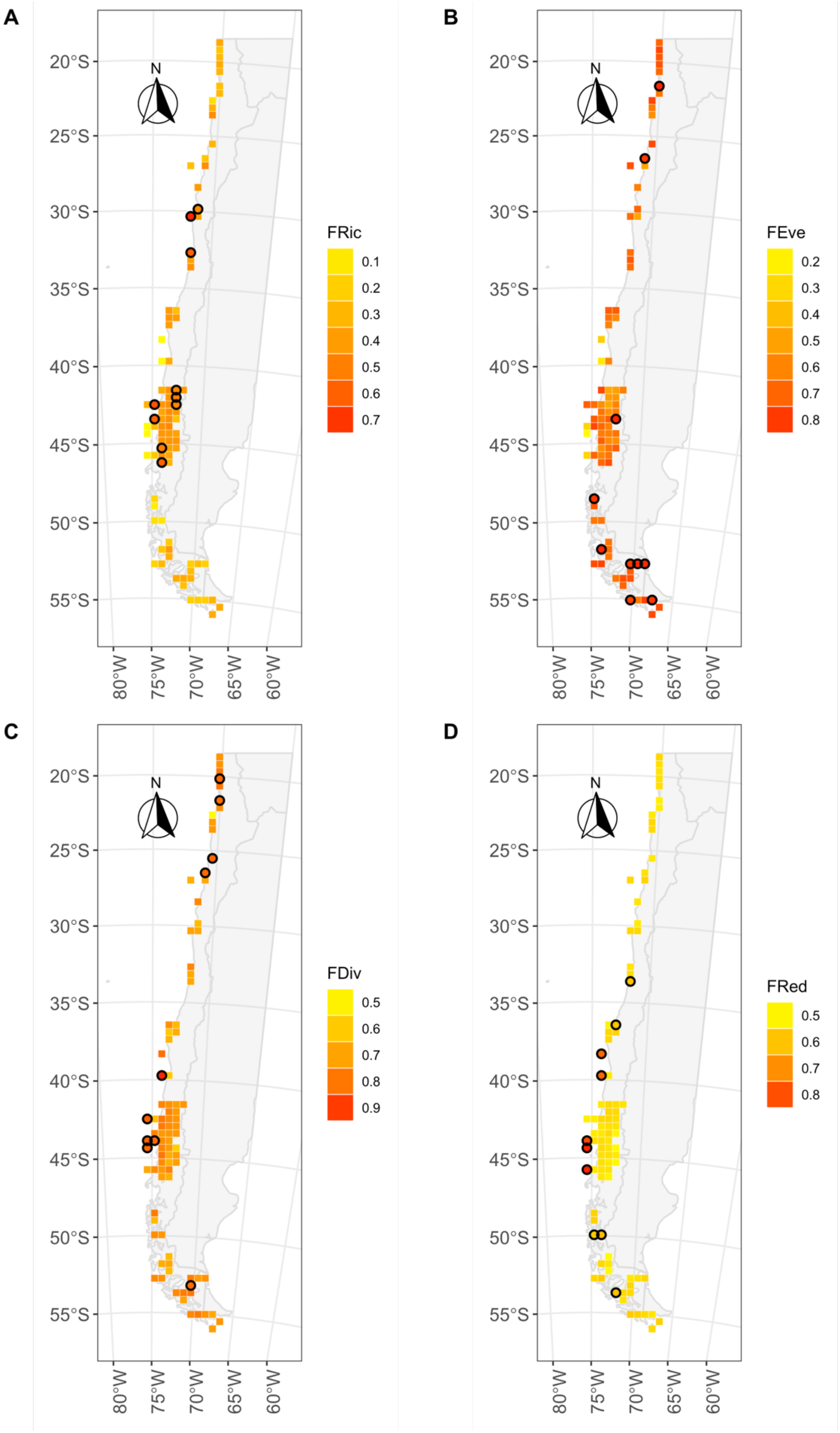


Figure 21. Gridded map showing the spatial distribution of each functional diversity metric and the Hotspots (defined as the 10% most diverse area for each metric), indicated through the black circles. **A)** FRic - Functional richness, **B)** FEve - Functional evenness, **C)** FDiv - Functional divergence, and **D)** FRed - Functional redundancy.

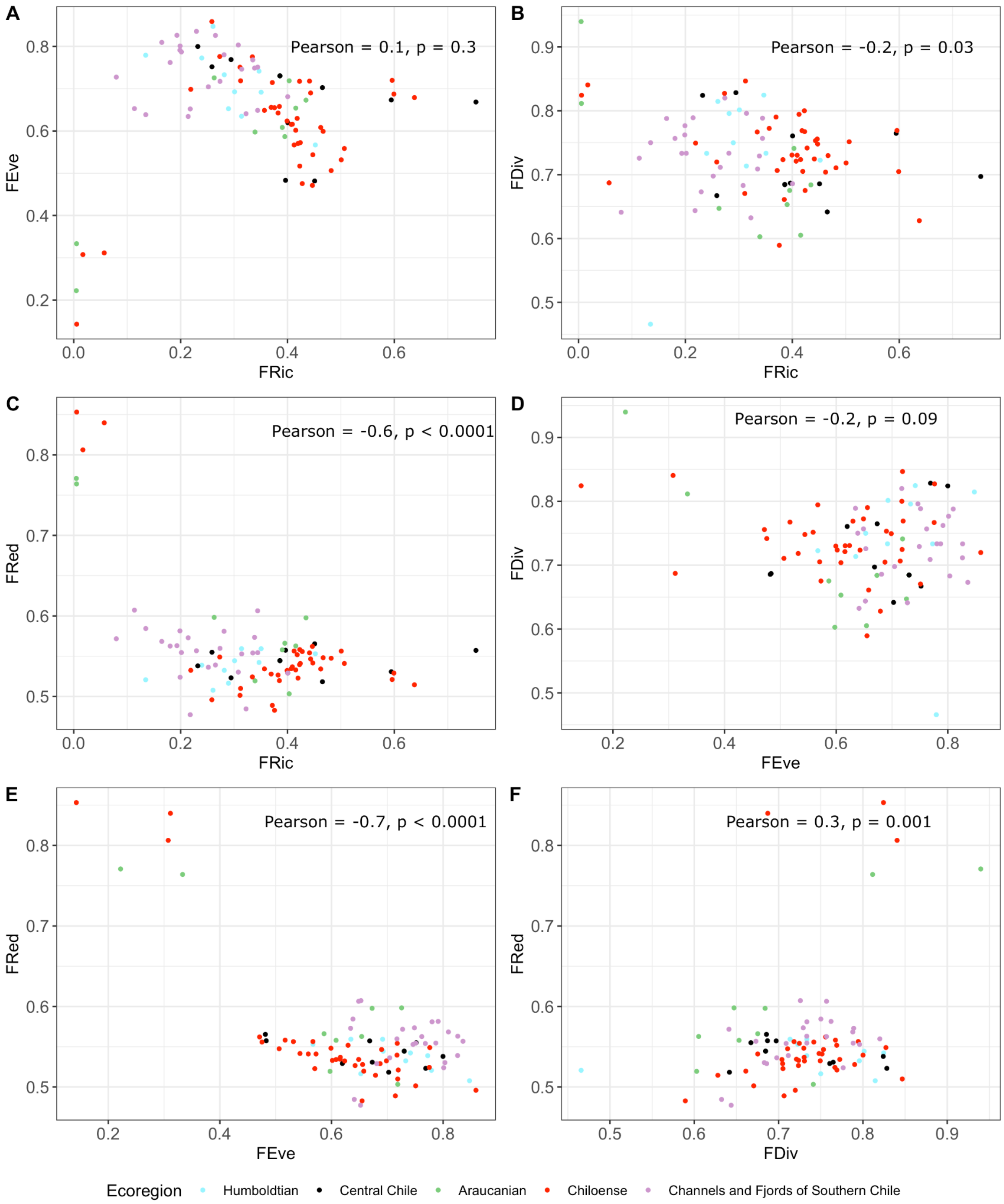


Figure 22. Complementarity between diversity functional diversity measures (FRic - Functional Richness, FEve - Functional Evenness, FDiv - Functional Divergence, and FRed - Functional Redundancy).

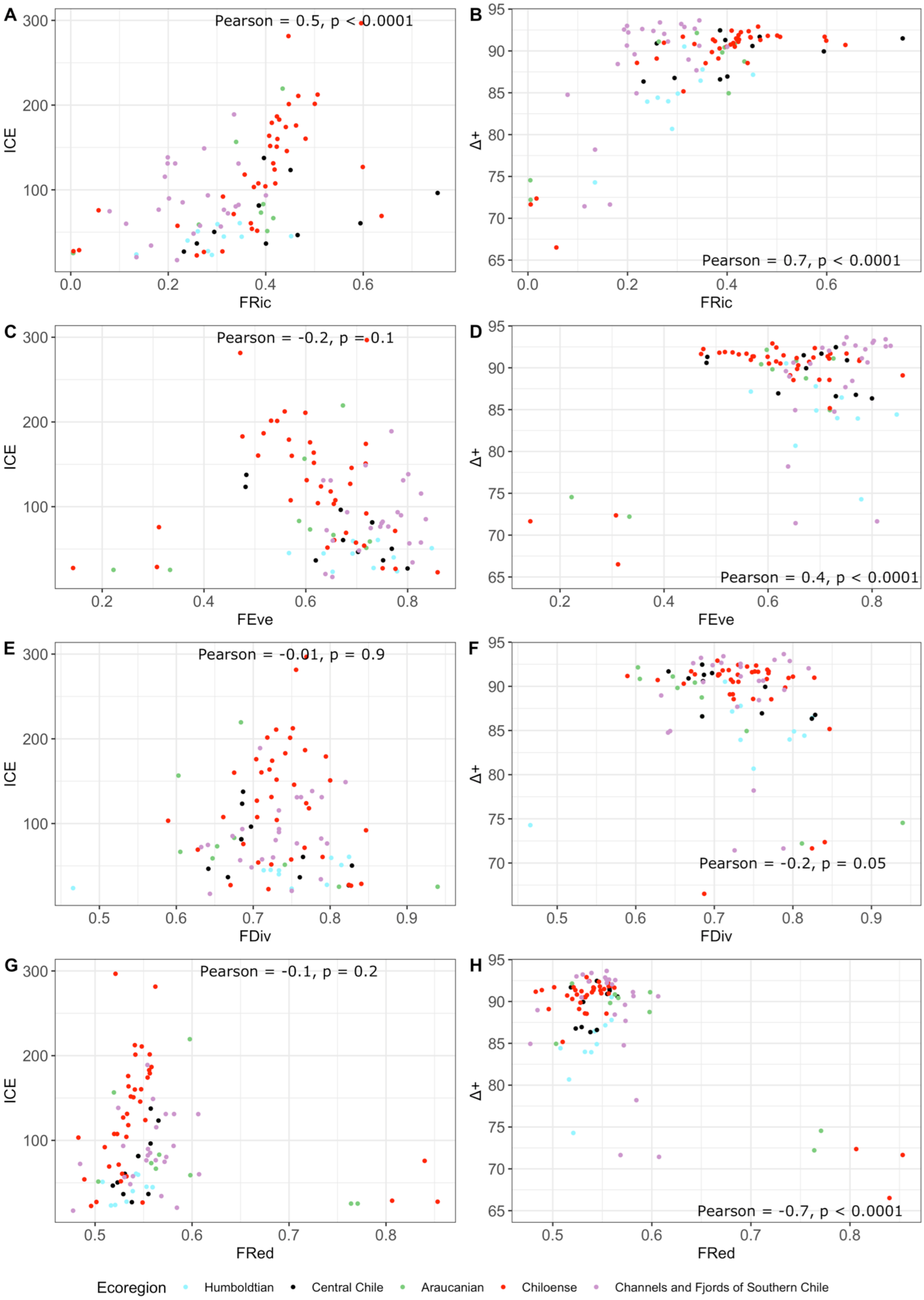


Figure 23. Complementarity between ICE (Incidence Coverage-based estimators), Δ^{+} (taxonomic distinctness), and the functional diversity measures (FRic - Functional Richness, FEve - Functional Evenness, FDiv - Functional Divergence, and FRed - Functional Redundancy).

Congruence among the measures of FD was observed between FDiv and FEve (two hotspots in common) and between FDiv and FRed (three hotspots in common; Figure 24A). From the three components of the FD (FRic, FEve, and FDiv), only FRic showed congruence with ICE (four hotspots in common; Figure 24B). From the three components of the FD (FRic, FEve, and FDiv), only FEve showed congruence with Δ^+ (five hotspots in common; Figure 24C). FRed showed congruence with ICE (one hotspot in common; Figure 24D). Hotspots showing congruence among FRic (or other FD metrics), richness ICE, and taxonomic diversity Δ^+ were not observed.

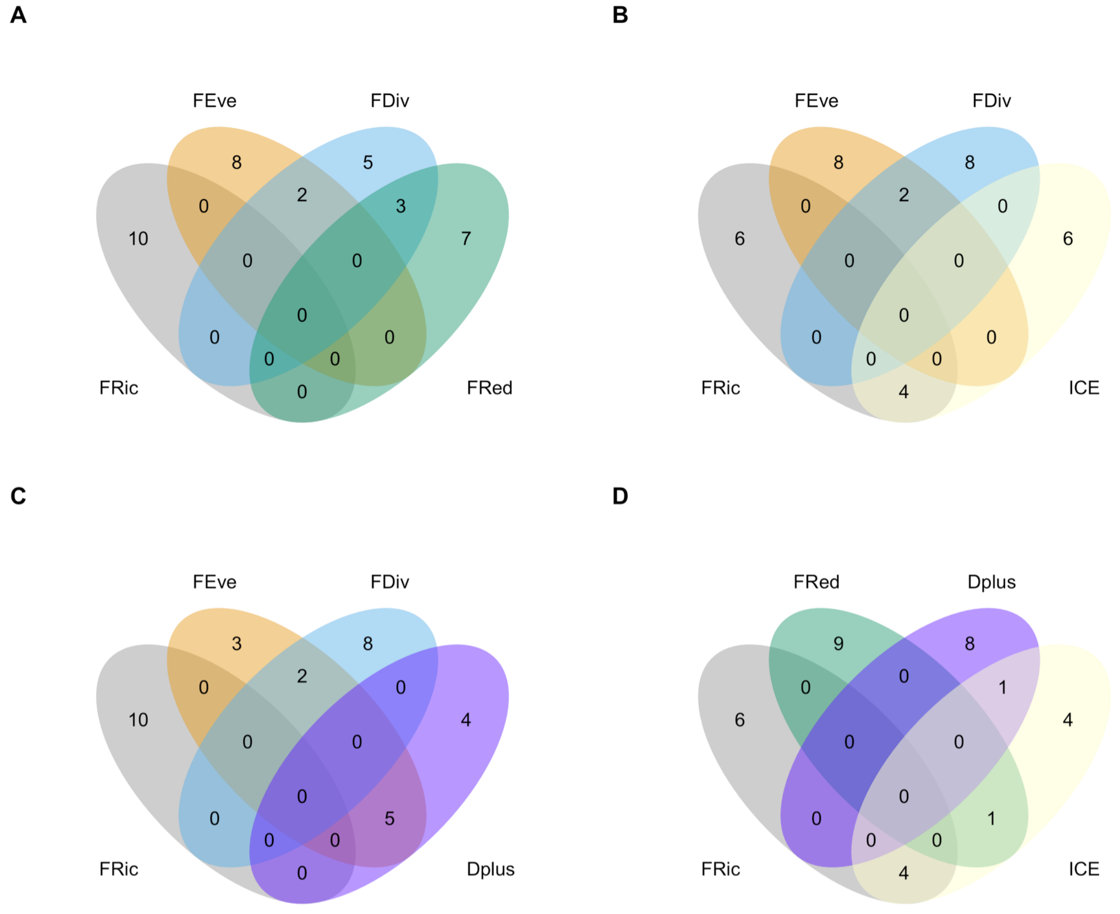


Figure 24. Congruence between: A) Functional diversity measures (FRic - Functional Richness, FEve - Functional Evenness, FDiv - Functional Divergence, and FRed - Functional Redundancy), B) The three components of functional diversity (FRic - Functional Richness, FEve - Functional Evenness, FDiv - Functional Divergence) and richness ICE, C) The three components of functional diversity (FRic - Functional Richness, FEve - Functional Evenness, FDiv - Functional Divergence) and taxonomic diversity (Dplus - Taxonomic distinctness), D) Functional richness (FRic), Functional redundancy (FRed), richness ICE, and taxonomic diversity (Dplus).

4.5. Discussion

4.5.1. Latitudinal patterns in functional diversity

This research is the first in considering functional diversity (FD) of Chilean benthic marine invertebrates covering the entire eco-geographical gradient, contributing to the knowledge of the marine ecosystem of the Southern Hemisphere and its functioning and the global patterns of diversity.

Different latitudinal patterns were observed for the four FD indices (Figure 20). This finding supports recommendations to measure each component of functional diversity independently and simultaneously (Schleuter et al. 2010, Legras et al. 2018) because they consider different aspects of FD (Mason et al. 2005). Research carried out by Garaffo et al. (2020) did not describe any pattern with latitude for FRic and FRed along rocky shores in the Argentinian coastline. Thus, different results are observed along the latitudinal gradient of the Atlantic and Pacific of South America, depending on the FD index used. FD indices might be explaining different functional responses from benthic invertebrates to environmental drivers in the South Hemisphere.

From the four functional diversity metrics used, only FRic showed a significant latitudinal pattern, peaking in the Central Chile and Chiloense ecoregions (Figure 20A). However, this pattern was weak and mainly influenced by only a few grid cells with high values of FRic (ranging between 0.5 to 0.8); all other grid cells had values of FRic less than 0.5 (Figure 20A), regardless of latitude. This finding suggests that the communities of benthic marine invertebrates occupy a small volume of functional trait space. According to Legras et al. (2018), FRic decreases when the species with the extreme traits values forming the functional trait space are impacted. However, FRic detects impact after a long time because changes in the volume of functional space occur only when the most extreme traits are affected (Legras et al. 2018). In addition, FRic peaked at similar latitudes than the nonparametric estimator's species richness: ICE and second-order Jackknife (Chapter 3) between 42° and 43° S in the Chiloense ecoregion. It might be related to the influence of species richness on FRic (Mason et al. 2005).

FEve and FDiv did vary systematically with either latitude or longitude, with values higher than 0.5 throughout the latitudinal gradient (Figures 20B, C). The highest values of FEve were observed at the latitudinal extremes of Chile, in both the Humboldtian and the Channels and Fjords ecoregions (Figure 20B). Similar to the current results, a poleward increase of FEve and a contrary pattern with FRic has previously been recognised in benthic invertebrate communities in both hemispheres (e.g. Schumm et al. 2019, Edie et al. 2018, Berke et al. 2014). Thus, the observed patterns of FEve and FRic seem to be actual rather than simply artefacts of sampling. Bon et al. (2021) mainly observed low to moderate values of FRic, high values of FDiv (> 0.7) and moderate to high values of FEve in communities of benthic macrofauna in coastal areas at 23° S (Mejillones Bay, Humboldtian ecoregion); similar levels to those observed in the current study at the same latitude (Figures 20B, C). Despite the similarities with Bon et al. (2021), the current results might neglect some local differences between small areas due to the diversity of the ecosystem associated with the environmental features of the upwelling centres and shallow oxygen minimum zones (OMZs) representatives in the Humboldt Current in northern latitudes (HCS; Thiel et al. 2007). In the same area studied by Bon et al. (2021), Pacheco et al. (2011) observed differences in the feeding traits modalities between communities of benthic marine invertebrates in a short depth gradient (10 to 50 metres). Shallow bottom communities were composed of carnivores, commensalism, surface deposit feeders, and omnivores, suggesting diverse food sources; on the contrary, deeper communities (OMZ) were composed of subsurface and interface deposit feeders related to suspended organic matter as the primary source of food (Pacheco et al. 2011). Thus, benthic marine invertebrates in northern latitudes might be responding to the high environmental stress (e.g. oxygen depletion), maintaining communities occupying a small volume of functional space but being highly adapted to the environmental conditions and functionally successful.

According to Mason et al. (2005), high FEve might indicate that the species are better distributed in the functional trait space, using the available resources and consequently being highly productive. FDiv, on the other hand, showed high values along the gradient, not showing any significant pattern with latitude. High FDiv might be related to communities with a low competition per resource (Mason et al. 2005), where dominant species in the community present a high niche differentiation (Dimitriadis et al. 2012). However, using the relative frequency of the species instead of species abundance or biomass might produce bias in the FEve and FDiv, and consequently, their interpretations should be taken with precautions. Some studies have even shown different results in FD, depending on species abundance or species biomass used in the analysis (e.g. Gusmao et al. 2016, Darr et al. 2014). The variability of the obtained values using abundance or biomass may affect the interpretations if the aim is to observe environmental differences between polluted or unpolluted areas (e.g. Gusmao et al. 2016) or in an environmental gradient (e.g. salinity, Darr et al. 2014).

Moderate FRed was generally observed along the latitudinal gradient (0.5-0.6). FRed was not significantly related to latitude (Figure 20D), but it did vary with longitude, tending to be higher toward western longitudes (Figure S2D). This pattern with longitude was contrary to the one shown by FRic; therefore, communities with a small volume of functional space presented the highest functional redundancy (Figures S2A, D). Only as a reference, these grid cells were located at around 45° S (Figure 20A, D). These communities were composed of a low richness (ICE; see Chapter 3). Thus, this pattern might be highly influenced by the richness, where small communities with a few species presented a higher redundancy in their biological traits. However, the current results might also indicate that the studied benthic communities present certain resilience and capacity to deal and recover from perturbations (Micheli & Halpern 2005, Biggs et al. 2020), and consequently more stable communities and ecosystem functioning (Biggs et al. 2020).

4.5.2. Hotspots of functional diversity and complementarity with richness and taxonomic diversity

Areas identified as hotspots of FD mainly differed spatially according to each FD metric (Figure 21). It is the first-time using FD measures to identify hotspots of benthic marine invertebrates in Chile.

The latitude between 42° to 46° S located in the Chiloense ecoregion presented the highest number of FD hotspots, with seven FRic hotspots, one FEve hotspot, four FDiv hotspots, and three FRed hotspots (Figures 21A-D). The Chiloense ecoregion has been widely described as a hotspot of benthic marine invertebrates for Echinodermata and Demospongiae (Lancellotti & Vásquez 2000), Anthozoa (e.g. North part of the fjords Patagonian System; Häussermann 2006), and Polychaetes (Hernández et al. 2005). As was discussed in Chapter 3, the real importance of this area in terms of species diversity is still in discussion due to the strong sampling effort and its effect on measures based on species richness (e.g. Lancellotti & Vásquez 2000, Häussermann 2006). However, the latitude at around 42° S is relevant because it represents a break between north and south latitudes. For instance, in terms of oceanographic features, the Antarctic circumpolar current is divided into the Humboldt Current and Cape Horn Current at this latitude (Hernández et al. 2005) as well as, south of 39° S, the environmental heterogeneity increases and gradients in salinity and temperature are stronger due to geographic changes, such as the increase of the number of rivers, estuaries, channels and fjords, and an increment of precipitation (Camus 2001). According to Hernández et al. (2005), the diversity in biotopes increases from 41° S, creating different habitats available to more diverse benthic communities.

Moreover, in the Chiloense ecoregions since 1980, the aquaculture of introduced species such as *Salmo salar* (Atlantic salmon)*,* *Oncorhynchus kisutch* (Pacific salmon) and *Oncorhynchus mykiss* (rainbow trout), and the native mussel *Mytilus chilensis* (Mutschke et al. 2016) has been intensified. The aquaculture of salmon has increased the input of nitrate, phosphate and carbon in the system (Sepulveda et al. 2005, Pantoja et al. 2011, Iriarte et al. 2010, Mayr et al. 2015). Therefore, with all these factors present in the same area (FD hotspots + environmental drivers + human pressure), understanding why this zone is important for the diversity of benthic invertebrates and how these communities, even occupying small functional space, might maintain high levels of diversity in the time are key.

The latitudinal band between 20° to 33° S represents an area of hotspots of FD components (FDiv, FEve and FRic; Figures 21A-C). The latitudes 20° to 22° S and 30° S are important centres of upwelling in the HCS, associated with high levels of nutrients, and high primary productivity, sustaining important pelagic fisheries (Thiel et al. 2007) such as the *Engraulis ringens* (anchovy) and *Trachurus murphy* (jurel). Miloslavich et al. (2011) observed at 22° S a high diversity of marine species (including marine mammals, reptiles, fishes, and invertebrates). The latitudinal band 30° to 33° S located in the Central Chile ecoregion, coincides with one of the biogeographical breaks for marine taxa proposed by Camus (2001) and this area was also considered by Myers et al. (2000) as a priority for conservation purposes, due to the observation of hotspots of species diversity of marine mammals such as *Tursiops truncatus* (bottlenose dolphin), *Otaria flavescens* (Patagonian sea lion), and *Lontra felina* (marine otter), birds such as *Spheniscus humboldti* (the Humboldt penguin), and important Chilean endemic species of benthic invertebrates, for instance *Concholepas concholepas* (Chilean abalone), and *Fissurella costata* (Keyhole limpet; Lenninger 2015), and non-commercial benthic invertebrates such as molluscs, echinoderm, crustaceans, and brachyuran (Fernández et al. 2000). Thus, the current findings support the importance of these areas for local and global diversity, and they may be relevant for decision-makers.

Toward higher latitudes were located hotspots of FD such as FEve, FDiv and FRed, mainly in the Strait of Magellan and south of Tierra del Fuego (Figures 21B-D). The Magellanic ecosystem is highly complex and diverse in habitats and species diversity (Artnz & Rios 1999, Montiel et al. 2011), is important in species diversity of molluscs (Aldea et al. 2020), seaweed flora (Santelices & Marquet 1998, Fernández et al. 2000), and marine mammals (Fernández et al. 2000). However, FD hotspots of benthic marine invertebrates have not been described for these areas until now.

The congruence among hotspots of FD was only observed in two hotspots of FEve and FDiv and between three hotspots of FDiv and FRed (Figure 24A). This low congruence between these FEve and FDiv hotspots might be related to these measures are not influenced by species richness (e.g. Pavoine et al. 2013), and they are independent between them because they consider different aspects of FD (Mason et al. 2005). Regarding the match between FDiv and FRed hotspots, Mouchet et al. (2010) argued that those communities composed of dominant species showing high niche differentiation and consequently low competition per resource (i.e. high FDiv) might be formed by functionally similar species (i.e. moderate to high levels of FRed). Thus, these hotspots areas might maintain ecosystem services and processes in better conditions, being resistant and resilient to future species loss and some degrees of species extinction (Diaz et al. 2007). Moreover, conserving and preserving these hotspots areas might also be relevant to enhance the quality and quantity of Chilean ecosystem functioning.

FD hotspots were also different to those hotspots of richness (ICE) and taxonomic diversity (taxonomic distinctness) (Figures 24B-D). Hotspots of richness and taxonomic diversity were mainly located in the Chiloense ecoregion between 41.5° to 46° S, and in the Channels and Fjords ecoregion south 52° S, respectively (Chapter 3). As a result, there was very little congruence between hotspots of richness, taxonomic, and FD. Four hotspots of FRic were congruent with ICE. (Figure 24B) These communities with a high number of species (ICE) and high FRic may be mainly composed of more specialist organisms and may be associated with high available resources and diversity of habitats (Mason et al. 2008). The availability of resources such as food and habitat in the Chiloense ecoregion have been already documented (e.g. Hernández et al. 2005, Zapata-Hernández et al. 2016, Villalobos et al. 2021). Thus, these findings related to FD hotspots support the general knowledge that Chiloense ecoregion corresponds to an area of high biodiversity (e.g. Fernández et al. 2000, Häussermann 2006), and it is not only the effect of the intense sampling effort.

The addition of new hotspots through measures of FD to those hotspots based only on the species count, or species presence, have been observed in macroecological studies; for instance, for marine mammals using FRic (Albouy et al. 2017), for fishes using Rao quadratic entropy (Stuart-Smith et al. 2013), for sharks using FRic (Lucifora et al. 2011). According to Orme et al. (2005), lack of congruence among hotspots, including different aspects of the diversity, has implications for their use as a conservation tool. These authors argued that finding high congruence among different diversity hotspots may not be considered an aim in conservation because if the congruence is high, it is assumed that any measure of diversity can be used as a surrogate for any other diversity aspect. In this manner, considering different aspects of diversity allows us for more holistic spatial planning.

In terms of complementarity, the three components of FD (FRic, FEve, and FDiv) exhibited a weak correlation between them (Figures 22A, B, D). Thus, these three components showed independence from each other (Mason et al. 2005, Villéger et al. 2008). FEve and FDiv were not correlated to the measure of richness (ICE; Figures 23C, E). Bon et al. (2021) also observed a negative relationship between FEve, FDiv and species richness. These benthic marine invertebrate communities were composed of a lower number of species highly adapted and performing a range of biological traits necessary to tolerate the environmental conditions (e.g. OMZ; Bon et al. 2021). A negative correlation between FEve and species richness was also observed by Zhong et al. (2020) in benthic macrofaunal communities of an estuarine zone of high environmental dynamics. The authors found a high diversity of species associated with low FEve. They argued that communities with high species diversity might not be functionally diverse. Törnroos et al. (2015), on the other hand, determined that even when the taxonomic richness of benthic marine invertebrates can significantly decline along a natural environmental gradient, the communities can still be functionally diverse. For instance, these authors observed that only 4% of the total taxa expressed 66% of the total traits' modalities in marine benthic communities in the Baltic sea.

Only FRic was strongly and positively correlated to ICE (Figure 23A) and taxonomic distinctness (Figure 23B). However, FRic reached an asymptote at around 0.5 with increased species richness and presented low to moderate values with the rise in taxonomic distinctness. Communities with high species and taxonomic diversity (e.g. ICE and taxonomic distinctness) can maintain populations without increasing the niche volume (Mason et al. 2008) and consequently present low or moderate FRic. These communities may be composed mainly of generalistic niche species (Mason et al. 2008), which do not use all the available niche space and resources (Mason et al. 2005, Morelli et al. 2018). On the contrary, the asymptotic relationship between FRic and richness (ICE) might be attributed to the intrinsic functional redundancy present in the communities (Petchey & Gaston 2002). At high species diversity levels, the new species included in the community tend to have similar functional traits to the species already present (i.e. moderate FRed, Micheli & Halpern 2005, Cornwell et al. 2006), and consequently, the volume of functional space does not increase (Cornwell et al. 2006). These communities might be modulated by the habitat filtering processes, where the environment and its biotic and abiotic features allow the coexistence of tolerant species presenting strategies to determinate environmental conditions; besides, the environmental conditions also exclude non-tolerant species (Cornwell et al. 2006). Species in communities driven by habitat filtering use less volume of functional traits space, reducing the spread of their trait values (Cornwell et al. 2006). Therefore, this might mean that the range of biological traits performed by the benthic invertebrates in the studied communities is limited to certain functions and combinations of traits that are biologically and ecologically possible.

The moderate levels of FRed observed in general (FRed mainly between 0.5 to 0.6; Figure 20D) along the gradient influenced the relationship of this FD measure with the taxonomic distinctness. Taxonomic distinctness is a measure of taxonomic distance between species in a community, and based on the Linnaean taxonomic classification (i.e. phylum, class, order, family, and genus; Griffin et al. 2013). It might also be considered as a proxy of phylogenetic diversity (Clarke & Warwick 1999) and may be used in a lack of well-developed phylogenies for many taxa (Srivastava et al. 2012). Thus, the expectation from the negative relationship between FRed and taxonomic distinctness is that with high values of taxonomic distinctness, and potentially more phylogenetic diversity, the biological traits performed by the species in a community would be less redundant (i.e. a more diverse range of traits than a taxonomically homogeneous community). Srivastava et al. (2012) argued that communities with a high phylogenetic diversity might be composed of species with less overlapped functional traits. These species might present less interspecific competition because they use the available functional niche space (i.e. niche complementarity), contributing to the ecosystem functioning (Srivastava et al. 2012). Although FRed was negatively correlated with taxonomic distinctness, moderate FRed was observed in relationship with higher taxonomic distinctness; it reveals that these communities are taxonomically and potentially phylogenetically diverse with some levels of interspecific competition, and at the same time, the communities present certain levels of resilience in front of changes in the environment or species loss (Micheli & Halpern 2005, Biggs et al. 2020).

To conclude, Chilean communities of marine benthic invertebrates occupy a small volume of functional trait space. At the same time, these communities are highly productive because they are using the available resources (e.g. food, habitat), presenting a reduced competition for them. In general, these communities have moderate levels of resilience in front of changes in the environment or species loss. Hotspots of FD located between 20° to 33° S and south of 50° S are revealing new hotspots areas. Correlation between FD and taxonomic diversity showed the independence between the three components of FD (FRic, FEve, and FDiv).

4.6. Supporting information

Appendix S3. List of references used to construct the biological traits dataset used in Chapter 4.

Appendix S4: Metadata biological trait database. Link available from ORDA: https://doi.org/10.15131/shef.data.19195967.

Appendix S5: Biological traits database. Link available from ORDA: https://doi.org/10.15131/shef.data.19195967.

Figure S2. The relationship between longitude and **A)** FRic - Functional richness, **B)** FEve - Functional evenness, **C)** FDiv - Functional divergence, and **D)** FRed - Functional redundancy. Black line represents the fitted Generalised Additive Model (GAM), and the grey bits the interval confidence.

5. How do key environmental drivers and human activities influence the spatial patterns of benthic marine invertebrates in Chile?

5.1. Abstract

Understanding the marine ecosystem functioning is possible by documenting ecogeographic gradients in natural and anthropogenic drivers of benthic community structure and dynamics. Multiple might be the drivers associated with diversity patterns of marine invertebrates along the Chilean gradient. Key environmental drivers and anthropogenic activities influencing the diversity patterns of benthic marine invertebrates along with the full extent of Chile are identified. I use Random Forests analysis to identify the importance of environmental factors and activities in explaining observed patterns in diversity measures: species richness, taxonomic diversity and functional diversity. The key environmental drivers include environmental stress (oxygen at maximum bottom depth, sea bottom nitrate and sea surface nitrate), hydrographic variability (sea bottom temperature), and primary productivity (net primary productivity of carbon). A negative relationship between diversity and environmental stress is observed; in contrast, a positive relationship between PP and temperature with diversity is found. Environmental stress is the primary driver influencing the different diversity measures in the northern latitudes of Chile. These communities present a lower species richness and taxonomic diversity. PP is the key driver influencing the high taxonomic diversity towards southern latitudes, while hydrographic variability influences the high functional and taxonomic diversity levels towards the most austral latitudes. I argue that the benthic communities are highly adapted to environmental stress and hydrographic variability. Diversity does not decrease with aquaculture and the human population as the most important anthropogenic activities influencing the diversity patterns. I also argue that the

species adaptations to environmental heterogeneity might help these communities to tolerate inputs of inorganic nutrients and organic matter from aquaculture.

5.2. Introduction

Coastal and estuarine ecosystems, such as those observed throughout the eco-geographical gradient of Chile, are characterised by diverse biological interactions and high environmental variability, as well as by a high degree of coupling between benthic and pelagic habitats (Griffiths et al. 2017). Benthic marine invertebrates contribute to critical functions in these ecosystems, including nutrient cycling (carbon, nitrogen, phosphorous), the transport, burial, and metabolism of contaminants, secondary production, and via processes such as bioturbation and diffusion (Snelgrove 1998, Griffiths et al. 2017, Stief 2013). At the same time, the richness, abundance, and functional structure of benthic invertebrate assemblages are affected by their surrounding biotic and abiotic environment (McArthur et al. 2010), both of which may, in turn, be impacted by anthropogenic activities (Griffiths et al. 2017). Documenting ecogeographic gradients in the natural and anthropogenic drivers of benthic community structure and dynamics is essential to understanding marine ecosystems' functioning (Godbold & Solan 2009), with implications for effective management and policy decisions (Raffaelli et al. 2003). It becomes pressing in the face of global environmental change and the steady increase of anthropogenic pressures throughout coastal and marine areas (Ellingsen & Gray 2002).

In Chile, as documented in Chapters 3 and 4 of this thesis, species richness, taxonomic diversity and functional diversity (e.g. Functional richness - FRic) of marine benthic invertebrates mostly peak between 42° to 46° S, in the Chiloense ecoregion. There is also evidence for lower species richness (Carrasco 1997, Carrasco & Moreno 2006, Hernández et al. 2005, Laudien et al. 2007, Bon et al. 2021) and taxonomic diversity towards northern latitudes (Rivadeneira et al. 2011, Chapters 3). However, the results observed in Chapter 4 regarding functional diversity could bring new information about the functional structure of northern communities. The lack of studies on understanding the factors generating these patterns in the benthos at large spatial scales has long been recognised (e.g. Fernández et al. 2000).

Studies encompassing the 39° of latitudinal gradient have related peaks of species richness to the diversity of biotopes in the Chiloé Archipelago and the divergence of current systems between Humboldt and Cape Horn at around 41° S (e.g. Lancellotti & Vásquez 2000, Valdovinos et al. 2003, Hernández et al. 2005). At the local scale, the high biodiversity of southern areas such as the Inner Sea of Chiloe and the System of Patagonian Fjords is related to the availability of habitat due to the high presence of reef-forming species such as the cosmopolitan cold-water coral *Desmophyllum dianthus* (e.g. Zapata-Hernández et al. 2016). When this species is highly abundant, it can form reef-like structures and provides habitat to organisms (Miller et al. 2011), such as a variety of Sipuncula, bivalves *Ennucula grayi*, *Xylophaga dorsalis*, and the Echinoidea *Tripylaster philippii* (see Zapata-Hernández et al. 2016 for more details in term of species). Some findings also suggest that hydrographic variability (e.g. salinity and temperature gradients) and habitat heterogeneity (e.g. organic matter, sediment texture, and availability of hard bottom) might help to understand the structure of benthic marine invertebrate communities in southern Chile's Fjords ecosystems (e.g. Quiroga et al. 2012, 2016, Zapata-Hernández et al. 2016, Jordà Molina et al. 2019). Moreover, toward southern latitudes, habitat filtering (i.e. biotic and abiotic features allow the coexistence of species presenting strategies to environmental conditions; besides, the environmental conditions also exclude non-tolerant species (Cornwell et al. 2006)) might drive the communities of benthic marine invertebrates. These communities may be expected to display biological traits adapted to the environmental heterogeneity driven by the pronounced salinity and thermal gradients and the high primary productivity (evidenced by high chlorophyll-a levels) observed in southern Chile (e.g. Iriarte et al. 2007, 2010, González et al. 2010, Villalobos et al. 2021).

The low diversity of Chilean benthic invertebrates towards northern latitudes, on the other hand, has previously been attributed to environmental characteristics of the Humboldt Current System (HCS) in the South Pacific. The area corresponding to the HCS is characterised by a dominant northward flow of subantarctic waters and an upwelling system of cold and nutrient-rich waters whose origin is equatorial (Thiel et al. 2007). Along the HCS, some areas have a range of dissolved oxygen from hypoxic to anoxic concentrations; they are considered oxygen minimum zones (OMZs; Thiel et al. 2007). Moreover, the occurrence of El Niño Southern Oscillation (ENSO) events adds complexity and interannual variability to coastal and marine ecosystems (Escribano et al. 2004). During non-ENSO events (i.e. under normal environmental conditions), lower species richness is observed in the communities of benthic invertebrates in communities in shallow coastal water (e.g. Bon et al. 2021) and in the continental shelf and slope (e.g. Gallardo et al. 2004; Palma et al. 2005, Hernández et al. 2005, Rivadeneira et al. 2011). Benthic invertebrate communities are also affected by the three water masses present along the HCS (Equatorial Subsurface Water, Antarctic Intermediate Water, and the Pacific Deep Water; Palma et. al 2005). The increase of temperature due to the ENSO event during 1997-98 caused changes in benthic invertebrate communities in shallow waters under normoxic conditions, reducing the species richness (Laudien et al. 2007). On the contrary, the increase in oxygen levels during ENSO periods increases the abundance, species richness (Laudien et al. 2007) and the macrofaunal biomass (Escribano et al. 2004) in communities that inhabit OMZs. Changes in the community structure, such as the increase of bioturbation during ENSO (Escribano et al. 2004, Gallardo et al. 2004), are also recognised, mostly due to the dominance of polychaete species such as *Cossura chilensis* (Gallardo et al 2004). However, less is known about the levels of diversity towards northern latitudes in systems influenced by the Humboldt Current (Thiel et al. 2007).

As shown above, multiple potential explanations exist for the observed ecogeographic gradients in Chilean benthic diversity. However, a more comprehensive investigation is warranted given that Chilean benthic marine ecosystems are highly diverse, are key in the maintenance of important economic activities (fisheries, aquaculture, and tourism), and are influenced by diverse human activities (Escribano et al. 2003). For example, overfishing commercial and non-commercial species, coastal and development (e.g. domestic sewage and industrial waste outfalls), and introduction of exotic species (Snelgrove 1998) can all impact benthic assemblages. In addition, estuaries and coastal ecosystems may be affected by oxygen decreases caused by increasing nutrient loads (nitrogen and phosphorus) and organic matter from agriculture, sewage and fossil fuel combustion (Breitburg et al. 2018). The increase in the number and severity of anthropogenic stressors threatens the ecosystems and their functioning, generating accumulated disturbance which diminishes ecosystem resilience (Villnäs et al. 2013). Thus, a better understanding of how human pressures may modify the structure and functions of ecosystems is necessary to implement successful strategies of management that reduce or adapt to anthropogenic-driven changes in coastal and marine ecosystems (Griffiths et al. 2017).

The main aim of this chapter was to identify key environmental drivers and anthropogenic activities, including measures of protectiveness such as protected areas (including terrestrial and marines) and the territorial user rights for fishers (TURFs), which might influence diversity patterns of benthic marine invertebrates along with the full extent of the Chilean coast and continental shelf. Environmental drivers involve abiotic factors related to oceanographic, geomorphic and hydrographic processes, measurable from sediment and water columns, including sediment grain size, organic matter content, pH, redox potential, phosphorus and nitrogen contents, temperature, salinity and oxygen (McArthur et al. 2010). In addition, I also consider biotic factors associated with the interaction between organisms and the environment through processes such as nutrient cycling, bioturbation, calcification, and feeding methods (e.g. chlorophyll, calcium carbonate and total organic Carbon; McArthur et al. 2010). Thus, I define environmental drivers as the interaction between factors (abiotic and/or biotic), including environmental stress (natural or anthropogenic eutrophication and hypoxia), primary productivity, habitat heterogeneity, and hydrographic variability. I also consider key anthropogenic activities expected to directly (e.g. aquaculture) or indirectly (e.g. proximity to centres of high human population density) impact benthic communities along Chile's coastline and continental shelf. The expectation is that those benthic communities closer to anthropogenic activities and populated areas may suffer the effects of sewage, garbage, tourism, and excess nutrients, and their diversity may be reduced. I use Random Forests to identify the importance of different drivers and activities in explaining observed patterns in four measures of diversity: (1) Species richness, represented by the incidence Based on Coverage Estimator (ICE) (Chapter 3), (2) Taxonomic diversity represented by Taxonomic Distinctness ($\Delta+$) (Chapter 3), and (3) Functional diversity, represented by Functional Evenness (FEve) and Functional Redundancy (FRed) (Chapter 4). These metrics have been selected because they represent different dimensions or aspects of diversity, and the same driver might influence distinct aspects of diversity in different ways (e.g. Levin & Gage 1998). I assess whether different drivers are more associated with particular Chilean ecoregions due to the differences in environmental factors, using Generalised Additive Models to represent how the environmental factors vary with latitude.

5.3. Materials and Methods

5.3.1. Benthic diversity data

The data and processing steps to derive spatial estimates of species richness, taxonomic diversity, and functional diversity of Chilean marine benthic invertebrates are described in full in Chapters 3 and 4. In brief, the database of the benthic community, fully described in Chapter 2, was used to obtain different aspects of the diversity. This database was generated by aggregating data from five different sources. A total of 34,179 occurrence records for 762 species of benthic marine invertebrates, from a broad range of taxa including Mollusca, Annelida, Arthropoda, Foraminifera, Echinodermata, Porifera, Cnidaria, Bryozoa, Brachiopoda, and Nemertea. Each species occurrence was georeferenced and the dataset was gridded into equal-area cells of 55 x 55 km. Latitude and longitude were projected as Albers Equal Area Conic (ESRI projection 102033), because of the geographic position and elongated shape of Chile.

Each grid cell was assigned to one of the five ecoregions proposed for Chile according to the classification of the global continental shelf developed by Spalding et al. (2007). This classification divided the global continental shelf into 62 provinces and 232 ecoregions. The ecoregions correspond to areas with relatively homogeneous species composition (Spalding et al. 2007). Two provinces and five ecoregions represent the continental shelf of Chile. The Warm temperate Southeastern Pacific Province is shared between Peru and Chile. This province ranges from 18º to 41.5º S and includes the Humboldtian, Central Chile, and the Araucanian ecoregions. The Magellanic Province, from 41.5º to 56º S, is divided into the Chiloense and the Channels and Fjords ecoregions. The limits of each province and their ecoregions in Chile were based on Chilean research developed by Fernandez et al. (2000), Ojeda et al. (2000), and Camus (2001).

Diversity measures were chosen using the complementarity criteria between metric, the low congruence between diversity hotspots, and the diversity patterns with latitude observed in Chapters 3 and 4. Thus, these metrics should capture different aspects of benthic diversity. The four aspects represented were (1) species richness through the nonparametric incidence-based coverage estimator (ICE), (2) taxonomic diversity using taxonomic distinctness, and (3) functional diversity through Functional Evenness (FEve), and Functional redundancy (FRed). Functional richness was not chosen due to the high complementarity with ICE and taxonomic distinctness (Chapter 4); moreover, FRic presented a similar pattern with ICE and taxonomic distinctness (Chapter 3 and 4). On the other hand, FDiv did not show any pattern with latitude (Chapter 4).

5.3.2. Environmental variables data

The environmental variables considered as possible drivers of diversity were collected using the same spatial grid as the benthic diversity data. A database of sediment and water variables was then constructed from five sources: three from environmental monitoring along the Chilean coast and continental shelf, one from an annual cruise throughout Patagonian

Fjords, and the final source was the global marine data layers available via Bio-ORACLE (Tyberghein et al. 2012, Assis et al. 2018).

The sediment covariates were obtained from the Chilean National Fisheries Service (SERNAPESCA) survey, which monitors sediments directly within the area covered by aquaculture installations. The second survey, run by the Fisheries Development Institute of Chile (IFOP), is also concerned with sediments influenced by aquaculture. However, IFOP locates sampling stations outside the farms (e.g. between two farms or in the centre point among a group of farms). The third survey, run by the Department of Maritime Territory and Merchant Marine of Chile (DIRECTEMAR), covers sediment and the water column near the coastline. The fourth source is the Marine Investigation Cruises in Remote Areas (CIMAR), run by the National Oceanographic Committee (CONA) focused on the Patagonian Fjords of Chile (Silva & Palma 2006). Georeferenced data were available for SERNAPESCA from 2014 to 2017, to IFOP from 2012 to 2017, to DIRECTEMAR from 2013 to 2015, and to CIMAR from 1995 to 2010 (Tables 5, S2). Variables recorded were the percentages of gravel, sand, and mud, the percentage of organic matter, the pH, redox (mV), and temperature (℃) of the sediment (Tables 5, S2). The mean value was taken when multiple values were available for any variables within a grid cell.

Additional environmental data layers were obtained from Bio-ORACLE, a global dataset composed of 23 GIS rasters with data in a spatial resolution equal to 5 arcmins (Tyberghein et al. 2012, Assis et al. 2018). The data mostly corresponds to an average over a focal period or values derived from DIVA (Data Interpolating Variational Analysis) interpolation over many data points. The time coverage and more information of the type of data obtained in Bio-ORACLE are shown in tables 5 and S2. To access to Bio-ORACLE data, in R (R Core Team 2021), the `sdmpredictors` R package (Bosch & Fernández 2021) was used to obtain data on chlorophyll-a concentration ([chl-a] mg/m^3), chlorophyll concentration ([chl] mg/m^3), Sea Bottom Temperature (SBT °C), seawater salinity (B salinity PSS), sea bottom nitrate concentration ([B Nitrate] umol/m^3), seawater phosphate concentration ([B Phosphate] umol/m^3), seawater dissolved oxygen concentration ([O_2] umol/m^3), seawater Carbon phytoplanktonic concentration ([C phyto] umol/m^3), seawater net primary productivity of Carbon ([PP] g/m^3/day), and seawater Silicate concentration ([Silicate] mol/m^3). These variables represent the mean values at maximum bottom depth (MBD) (Tables 5 and S2). I also obtained data of the water column for the mean Sea Surface Temperature (SST °C), the mean salinity (PSS), mean sea surface nitrate concentration ([Nitrate] umol/m^3), and mean pH (Table 5, S2).

Environmental variables of the sediment were interpolated for grid cells missing values due to data gaps in some grid cells. The interpolation was carried out using the Nearest Neighbour model in the `gstat` package (Pebesma 2004, Gräler et al. 2016) with a minimum of 3 and maximum of 10 neighbouring observations to fit, and the function `interpolate()` in the `raster` package (Hijmans 2021). After the interpolation, three sediment variables - pH, temperature (°C), and redox (mV) - were removed from the dataset because they did not have enough data to fill all the gaps (Table S2).

Table 5. Details of the sediment and water column variables considered to be potential environmental drivers of Chilean benthic diversity. Expected relationship indicates whether a direct or indirect relationship is expected between the environmental driver and benthic diversity, with further details of the expected relationship provided in the final column (Compiled by author).

Covariate and variable name	Unit	Matrix	Time coverage	Type of data	Data source	Expected relationship	Environmental driver associated / Importance notes
Gravel	%	Sediment	1995 - 2017	Average / Time period	SERNAPESCA IFOP DIRECTEMAR CIMAR	Direct - Species, taxonomic and functional diversity (FD) increase with the increase of grain size, and also with the increase of habitat heterogeneity (Ellingsen & Gray 2002, Mastrototaro et al. 2008).	Granulometry is related to **environmental / habitat heterogeneity.** ● Important driver of beta and gamma diversity of benthic invertebrates in soft bottoms (e.g. Ellingsen & Gray 2002, Mastrototaro et al. 2008). ● Beta and gamma diversity increase with the increment of habitat heterogeneity driven by the granulometry (Ellingsen & Gray 2002). ● Communities from muddy bottoms, also rich in organic matter, were less diverse in species richness than those inhabiting coarse sediments and higher bottom heterogeneity (Mastrototaro et al. 2008).
Mud	%	Sediment	1995 - 2017	Average / Time period	SERNAPESCA IFOP DIRECTEMAR CIMAR		
Organic matter	%	Sediment	1995 - 2017	Average / Time period	SERNAPESCA IFOP DIRECTEMAR CIMAR	Indirect - Species richness decreases with a gradient of OM (Mastrototaro et al. 2008, Hyland et al. 2005). Taxonomic diversity decreases with the increase of OM content. FD (e.g. FEve) decreases with the increase of OM content (Bon et al. 2021).	Organic matter (OM) is related to **Environmental stress.** ● Increase of OM content in the water column, exceeding the metabolic capacity of metazoan consumers, results in the non-metabolization of an important proportion of the organic matter which might reach the sediment and be accumulated until the oxygen depletion or hypoxia (Levin et al. 2009). ● Villnäs et al. (2013) determined that variations on sediment OM content explained the variability on ecosystem functions related to the macrobenthic species nitrification/ denitrification capacity in ecosystems affected by repeated hypoxia.

Covariate and variable name	**Unit**	**Matrix**	**Time coverage**	**Type of data**	**Data source**	**Expected relationship**	**Environmental driver associated / Importance notes**
							● Under environmental stress communities are reduced in number of species, performing a small range of functional traits necessary to tolerate high stress levels (e.g. Bon et al. 2021).
Mean Sea Bottom Temperature (SBT)	℃	Mean value at maximum bottom depth in the water column	2000 - 2014	Average / Time period	Bio-ORACLE	Direct - Species, taxonomic and FD increase with the increase of SBT (following the patterns of Sea Surface Temperature; e.g. Tittensor et al. 2010, Rivadeneira et al. 2011).	Sea Bottom Temperature (SBT) is related to the **Hydrographic variability**. ● Important factor in the estimation of temporal and spatial benthic flux variation, benthic-pelagic coupling and ocean warming prediction at high latitudes (e.g. Belley & Snelgrove 2016).
Mean Nitrate concentration [Nitrate]	$umol/m^3$	Water column	1928 - 2008	Data Interpolating Variational Analysis (189,530 data points)	Bio-ORACLE	Indirect - Species richness decreases with a gradient of nutrients. Taxonomic diversity decreases with the increase of nutrients. FD (e.g. FEve) decreases with the increase in eutrophicated environments (Bon et al. 2021).	Nitrate concentration is related to **Environmental stress** due to eutrophication. ● Eutrophication has its origin in the increase of nutrients availability such as nitrogen and phosphorus in the system. ● Eutrophication can be related to the natural processes induced by winds along the continental margin defined such as coastal upwelling, or be facilitated by the discharge from estuaries and rivers nearby to human activities (e.g. agriculture, mining, cities, which can provoke an excessive growth of phytoplankton (Levin et al. 2009)). ● Nutrient loading has a direct impact on the benthic - pelagic coupling and as result effects on ecosystem functioning (Griffiths et al. 2017).
Mean Bottom Nitrate concentration [B Nitrate]	$umol/m^3$	Maximum bottom depth in the water column	2000 - 2014	Average / Time period	Bio-ORACLE		

Covariate and variable name	Unit	Matrix	Time coverage	Type of data	Data source	Expected relationship	Environmental driver associated / Importance notes
Mean dissolved Oxygen concentration [O_2]	$umol/m^3$	Maximum bottom depth in the water column	2000 - 2014	Average / Time period	Bio-ORACLE	Direct - Low diversity of species is expected under low dissolved oxygen levels (e.g. Rivadeneira et al. 2011, Palma et al. 2005). FD (e.g. FEve) decreases with the decrease of oxygen dissolved concentrations (Bon et al. 2021).	Low levels of oxygen are related to **Environmental stress.** ● Oxygen is the main environmental regulator of inorganic nutrients fluxes through the sediment-water interface, as well as oxygen regulates the magnitude to which diffusion and bioturbation control the nutrient fluxes (e.g. Griffith et al. 2017). ● Low levels of oxygen dissolved influence benthic invertebrate communities in the continental shelf and slope of the Humboldt Current System (Palma et al. 2005).
Mean Chlorophyll-a concentration [Chl-a]	mg/m^3	Maximum bottom depth in the water column	2000 - 2014	Average / Time period	Bio-ORACLE	Direct - Species, taxonomic and FD increase with the growth of chlorophyll a (e.g. Cusson et al. 2007, Zhong et al. 2020).	Chlorophyll-a and mean net primary productivity of Carbon are related to **Primary Productivity** (PP). ● Species richness and Shannon-Wiener diversity were influenced by gradients of primary productivity (e.g. Canadian Arctic Archipelago, Cusson et al. 2007). ● High diversity of taxa in (including invertebrates, bony fishes, rays and sharks) were related to the benthic food webs supported by the Carbon originated from surface phytoplankton (Zapata-Hernández et al. (2016).
Mean net primary productivity of Carbon (PP)	g/m^3 $/ day$	Maximum bottom depth in the water column	2000 - 2014	Average / Time period	Bio-ORACLE	Direct – Species richness (e.g. Zapata-Hernández et al. 2016).	

Covariate and variable name	Unit	Matrix	Time coverage	Type of data	Data source	Expected relationship	Environmental driver associated / Importance notes
Mean Silicate concentration [Silicate]	$umol/m^3$	Maximum bottom depth in the water column	2000 - 2014	Average / Time period	Bio-ORACLE	Unknown for species richness and taxonomic distinctness. Direct - Positive relationship was observed between FD (functional richness) and nutrient flux of silicate and phosphate (Belley et al. 2016).	Silicate is related with **Environmental stress** and **Primary productivity.** ● Under eutrophication in coastal areas, silicate can limit the primary productivity in ecosystems dominated by diatoms (Chauvaud et al. 2000). ● Biological traits such as type of feeding and ecosystem engineering (e.g. tube building) can affect the silicate flux (Marinelli 1992).
Mean pH	Acidity of the ocean	Water column	1910 - 2007	Data Interpolating Variational Analysis (117,833 data points)	Bio-ORACLE	It could potentially decrease the marine biodiversity, impacting on tolerant species, reducing the taxonomic diversity and the loss of key species, which influence on ecosystem functioning (Widdicombe & Spicer 2008)	pH is related to ocean **Acidification (Ac).** ● In the ocean and coastal waters, the increase of acidification and temperature and their combination with low oxygen conditions affect biogeochemical, physiological and ecological processes (Breitburg et al. 2018). ● Ac. may impact species tolerance to temperature, salinity, contamination, and disease (Widdicombe & Spicer 2008). ● Ac. affects mainly benthic calcifiers species such as coral reefs. Over time, it will affect the community structure and decrease biodiversity (Anderson et al. 2011). ● Ac. may indirectly affect benthic organisms by processes such as competition, prey, predation and quantity and quality of food supply (Anderson et al. 2011).

5.3.3. Human activities data

Human activities were collected using the same spatial grid for benthic diversity and environmental drivers. The anthropogenic activities covered a range of marine and terrestrial activities that may impact benthic communities (Tables 6 and S3). The human population density was also considered an overall indicator of human pressures. Each cell's nearest distance (in km) was calculated to account for human activities near, but not within, focal grid cells. The distances were derived using the function `gridDistance()` in the package `raster` (Hijmans 2021), which calculates distances through neighbouring raster cells' centres. The new variables were preceded by the letters "df" indicating distance from. In addition, average by neighbourhood was calculated in the 3 x 3 neighbourhood of grid cells centred on each focal cell using the `focal()` function in the package `raster`. The new variables were preceded by "Mean focal". The considered activities are described and defined in tables 6 and S3.

Aquaculture data were obtained from a shapefile provided by SERNAPESCA and updated to April 2020. Firstly, the geographical coordinates (longitude and latitude), and farm size (i.e. area of the water concession in km^2) of centres of aquaculture whose status was categorised as "granted" between 1980 to 2019 were considered. The aquaculture installations were classified by the taxonomic group, namely salmonids (e.g. *Salmo salar, Oncorhynchus kisutch* and *Oncorhynchus mykiss*), molluscs (e.g. *Mytilus chilensis, Aulacomya atra* and *Argopecten purpuratus*), abalone (e.g. *Haliotis rufescens* and *Haliotis discus hannai*), Echinodermata (e.g. *Loxechinus albus*), other fish (e.g. *Scophthalmus maximus,* and *Seriola lalandi*), and algae (e.g. *Gracilaria chilensis*).

Small harbours data were obtained from a shapefile provided by SERNAPESCA, updated to August 2019. Each small harbour's geographical coordinates (longitude and latitude) and code were recorded. The Chilean Fisheries and Aquaculture Law (FAL; SUBPESCA 1991) defines small harbours as a productive, economic, and social and cultural unity located in a specific geographical area, in which direct and indirect activities related to artisanal fisheries are developed.

Mining data were obtained using a shapefile provided by the Laboratory of Geography of the Universidad de la Frontera, Chile, which included the geographic coordinates (longitude and latitude) of each mine, the name, and the type of extracted mineral. A total of 162 mines account for mining activity along the length of Chile, with around 800 mining tailings are mainly located towards the northern and mid-latitudes. The activity is mostly focused on Copper and Iron, and they are mainly located inland and close to the chain of mountains, Los Andes.

Human population density was obtained from the WorldPop Dataverse Repository available from www.worldpop.org. This open-access database provides population density estimates (i.e. people per km^2) at 1km^2 resolution (Sorichetta et al. 2015). The average of the human population by grid cell was estimated. It can be considered an indirect measure of anthropogenic impact due to the proximity of important cities to the coast.

Protected Areas (PAs) data were obtained from the shapefile available on the World Database on Protected Areas (WDPA; https://www.protectedplanet.net/country/CHL) in August 2020 (UNEP-WCMC 2020). The geographical coordinates (longitude and latitude) of each marine and terrestrial protected area and the area (km^2) were added to the database. Terrestrial protected areas were also considered because some are adjacent to the coast due to Chilean geography; the longest distance is 356 km from east to west. As a result, most protected areas are close to the coastline. Thus, the protection of landed areas is expected to limit land-based activities that may impact benthic communities. According to the Atlas of Marine Protection, which based their classification on a stricter categorisation of Marine Protected Areas (MPAs) than the U.N.'s WDPA, only 5.8% of the total area of Continental Chile is covered by MPAs, with most occurring towards Southern latitudes. Thus, the Chilean MPA network, at least in its continental area, is relatively small. Squeo et al. (2012) argued that a multi-scale approach encompassing terrestrial and marine ecosystems would help reach the biodiversity target of achieving 10% of all ecosystems fully protected according to the Convention on Biological Diversity recommendations in 2006. Thus, considering terrestrial PAs and MPAs together may be relevant for benthic marine biodiversity.

Territorial Use Rights for Fisheries data were obtained from a shapefile provided by SERNAPESCA. The geographical coordinates (longitude and latitude) and the code (i.e. unique code given to each TURF) of only those TURFs whose status was categorised as "granted" were considered. TURF is an area-based management system that allows the access and exploitation of resources to determined individuals or groups of fishers (Nguyen Thi Quynh et al. 2017). TURFs are a form of co-management, where fishers are assigned to small-scale fisher unions in specific coastal areas (Castilla 1994) for the management of inshore benthic resources strongly exploited by small-scale fisheries (Castilla et al. 1998, Gelcich et al. 2008b).

Table 6. Details of the human activities considered to be potential drivers of Chilean benthic diversity. Expected relationship indicates whether a direct or indirect relationship is expected between the human activities and benthic diversity, with further details of the expected relationship provided in the final column (Compiled by author).

Activity	Covariate and variable name / Definition	Unit (by grid cell)	Matrix	Time coverage	Data source	Expected relationship	Importance
Aquaculture	Total aquaculture area / Total area occupied by all aquaculture concessions of any taxa df salmon aquaculture df aquaculture / Distance from any type of aquaculture	km^2 km km	Sea	1980 - 2019	SERNAPESCA	Indirect-Decrease of Species diversity due to decrease with the increase in OM (Villalobos et al. 2021). Direct- Increases in distance from aquaculture farms will increase the biotic parameters (e.g. species richness; Kalantzi & Karakassis 2006, Borja et al. 2009).	● **Aquaculture** provokes anthropogenic gradients of disturbance, affecting the physicochemical of the sediment, benthic macrofaunal community composition and net benthic ecosystem functioning (Godbold & Solan 2009). ● The habitat degradation, due to the excessive accumulation of OM under salmon farms has revealed, that the low quality of OM of the sediments is related to a low species diversity of benthic marine invertebrates in areas under high aquaculture pressure (e.g. Northern Patagonian Fjords; Villalobos et al. 2021). ● Anthropogenic eutrophication also can include the organic enrichment of the water column and seabed due to the nitrogen and phosphorus released to the environment through the excretion, faeces, and uneaten food due to salmon aquaculture (Soto & Norambuena 2004, Niklitschek et al. 2013, Quiñones et al. 2019).
Small harbours	Total number of small harbours / Sum of the total number of small harbours per grid cell. df small harbours	number km	Sea/Earth	Updated August 2019	SERNAPESCA	Indirect - Fishing activity related to small harbours is expected to impact benthic invertebrate communities, decreasing their populations. Higher df small harbours, higher would be the diversity.	● Benthic fisheries impact the population of coastal and marine invertebrates directly, for example, through the overfishing of sea urchins (e.g. *L. albus* and *Arbacia dufresnii*) and mussels (Chilean abalone, *C. concholepas*). ● Benthic fisheries at a small scale do not provoke damages in the habitat of non-target species because it is done through diving (Gelcich et al. 2008b).

Activity	Covariate and variable name / Definition	Unit (by grid cell)	Matrix	Time coverage	Data source	Expected relationship	Importance
Mining	Total number of copper mines / Sum of the total number of Cu mining.	number	Earth	Unknown	Laboratory of geography (UFRO)	Indirect - The increase in the number of mining and the related tailings, decrease the species, taxonomic and functional diversity of benthic invertebrates. Direct - The increase in distance from mining will increase diversity aspects.	● Lancellotti and Stotz (2004) argued that although extractive activity of **Mining** occurs in land, its effects also may be observed in the coast, where there are mineral deposits. ● Mining is not subject to proper environmental legislation with the aim to protect the coastal and marine ecosystems from mining discharges, even when the effects on marine communities have been evidenced (e.g. Castilla 1983). ● Mining activity and mining tailing have effects on biological diversity, decreasing the diversity of species of marine invertebrates (Castilla 1983; Ramirez et al. 2005, Fariña & Castilla 2001, Rodríguez et al. 2021), reducing the number of taxa and densities of meiofauna (Lee & Correa 2005), affecting the trophic structure of benthic communities, being mostly represented by deposit feeders (e.g. *Lumbrineris bifilaris* and *Diastylis tongoyensis*; Lancellotti & Stotz 2004), and decreasing the populations of sessile species on rocky intertidal communities (Fariña & Castilla 2001).
	Total number iron mines / Sum of the total number of Fe mining.						
	df mining / Distance from any mining.	km					
	Mean focal mining / Average by neighbourhood	number					
Human population density	Mean human population density / Number of individuals by grid cell	density	Earth	2015	WorldPop Dataverse Repository	Indirectly - Higher human population density and the proximity of human population will decrease the species richness, taxonomic	● Nitrogen discharges to coastal waters are expected to increase as human population and agricultural production increase (Breitburg et al. 2018). ● A high coastal population density could be associated with a higher discharge of sewage from human settlements and industries, as
	df human population	km					

Activity	Covariate and variable name / Definition	Unit (by grid cell)	Matrix	Time coverage	Data source	Expected relationship	Importance
	Mean focal human population / average by neighbourhood	density				diversity, and FD.	coastal cities present a high touristic activity due to the proximity to beaches.
Protected areas (PA)	PA area	km^2	Sea/Earth	Updated August 2020	World Database on Protected Areas	Direct - Large area of PAs, and the proximity to PAs have a positive impact on species richness, taxonomic distinctness, and FD.	● The species response to Pas may also depend on their life-history traits and the ability to dispersion larvae in juvenile and adult stages (Micheli et al. 2004).
	df PA	km					
	Mean focal PA area / average by neighbourhood	km^2					
Territorial Use Rights for Fisheries (TURFs) +	df TURFs	km			SERNAPESCA	Direct - the proximity to TURFs has a positive impact on species richness (Gelcich et al. 2008b), taxonomic distinctness, and FD.	● TURFs positively impact the recovery of benthic target-species populations strongly overexploited in the past, such as the gastropod *C. concholepas* (Gelcich et al. 2008b). ● An increase in species abundances, body size, and recruitment of benthic invertebrates is observed inside these areas (Castilla et al. 1998, Gelcich et al. 2008b).

5.3.4. Analysis of correlation between variables

Before modelling relationships between diversity and environmental factors or anthropogenic activities, following Thompson et al. (2021), pairwise Pearson correlation coefficients were calculated across both sets of predictor variables to identify highly collinear variables (Figures S3A, B). Additional spatial covariates were also included to both sets to account for additional spatial structure in the data. Latitude, longitude and distance from shore were correlated with the set of sediment and water variables. Latitude and longitude were correlated with the set of human activities. When pairwise correlations were high ($|r| > 0.7$) one of the covariates was removed from inclusion in models. To decide which covariate to remove, the covariate representing a direct measure from the environment (e.g. nitrate concentration, area of salmon farms) was retained (Thompson et al. 2021) in preference to indirect measures of impact, such as variables related to spatial effects like latitude, longitude or the distance from the coast.

After the Pearson correlation analysis, 11 environmental covariates were chosen to be fitted in the Random Forest (RF) models (Table 5, Figure S3A), and 19 anthropogenic activities, including also those related to distance from and mean focal were added to the RF models (Table 6, Figure S3B).

5.3.5. Relationship between taxonomic and functional diversity, and environmental drivers and human activities

Random Forest (RF) analysis (Breiman 2001) was performed to explore the relationship between the gridded species richness, taxonomic and functional diversity values obtained in chapters 3 and 4 respectively, and environmental factors and human activities. RF is a machine learning technique which does not assume linearity between the predictor and explanatory variables (Kocsis et al. 2018). RF is a group of regression trees (i.e. for continuous variables) which are constructed taking a bootstrapped sample from the data to congregate the most homogeneous covariates in the same group (Thompson et al. 2021). The model randomly selects a subset of the covariates to determine each node of a tree (Thompson et al. 2021).

The RF model was constructed in the form diversity index ~ covariate 1 + covariate 2 + covariate 3 … + covariate n in the `ranger` package (Wright & Ziegler 2017). The number of trees used was 200, and the argument mtry (i.e. the number of variables tried at each node) was set to 3 (Couce 2021, personal communication, 24 August). The argument quantreg =

TRUE was used to estimate the prediction error variance. To obtain the relative importance of the covariates in each fitted RF, the impurity approach was used, which is based on minimising the variance of the response variable every time that a covariate is used for a node (Thompson et al. 2021). The MSE (mean square error), the R^2, and the relative importance of each covariate were extracted from each RF model.

Partial dependence plots were used to show the model predictions of the four chosen diversity metrics (ICE, Δ^+, FEve, and FRed) in response to the three most important covariates determined by node impurity in each the RF model. In addition, partial plots for the total area of PAs, distance from PA, and from TURFs for the four diversity metrics were performed. This has the aim to observe the different aspects of the diversity in relationship to these measures of conservation implemented in Chile. The `partial()` function in the package `pdp` (Greenwell 2017) was used for visualising the partial dependence of the response variable on a single predictor.

5.3.6. Latitudinal patterns in important covariates

The most important environmental variables identified by the RF analyses were analysed as a smoothed function of the latitude and the longitude of each grid cell using Generalised Additive Models (GAMs), of the form covariate ~ s(latitude) + s(longitude). Latitude and longitude were both included as separate smooth terms, with latitude the primary variable of interest (because it represents an eco-geographical gradient) and longitude included to account for additional spatial structure in the data. Smooths were fitted using restricted maximum likelihood (REML). GAMs were chosen because they are flexible, with smooth functions allowing the response curve to be fitted for the predictor variable without assuming a distinct functional form (Lawler et al. 2006). GAMs were fitted using the package `mgcv` (Wood 2003, 2004, 2011, 2017, Wood et al. 2016) in R. The F test statistic, and its significance, as well as the R^2, and the effective degrees of freedom (edf - an indication of the extent of nonlinearity of the fitted smooth) were all extracted from the model.

5.4. Results

5.4.1. Relationship between diversity and environmental factors

According to the RF model (RF: MSE = 2656, $R^2 = 0.3$), the mean dissolved O_2 concentration at maximum bottom depth (MBD), the mean nitrate concentration at MBD ([B Nitrate]) and sea surface nitrate, were the most important variables explaining variation in the species richness measure (ICE; Figure 25A). In terms of the model prediction, ICE showed a sigmoid increase with increasing O_2 at MBD (> 275 umol/m^3, Figure 26A), decreased with increasing [B Nitrate] (> 25 umol/m^3, Figure 26B), and increased initially with sea surface nitrate up to ~ > 6 umol/m^3, and increased again above > 9 umol/m^3 (Figure 26C).

Taxonomic distinctness (RF: MSE = 18, $R^2 = 0.5$) was driven primarily by mean net primary productivity of Carbon at MBD (PP), [B Nitrate], and the Sea Bottom Temperature (SBT) (Figure 25B). Taxonomic distinctness reached an asymptotic as PP increased (> 0.01 g/m^3/d^1, Figure 26D), decreased with increasing [B Nitrate] (> 30 µmol.m^{-3}, Figure 26E), and increased initially with SBT up to ~ 7.5 ℃, before decreasing as SBT increased above 7.5 ℃ (Figure 26F).

Important drivers of Functional Evenness (FEve, RF: MSE = 0.01, $R^2 = 0.3$) were SBT, O_2 concentration at MBD and [B Nitrate] (Figure 25C). This measure of functional diversity increased with increasing SBT to ~ 7.5 ℃, then decreased with increasing SBT > 7.5 ℃ (Figure 26G), and increased with increasing O_2 at MBD (> 300 µmol/m^3, Figure 26H). FEve also decreased with increasing [B Nitrate] (> 20 µmol/m^3, Figure 26I). Functional Redundancy (FRed, RF: MSE = 0.003, $R^2 = 0.4$) was more closely related to SBT, [B Nitrate], and PP (Figure 25D). FRed decreased with the increasing SBT, reaching an asymptote around 5 ℃ (Figure 26J). This measure of functional diversity increased with increasing [B Nitrate] (> 30 µmol/m^3, Figure 26K), and decreased with increasing PP (Figure 26L).

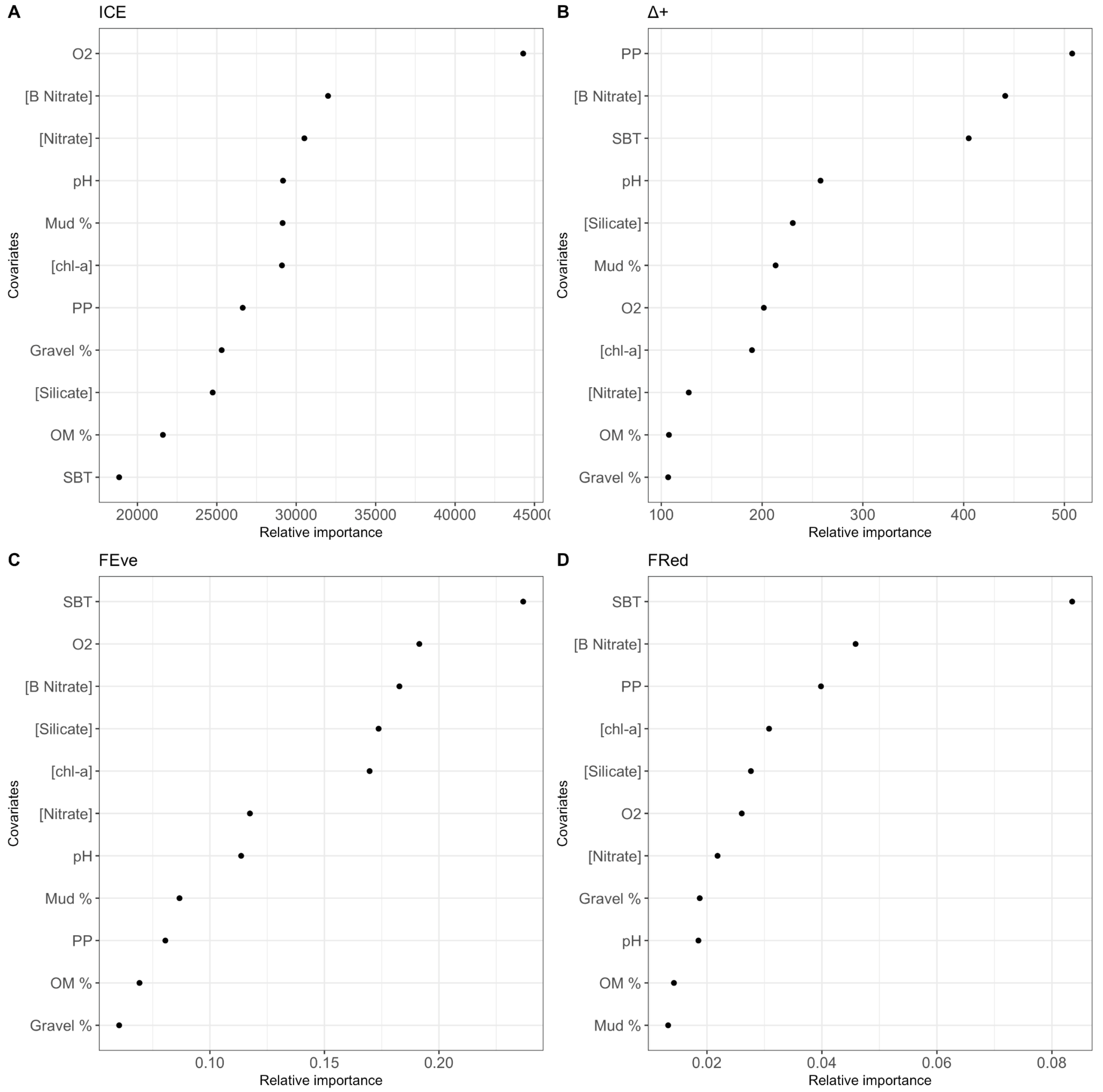


Figure 25. The importance of the environmental drivers based on node of impurity showing their influence on **A)** The Incidence Coverage - Based Estimator (ICE), **B)** Taxonomic Distinctness (Δ^+), **C)** Functional Evenness (FEve), and **D)** Functional Redundancy (FRed). The covariates are ordered in the y axis from the most important (top), to the least important (bottom) according to the Random Forest analysis.

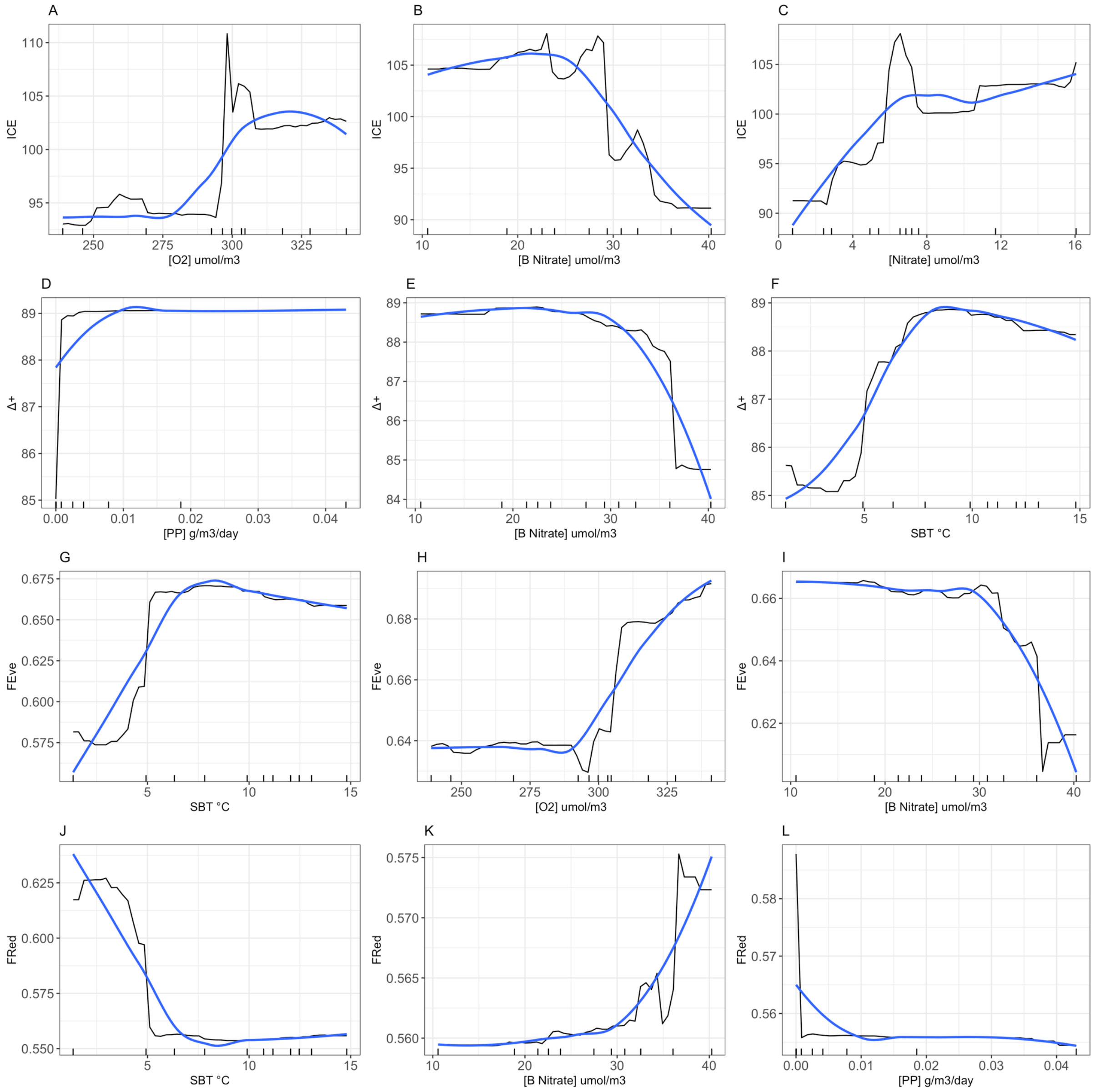


Figure 26. Partial dependence plots showing the model predictions (black lines) for the four diversity metrics: **A, B, C)** Incidence Coverage - Based Estimator (ICE); **D, E, F)** Taxonomic Distinctness (Δ^+); **G, H, I)** Functional Evenness (FEve); **J, K, L)** and Functional Redundancy (FRed) in relationship with the environmental drivers covariates (x-axis) representing the three most important according to each RF model. The blue line is the smoothed model prediction.

5.4.2. Latitudinal patterns of the ranked most important environmental factors

Considering the most important environmental factors influencing benthic diversity, oxygen at MBD presented a linear gradient from northern to southern latitudes (Figure 27A; GAM: F = 1398, edf = 1, $p < 0.0001$, $R^2 = 0.9$). [B Nitrate] was higher between 18° to 35° S (Humboldtian and Central Chile ecoregions) and decreased poleward, reaching the lower values after 45° S (Chiloense and Channels and Fjords ecoregions) (Figure 27B; GAM: F = 14, edf = 3, $p < 0.0001$, $R^2 = 0.7$). Sea surface Nitrate (Nitrate) presented a linear gradient from northern to southern latitudes (Figure 27C, GAM: F = 14, edf = 1, $p < 0.0001$, $R^2 = 0.7$). SBT peaked at 42° S (Chiloense ecoregion), decreasing in northern latitudes, reaching lower values at around 26° S (Central Chile ecoregion), and also decreasing poleward (Figure 27D, GAM: F = 6, edf = 3, p = 0.002, $R^2 = 0.4$). PP did not exhibit a significant trend with latitude (Figure 27E, GAM: F = 0.7, edf = 2, p = 0.5, $R^2 = 0.2$), although it slightly peaked at around 42° S.

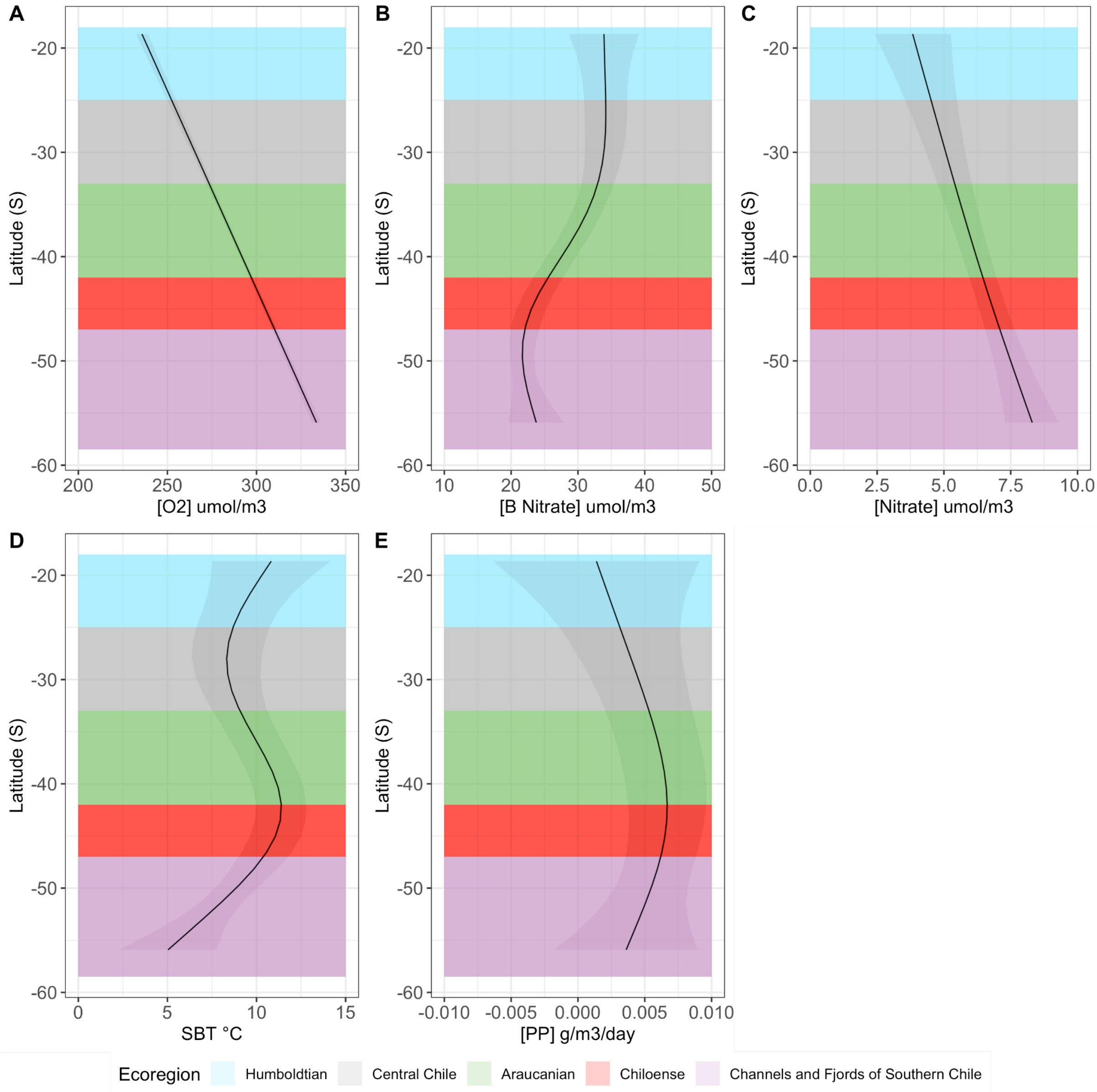


Figure 27. The relationship between latitude and **A)** O_2 (umol/m^3) at Maximum Bottom Depth (MBD) - [O_2], **B)** Nitrate umol/m^3 at MBD - [B Nitrate], **C)** Sea Surface Nitrate (umol/m^3) [Nitrate], **D)** Sea Bottom Temperature (°C) at MBD - SBT, and **E)** Net Primary Productivity of Carbon (g/m^3/day) at MBD - [PP]. Black lines represent the fitted Generalised Additive Models (GAMs), with the confidence interval in grey.

5.4.3. Relationship between diversity and anthropogenic activities

Species richness (ICE, RF: MSE = 2532, $R^2 = 0.3$) was most closely associated with the total aquaculture area, distance from salmon aquaculture, and the mean human population density (Figure 28A). ICE reached an asymptote as the total aquaculture area and the human population density increased (Figure 29A, C), and exhibited a sigmoid decrease with the increase in distance from salmon aquaculture (Figure 29B).

The most important drivers of taxonomic distinctness (RF: MSE = 22.3, $R^2 = 0.4$) were mean human population density, mean focal human population density, and distance from human population (Figure 28B). Taxonomic distinctness reached an asymptote as the human population density and the focal human population density increased (Figure 29D, E), and decreased reaching an asymptote with the increase in distance from human population (Figure 29F).

Functional Evenness (FEve, RF: MSE = 0.01, $R^2 = 0.2$) was most closely associated with mean human population density, mean focal human population density, and distance from human population (Figure 28C). FEve reached an asymptote as the human population density and the focal human population density increased (Figure 29G, H), and decreased until reaching a constant, to increase again with the increase in distance from human population (Figure 29I). The most important covariates explaining variation in FRed (RF: MSE = 0.003, $R^2 = 0.3$) were mean focal human population, mean human population density, and distance from human population density (Figure 28D). FRed decreased reaching an asymptote with the increase of focal human population density and human population density (Figure 29J, K), and increased with the increase of distance from human population (Figure 29L). The variable longitude, added to give some spatial structure to the model, was important according to all these RF models; however, it was not added to the RF models figures, because it does not represent a direct measure.

According to the RF models (Figure 28), none of the variables associated with PAs and TURFs were ranked as the most important. The partial plots showed that ICE and taxonomic distinctness increased, reaching an asymptote as the total area of PAs increased above 1500 km^2 (Figures S4A, D), and showed a sigmoid decrease with increasing the distance from PAs, reaching smaller values at around 200 km (Figures S4B, E). ICE decreased with distance from TURFs, at around 100 km of distance, then slightly increased with further increases in distance (Figure S4C). Taxonomic distinctness peaks at 100 km of distance from TURFs; then, it decreases with the distance (Figure S4F). FEve and FRed decreased with the increase of area of PAs, reaching an asymptote above 1000 km^2 (Figures S4G, J). FEve exhibited a sigmoid decrease with increasing the distance from PA, being lower at around 300 km of distance (Figure S4H), and it peaked at around 100 km from TURFs (Figure S4I). FRed increased with distance from PAs, reaching an asymptote (Figure S4K), and steadily increased with distance from TURFs (Figure S4L).

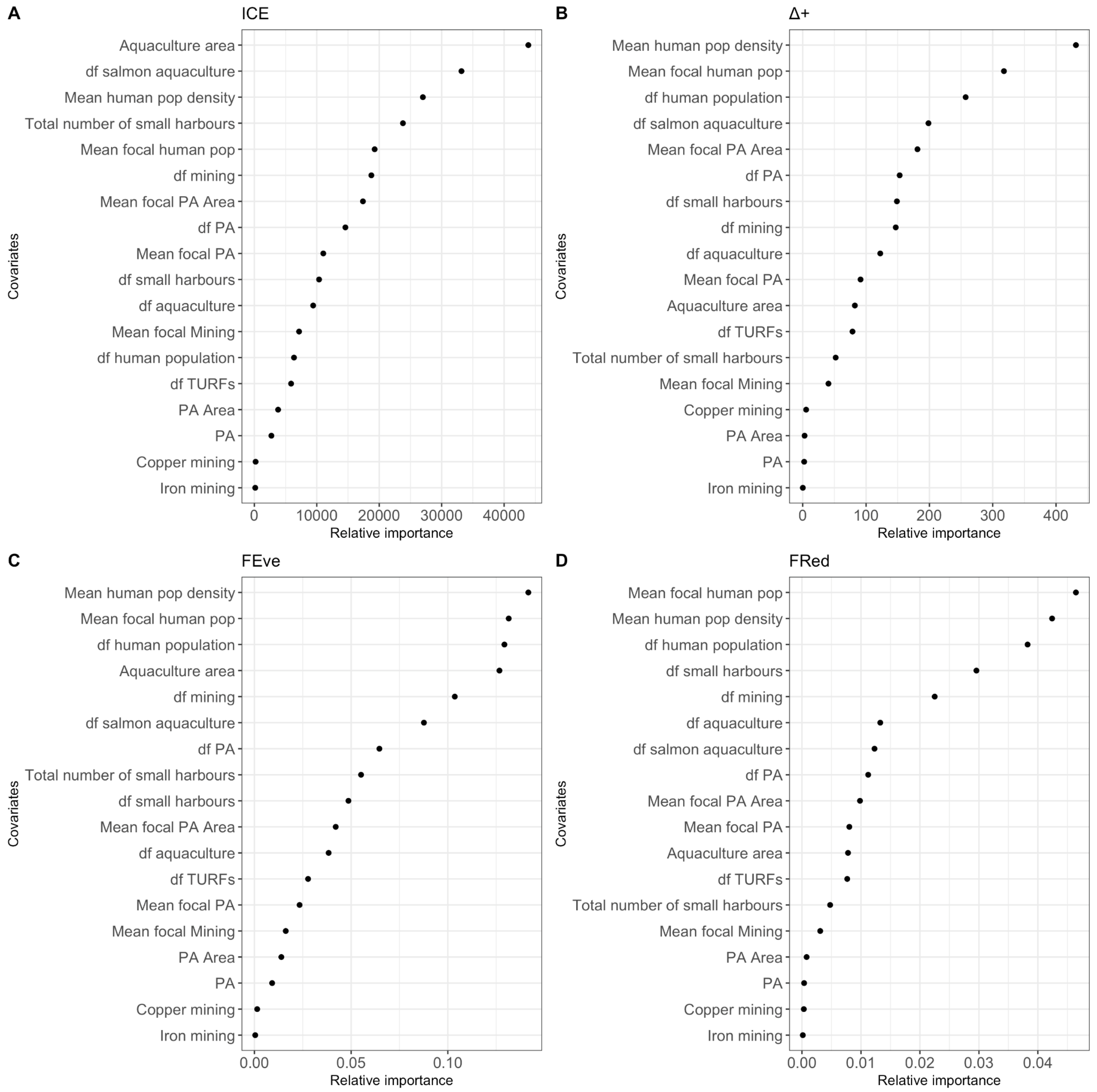


Figure 28. The importance of the human activities based on node of impurity showing their influence on **A)** The Incidence Coverage - Based Estimator (ICE), **B)** The Taxonomic Distinctness (Δ^{+}), **C)** Functional Evenness (FEve), and **D)** Functional Redundancy (FRed). The covariates are ordered in the y axis from the most important (up), to the least important (bottom) according to the Random Forest analysis.

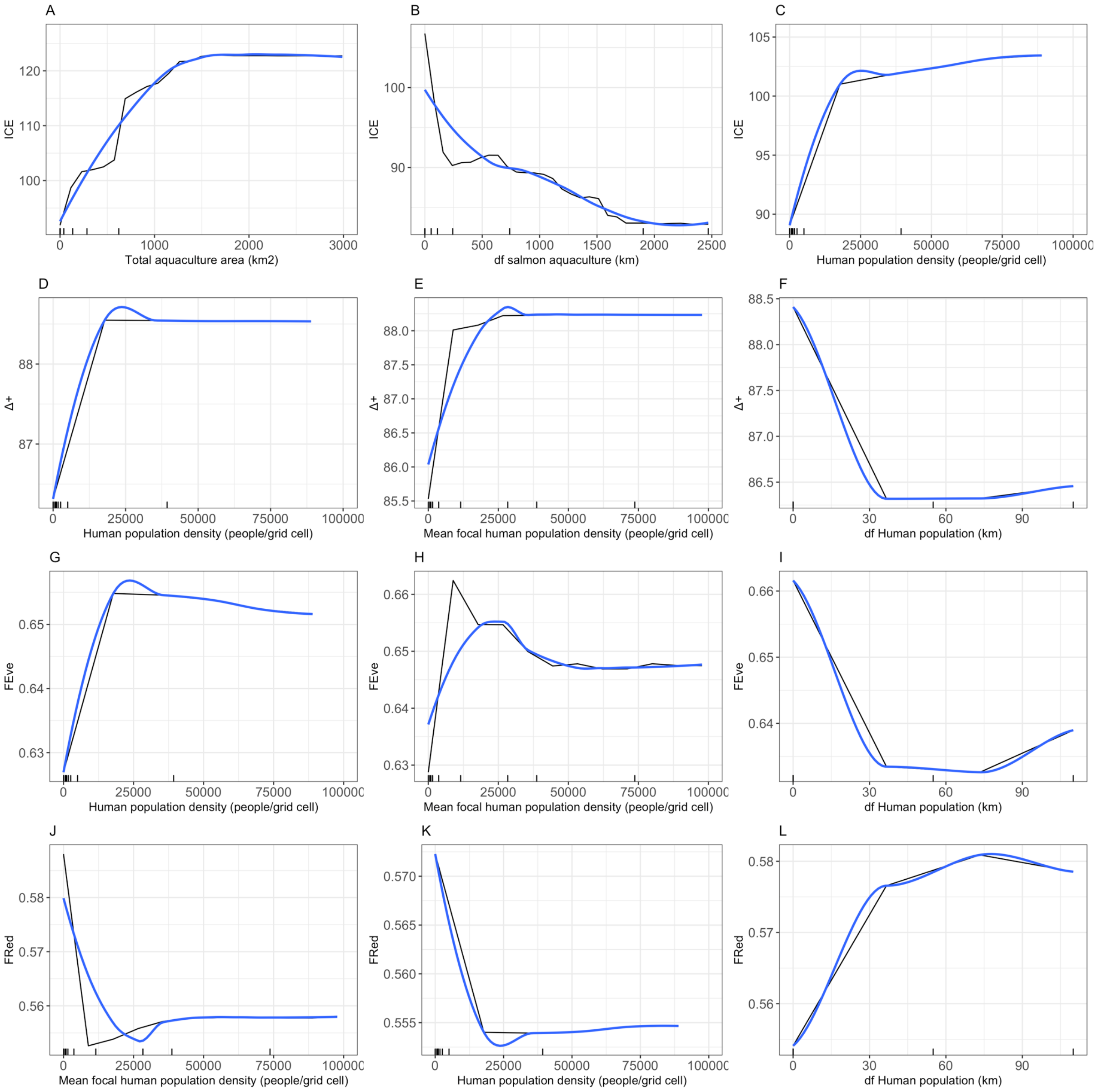


Figure 29. Partial dependence plots showing the model predictions (black lines) for the four diversity metrics: A, B, C) Incidence Coverage - Based Estimator (ICE); D, E, F) Taxonomic Distinctness (Δ^{+}); G, H, I) Functional Evenness (FEve); J, K, L) and Functional Redundancy (FRed) in relationship with the human activities covariates (x axis) representing the three most important according to each RF model. The blue line represents the smoothness of the model prediction.

5.5. Discussion

5.5.1. Environmental drivers

The results show (Figure 25) that key environmental drivers associated with benthic marine invertebrate communities along the Chilean coast and its continental shelf include those related to environmental stress (oxygen at maximum bottom depth (MBD), sea bottom nitrate [B Nitrate] and sea surface nitrate), hydrographic variability (sea bottom temperature, SBT), and primary productivity (net PP of Carbon (PP)). These key drivers influence different aspects of benthic diversity and different Chilean ecoregions, supporting previous arguments (Witman et al. 2008) that we should not expect a single explanation to determine patterns of species richness (i.e. diversity) at local or regional scales. The environmental factors identified as important are also related to two hypotheses explaining the diversity patterns in marine ecosystems and described by Tittensor et al. (2010). The stress hypothesis (related to oxygen depletion and nitrate increases) predicts a negative relationship between environmental stress and species diversity (Tittensor et al. 2010). The potential energy hypothesis (related to the PP and SBT), on the other hand, predicts a positive relationship between PP and temperature with species diversity (Tittensor et al. 2010).

Species richness (ICE), taxonomic (taxonomic distinctness) and functional diversity (FD, Functional Evenness - FEve) are each in part influenced by environmental stress. There was a direct relationship between oxygen dissolved and species richness and FEve; both measures increased with the increases of dissolved oxygen concentration (Figure 26). Species richness, taxonomic diversity and FEve had an indirect relationship with [B Nitrate]; these measures decreased with the increase of [B Nitrate] (Figure 26). Benthic ecosystems under environmental stress (e.g. deoxygenation and eutrophication) are found throughout Chilean coastal seas, encompassing the Humboldtian, Central Chile and Araucanian ecoregions (Figures 27A, B), corresponding to coastal upwelling system areas and their associated Oxygen Minimum Zones of the Humboldt Current (OMZs; Thiel et al. 2007). According to Bon et al. (2021), these coastal ecosystems may reach levels of eutrophication similar to the observed in highly polluted areas associated with anthropogenic eutrophication.

In northern latitudes, the low diversity might be explained by the environmental stress hypothesis (Tittensor et al. 2010, Witman et al. 2008) associated with oxygen dissolved depletion and nutrient excess (eutrophication). This hypothesis says that environmental stress modulates the populations of organisms. For example, depletion of dissolved oxygen, such as the observed in OMZs, affects the diversity of benthic marine invertebrate communities, reducing species richness (Levin & Gage 1998, Palma et al. 2005, Gooday et al. 2010, Sellanes et al. 2010, Bon et al. 2021), and taxonomic distinctness (e.g. peracarida; Rivadeneira et al. 2011). Under eutrophic conditions, on the other hand, lower species richness is also observed (Mastrototaro et al. 2008, Bon et al. 2021). Oxygen determines nutrients flux rates and their directionality regarding the conditions in the climate, and in turn, determines the degree to which biological processes such as bioturbation and diffusion take control of inorganic nutrients fluxes (Griffiths et al. 2017, Stief 2013). Thus, oxygen depletion seems to be a determinant factor for inorganic nutrient fluxes, benthic diversity levels, and the functional structure of benthic marine invertebrate communities in the northern latitudes of Chile.

Although FEve was also influenced by environmental stress, under dissolved oxygen depletion and increase of [B Nitrate], the values observed decrease to moderate levels of FD (Figures 26H, I). Thus, environmental stress modulates the functional structure of benthic invertebrate communities, but differently. Towards northern latitudes in Chile, Bon et al. (2021) also observed moderate to high levels of FEve, being moderate in the OMZ. The authors argued dissolved oxygen near hypoxia levels allows diversified functioning in benthic communities. I add that these communities might be structurally composed of a lower number of species highly adapted to stressful environmental conditions (hypoxia + eutrophication). In this manner, even under lower oxygen concentration, benthic activity performed by small communities of invertebrate species might contribute to the fluxes of [B Nitrate] (Figures 3A, B), accomplishing relevant and essential functions to the stability of the ecosystem functioning towards northern latitudes. For example, communities might be composed by surface deposit feeders (e.g. *Paraprionospio pinnata*, Gallardo et al. 2004), or burrower species, buffering the symptoms of eutrophication inhibiting the nutrients supply (McLenaghan et al. 2011). Molluscs and echinoderms, on the other hand, are more tolerant to environments reduced in oxygen dissolved than anthozoans and crustaceans (e.g. Steckbauer et al. 2015). Smaller benthic organisms with a short lifespan, such as foraminifera, have a high tolerance to environmental disturbance, colonising after hypoxic or anoxic events (Brower 2014), and being abundant in OMZs in Chile (e.g. *Nonionella* cf. *stella* and *Stainforthia*; Risgaard-Petersen et al. 2006).

Thus, to understand how the diversity aspects play different roles in the ecosystem functioning through Chilean upwelling systems, it might be needed to determine the functional structure of benthic invertebrate assemblages in zones associated with these complex and stressful ecosystems, which may be a future step in this research. Therefore, environmental stress related to eutrophication and hypoxia may be the primary driver influencing the different aspects of the diversity and community structure in the northern latitudes of Chile. Values of oxygen associated with hypoxia or anoxia in the area (i.e. < 65 umol Levin et al. 2009) were not observed, and findings only show lower concentrations of oxygen in northern latitudes than those observed towards southern latitudes (Figure 3A). Thus, it could be related to the size of the grid cells (55 x 55 km) and the average of oxygen and nitrate, neglecting those hypoxic and anoxic localities.

A direct relationship between PP and taxonomic diversity was observed (Figure 26D); taxonomic diversity increases, reaching an asymptote with primary productivity (PP) (Figure 26D). PP is associated with proxies such as net PP of Carbon [PP] and chlorophyll-a. High PP is observed toward southern latitudes, specifically in the Chiloense ecoregion, where [PP] peaks at around 43°S (Figure 27E). Zapata-Hernández et al. (2016) observed a high number of taxa, including invertebrates, bony fishes, rays and sharks from 100 to 460m of depth in the Inner Sea of Chiloe (ISCh), which they related in part to the benthic food webs supported by the carbon originating from surface phytoplankton. Higher species richness and Shannon diversity of benthic marine invertebrates have also been associated with an increased PP in the Canadian Arctic (Cusson et al. 2007). Thus, it seems reasonable to interpret the results as showing that PP is a key driver influencing the diversity of taxa in the Chiloense ecoregion. The importance of PP as a driver of taxonomic diversity is also associated with the role of the primary producers in the pelagic-benthic coupling and bottom-up effects in brackish waters (Dimitriadis et al. 2012), such as those located in the ISCh and the Patagonian fjords system.

Hydrographic variability, on the other hand, represented by SBT as an environmental factor, had a direct relationship with taxonomic diversity and FEve. Taxonomic diversity and FEve increase with increasing SBT until reaching an asymptote (Figures 26F, G). SBT follows a similar pattern with [PP] peaking in the Chiloense ecoregion (Figure 27D, E). Therefore, the high diversity in the Chiloense ecoregion might be related to the potential energy hypothesis. According to this hypothesis, the diversity of benthic invertebrate species is related to both PP and temperature (Tittensor et al. 2010, Witman et al. 2008). However, the importance of temperature as a relevant factor influencing the benthic marine invertebrate communities is disputed. Salinity rather than temperature has been considered as the main factor influencing the benthic communities of invertebrates through its relationship with freshwater inputs and stratification of the Chilean Patagonian Fjords (Quiroga et al. 2016, Villalobos et al. 2021) and in the Canadian Archipelago Arctic (Cusson et al. 2007, Witman et al. 2008). Therefore, the hydrographic variability driven by temperature and salinity gradients may be the primary driver influencing the benthic invertebrate communities in the south part of the Chiloense ecoregion and the Channels and Fjords ecoregion. These communities may be highly taxonomically diverse and functionally adapted to local gradients in both salinity and temperature.

5.5.2. Anthropogenic activities

A general decline of species richness, taxonomic and functional diversity due to anthropogenic activities and the human population was not observed. On the contrary, several diversity measures (species richness, taxonomic diversity and functional diversity (FEve)) are higher with an increased area used by aquaculture (Figure 29A), with closer proximity to salmon farms (Figure 29B), and with a higher nearby human population (Figure 29D-I). On a global scale, Tittensor et al. (2010) observed species richness hotspots of coastal and oceanic species (e.g. coastal fishes, tunas, cephalopods, squids, pinnipeds, cetaceans, foraminifera, among others) were located in areas with medium to high anthropogenic pressure. Moreover, a decrease in species richness is not always a sign of environmental stress; it could be more associated with the low nutritional quality of total organic content (TOC), the influence of salinity or grain size, low larval recruitment due to hydrographic features, disturbance related with natural events and biological interactions (Hyland et al. 2005). Even the increases of OM with high nutritional quality, until slightly moderate of environment carrying capacity, are a source of food for benthic communities; these communities can rise in species number and biomass to decline if the increase of OM exceeds the carrying capacity of the system (Conceptual model described by Hyland et al. 2005 based on Pearson & Rosenberg 1978). The nature of diversity measures used is also important. For example, Taxonomic distinctness is measured based on presence/absence data and would not detect the impacts of anthropogenic perturbations that primarily affect the relative abundance of species rather than variation in the taxonomic structure of assemblages (Bevilacqua et al. 2011). Nonetheless, FEve shows contrary responses to gradients of anthropogenic pressure (sewage discharges) in the South Atlantic of South America; evidencing differences between affected and not affected areas (Llanos et al. 2020) and not evidencing effects (Gusmao et al. 2016). Therefore, the magnitude of the effect, the spatial scale of the study, and the diversity metric used might all affect the observed relationship between diversity and anthropogenic drivers.

I expected benthic species richness, taxonomic diversity and functional diversity to decrease in areas strongly impacted by aquaculture or in the proximity of aquaculture (Brooks et al. 2001, Kalantzi & Karakassis 2006, Borja et al. 2009), especially towards Southern latitudes. However, the response of benthic communities to organic enrichment from aquaculture activity may be diverse, depending on hydrodynamic variables such as water depth and current velocity, and mud content (Borja et al. 2009) given the geographical context (Kalantzi & Karakassis 2006) and productive information such as farm volume, fish density, and food conversion ratio (Giles 2008). In Chile, marine phase salmon aquaculture is mainly developed in the transitional ecosystem encompassed by the archipelagos and the Patagonian Fjords and Channels of Southern Chile (Chiloense and Channels and Fjords ecoregions; Iriarte et al. 2010, Quiñones et al. 2019). As described before, this area is hydrodynamically active (i.e. high hydrographic variability). Salmon aquaculture effects are related to the input and accumulation of dissolved and solid residues in the water column and sediments and the retention of nutrients, such as nitrogen and phosphorus as a result of the excretion, faeces, and non-consumed food, which can exceed the carrying capacity of the ecosystems to incorporate these nutrients, resulting in anaerobic or anoxic processes (Niklitschek et al. 2013). A direct relationship was observed between species richness and nitrate; thus, higher species richness was related to an increase in nitrate (Figures 26C, 27C). This increase in nitrate towards the southern ecoregions can be related to natural inputs from freshwater, or it can be related to anthropogenic inputs due to salmon farms. Thus, how can benthic communities influenced by aquaculture tolerate the effects of this activity in Southern Chile? Kotta et al. (2007) argued that macrozoobenthos might respond less to nutrient concentrations in hydrodynamically active areas such as those observed in the Baltic sea, where the relationship between horizontal nutrient flows and vertical flux of organic matter affecting benthic communities is not simple. A similar explanation could hold in areas of the Chilean coast heavily threatened by this activity. Moreover, salmon aquaculture is still a relatively new activity in Chile, started during the early 1980s (Buschmann et al. 2009) but is developing much more rapidly this century; thus, its cumulative impact on benthic communities might not be evident at the broad spatial scale considered here. An alternative explanation is that benthic communities in these areas characterised by high hydrographic variability may already possess the biological traits required to tolerate levels of environmental stress such as eutrophication. For example, this might include biological traits relating to oxygen uptake and nutrient flux, mitigating anthropogenic impacts on ecosystem functioning (Belley et al. 2016). However, it does not guarantee that the communities will continue to function if the activity continues or increases. Therefore, a more complete study of the functional structure of benthic marine invertebrates might be key to understanding the levels of tolerance and adaptations to the conditions given by the environmental factors and anthropogenic drivers.

5.5.3. Protectiveness measures

PAs (PAs + MPAs) and TURFs were not generally important drivers of diversity (Figure 28). However, there are some broad trends. For instance, species and taxonomic diversity increase as the total PAs area increases, and species richness is higher in proximity to PAs and TURFs (Figures S4A-F). On the contrary, functional diversity indices do not increase with increasing PA area or proximity to both conservation measures (Figures S4G-L). In Chile, a positive impact on the recovery of benthic target-species populations, which were strongly overexploited in the past, such as *C. concholepas*, has been observed due to TURFs (Gelcich et al. 2008b) and PAs (Manríquez & Castilla 2001). TURFs have also increased the species abundances and biomass of non-target benthic species (Castilla et al. 1998, Gelcich et al. 2008b); thus, one of their main aims of restoring inshore assemblages is evidenced for benthic invertebrate species. The current findings are consistent with a positive response by species richness to these management tools. However, it was not possible to determine differences between different levels of protection and between management tools. For example, Lester and Halpern (2008) observed a higher density of organisms in fully protected MPAs than partially protected MPAs. In Chile, only 37.6 km^2 corresponds to fully MPAs (source: Atlas of Marine Protection available https://mpatlas.org/countries/CHL), a small portion of the total Chilean exclusive economic zone (1,975,760 km^2). Thus, considering the degree of protection of PAs and TURFs may be an essential next step in future research in Chile.

In Chile, TURFs and PAs have previously been shown to influence the functional structure of benthic invertebrate assemblages. For example, an increase in the area occupied by egg capsules, in the size of the eggs, in the number of larvae and the body size of *C. concholepas* is observed in PAs (Manríquez & Castilla 2001). TURFs have influenced the increase of body size in populations of overexploited species such as *C. concholepas* and the larval and juvenile recruitment of benthic invertebrate species (Castilla et al. 1998, Gelcich et al. 2008b). TURFs have also impacted trophic relationships, with evidence of competition between predators such as sea stars (*Heliaster helianthus* and *Stichaster striatu*s) and crustacea (e.g. *Cancer setosus*) due to the increase of abundance and biomass of key prey species (e.g. *H. helianthus*; Gelcich et al. 2008b). However, more than a positive impact, the higher abundance and biomass of top trophic species affect the rest of the species due to predation or competition (Micheli et al. 2004). As a result, these biological interactions modulate the communities in terms of species richness and density (Aldana et al. 2016). Joining these observations about the trophic structure of benthic invertebrates with the FD observed in this research would infer that the control of a specific trophic level and the intense focus on target-species impact the FD of benthic invertebrate communities within or in proximity TURFs and PAs. However, more is necessary, and this research could be the first step to better understanding these management tools and their effect on different diversity facets.

5.5.4. Functional redundancy: a key indicator of ecosystem functioning status

FRed might be a key indicator of ecosystem functioning throughout the Chilean marine and coastal ecosystem on a large scale. FRed exhibits a different pattern to the rest of the examined indices (Figures 26 and 29). FRed decreases with increasing, PP, SBT, mean focal human population density, and human population density, and increases with increasing [B Nitrate] and distance from the human population. Although FRed does not meet all the criteria to be recognised as an ecological indicator (e.g. its use is not straightforward (Hyland et al. 2005), due to its requiring ecological information of species), it may convey important information about the status of the ecosystem functioning in Chile.

Benthic marine invertebrate communities, showing some levels of resilience, may be responding to environmental gradients of SBT and salinity related to the increase of hydrographic variability of southern Patagonian fjords ecosystems (Iriarte et al. 2007) due to the interaction between inputs of surface freshwater, from rivers and precipitation, and deeper saline oceanic subantarctic waters (Iriarte et al. 2010). For instance, an increase in FRed with decreasing salinity was observed by Darr et al. (2014) in benthic marine communities of invertebrates inhabiting brackish waters of the Baltic sea. Under higher functional redundancy, benthic ecosystems were also more robust than those located in fully marine areas (Darr et al. 2014). In addition, even moderate levels of FRed (~0.5) in benthic marine invertebrate assemblages may lead to resilience against environmental fluctuations in brackish areas (Dimitriadis et al. 2012) and maintenance of ecosystem services and processes (Diaz et al. 2007). FRed also increases under eutrophication conditions (e.g. increase of [B Nitrate], northern upwelling systems). These benthic communities inhabiting stressful environments might be being highly adapted to these conditions, performing a similar range of functional traits, and allowing the support of ecosystem processes and services in the upwelling systems of Chile. Thus, these communities seem to be more tolerant to natural eutrophication because it has been a long-term environmental factor, which has allowed their adaptation to stressful conditions. However, FRed decreases with human drivers, such as the proximity to the human population or the increase in population density. Thus, benthic marine invertebrate communities may not be resilient to anthropogenic eutrophication (e.g. sewage discharges). Nevertheless, more is necessary to understand better the behaviour of FRed under anthropogenic pressure; for example, performing analysis at a small scale or making extra efforts to increase the species occurrences toward offshore areas in the continental shelf. FRed might therefore convey useful information about the stability of benthic marine invertebrate communities and ecosystem functioning in areas under natural or anthropogenic eutrophication, as well as those impacted by higher anthropogenic pressure, such as those located in the Humboldtian and Chiloense ecoregions.

To sum up, lower species richness and taxonomic diversity towards northern latitudes in the Humboldtian, Central Chile, and Araucanian ecoregions are explained by the environmental stress associated with the OMZs and eutrophication along the HCS. These small communities might be composed of species highly adapted to environmental stress. PP is the main driver influencing the higher taxonomic diversity of benthic marine invertebrates in the Chiloense ecoregion, and hydrographic variability represented by SBT gradient influences the communities towards the Patagonian fjords system (southern part of the Chiloense ecoregion and Channels and Fjords ecoregion). The levels of functional diversity of these communities located towards southern latitudes would allow the presence of species highly adapted to environmental gradients. In terms of human activities, species richness, taxonomic diversity, and functional diversity did not decline due to aquaculture and human population density (i.e. the most important drivers). Benthic communities in areas densely impacted by aquaculture might tolerate anthropogenic and natural eutrophication due to their functional adaptations to the hydrographic variability. Regarding protectiveness measures, only species richness and taxonomic diversity increase with PAs areas and with the proximity to PAs and TURFs. Finally, FRed showed a contrary pattern from the rest of the diversity metrics. Thus, FRed might be a key indicator of ecosystem functioning throughout the Chilean marine and coastal ecosystem and convey important information about the status of the ecosystem functioning in Chile.

5.6. Supporting information

Table S2. Details of the sediment and water column variables considered to be potential environmental drivers of Chilean benthic diversity. Expected relationship indicates whether a direct or indirect relationship is expected between the environmental driver and benthic diversity, with further details of the expected relationship provided in the final column. These variables were not considered in the model due to the high ($|r| > 0.7$) correlation with variables in table 5.

Table S3. Details of the human activities considered to be potential drivers of Chilean benthic diversity. Expected relationship indicates whether a direct or indirect relationship is expected between the human activities and benthic diversity, with further details of the expected relationship provided in the final column. These variables were not considered in the model due to the high ($|r| > 0.7$) correlation with variables in table 6.

Figure S3. Pearson correlation between **A)** environmental variables and **B)** human activities.

Figure S4. Partial dependence plots showing the model predictions (black lines) for the four diversity metrics: **A, B, C)** Incidence Coverage - Based Estimator (ICE); **D, E, F)** Taxonomic Distinctness (Δ^+); **G, H, I)** Functional Evenness (FEve); **J, K, L)** and Functional Redundancy (FRed) in relationship with measures of conservation such as Protected Area - PA (Terrestrial + Marine Protected Areas) and Territorial Use Rights for Fisheries - TURFs (TURFs + MEABR), in terms of the total PAs area, and the distance from (df) PA and TURFs. The blue line represents the smoothness of the model prediction.

6. General Discussion

Over the course of this research, I have explored the distribution patterns of benthic invertebrates throughout the eco-geographical gradient of Chile using different measures of diversity, with the final aim to identify key environmental drivers and anthropogenic activities influencing these patterns. In this general discussion, I first summarise my key findings. I expand upon the latitudinal patterns of the different diversity measures, and I discuss the congruence among hotspots and complementarity between diversity measures. I summarise the environmental drivers, and consider how diversity measures are impacted by anthropogenic pressures. Finally, I outline the future directions for benthic macroecological studies in Chile.

6.1. Key findings

I. Combining biodiversity data from the five complementary sources contained in the main integrated database (Chapter 2) led to a number of advantages, including expanding coverage across the entire latitudinal gradient of Chile between 18° to 57° S, which is essential given that describing the spatial distribution of benthic marine invertebrates across this gradient is our aim. The main database also gives new relevance to the data obtained through surveys and research programmes, which decision-makers consider in Chile. The exercise of collecting these data in a unique database is also helpful to estimate their quality and weaknesses, as well as the current lack of availability of major Chilean databases in global biodiversity aggregator databases such as OBIS.

II. Using the combined dataset, I showed that species richness, taxonomic distinctness (Chapter 3) and functional richness (FRic; Chapter 4) peaked at 43° S in the Chiloense ecoregion. FRic also peaks at 30° in the Central Chile ecoregion. Functional evenness (FEve) peaked towards the Humboldtian and Central Chile ecoregions (Chapter 4). FEve and Fred did not show any pattern with latitude.

III. Congruence between hotspots of species richness, taxonomic diversity and functional diversity was low (Chapter 4). Moreover, lack of complementarity of these different dimensions of diversity suggests that more than one should be considered in the environmental policies of Chile. My analysis highlights the importance of the

Humboldt Current System in terms of functional diversity and to the system of Patagonian fjords regarding taxonomic and functional diversities.

IV. Benthic invertebrate assemblages throughout the Chilean latitudinal gradient are composed of communities presenting a small volume of functional traits space (FRic ~ 0.5 and < 0.5); however, these communities are formed mainly by species tolerant to the environmental conditions, and they are using the available resources such as food and space (FEve > 0.5), presenting lower competition per resources (FDiv > 0.7). Moreover, these communities show moderate levels of resilience to changes in the environment and resistance to species loss (FRed ~ 0.5; Chapter 4).

V. The most important factors and environmental drivers influencing the benthic marine invertebrate communities were those related to environmental stress such as oxygen at maximum bottom depth (MBD), sea bottom nitrate [B Nitrate] and sea surface nitrate; hydrographic variability such as sea bottom temperature (SBT), and primary productivity such as net PP of Carbon [PP] (Chapter 5).

VI. The key anthropogenic activities driving the different facets of the diversity were aquaculture and the human population density; however, a decrease in diversity was not observed with these human pressures. Although measures of protectiveness such as PAs and TURFs were not important in driving diversity, both protectiveness measures seem to be more impact for species richness and taxonomic diversity (Chapter 5).

VII. FRed seems to be a key indicator of ecosystem functioning throughout the Chilean marine and coastal ecosystem on a large scale (Chapter 5). FRed appears to be responding to environmental gradients of SBT related to the increase of hydrographic variability and natural and anthropogenic eutrophication.

6.2. Diversity patterns of benthic marine invertebrate in Chile

The latitudinal band from 42° to 46° S, encompassing the Chiloense ecoregion, is already known for presenting higher diversity of species richness in benthic marine invertebrates (e.g. Cañete et al. 1999, Lancellotti & Vásquez 2000, Hernández et al. 2005, Häussermann 2006, Ibáñez et al. 2009, Chapter 3). The intense sampling effort from 41° to 46° S has rested relevance as a diversity hotspot (e.g. Lancellotti & Vásquez 2000, Häussermann 2006). In contrast, the lowest diversity is recognised towards northern latitudes (e.g. Carrasco 1997, Gallardo et al. 2004, Hernández et al. 2005, Palma et al. 2005, Carrasco & Moreno 2006, Rivadeneira et al. 2011, Chapter 3).

Using sample-based rarefaction/extrapolation (R/E) curves and nonparametric measures, I made the first attempt to reduce the influence of sampling effort on estimated species richness (Chapter 3). Although species richness, obtained using second-order Jackknife (Jackk 2) and Incidence Coverage-based estimator (ICE), peaked from 42° to 43° S, sample-based R/E curves also revealed the Channels and Fjords ecoregion as a potential area of high diversity. However, comparisons with estimations obtained in the Channels and Fjords ecoregion for molluscs and polychaetes using nonparametric measures (e.g. Montiel et al. 2011, Aldea et al. 2020) reveal that the current findings underestimate the actual diversity of this area. Even in well-studied regions, such as the Ross Sea in the Antarctic (Clarke et al. 2007), extra efforts to reduce species rarity and to fill gaps in taxa inventories (e.g. molluscs) are not enough to result in a complete dataset (Ghiglione et al. 2017). In less well-studied regions, any extra survey effort can dramatically increase the number of species in the repositories (e.g. Aldea et al. 2020). Better compilations using different sources of information collected along the entire latitudinal gradient of Chile and with different purposes would improve the species diversity estimations in the Channels and Fjords ecoregion and toward the northern latitudes. It gives relevance to open global databases such as OBIS to share and store data in the same place.

An alternative attempt to reduce the influence of sampling effort on diversity estimations was to use taxonomic distinctness (i.e. taxonomic diversity), because this measure is not biassed by differences in sampling effort (Clarke & Warwick 1998), and it is not dependent on species richness (Ellingsen et al. 2005). Taxonomic diversity peaked around 43°

S, with hotspots located south 52° S (Chapter 3). Using taxonomic distinctness, Rivadeneira et al. (2011) also recognised hotspots of peracarida at 54° S. Indeed, the south of Chile might be a source of evolutionary novelties, similar to the Antarctic region, which is an “evolutionary incubator” or origin point for many taxa (Clarke et al. 2004, Rivadeneira et al. 2011).

Functional diversity (FD) and its components Functional richness (FRic), Functional evenness (FEve), and Functional divergence (FDiv), were used to describe the distribution pattern of a different aspect of diversity based on the distribution of the species in the functional trait space. FD components showed different latitudinal patterns (Chapter 4), with FRic the only component following a similar pattern with species richness (Jackk 2 and ICE; Chapter 3), peaking at ~43° S in the Chiloense ecoregion. However, FRic also peaked at ~30° S. FEve was higher towards the extreme latitudes of Chile (Humboldtian and Channels and Fjords ecoregions), showing a contrary pattern with FRic. This finding revealed an area of high diversity towards northern latitudes. It also showed that Channels and Fjords ecoregion is an area of higher FD. A poleward increase of FEve and a contrary pattern with FRic have also been observed in benthic bivalves in both hemispheres (e.g. Schumm et al. 2019, Edie et al. 2018, Berke et al. 2014). Thus, the observed patterns in FEve and FRic in this thesis seem likely to be real rather than simply sampling artefacts.

The only published research considering FD components in Chile is a study of the coastal area around 23° S (Mejillones Bay, Humboldtian ecoregion; Bon et al. 2021). In this study, lower species richness and FRic, and local differences in FEve, were associated with hypoxic areas (Bon et al. 2021). Such local differences in FD will not be detected in my regional study due to the large size of the grid cell used. Rather, my results provide a general view of the benthic marine invertebrate communities in Chile. The finding that FRic, with a few exceptions, is low to moderate throughout the eco-geographical gradient suggests that the communities occupy a small volume of functional trait space. Thus, as was described by Legras et al. (2018), dominant species presenting the extreme values of traits, have been affected by long term perturbations, which can be associated with environmental drivers or anthropogenic pressure. On the other hand, even when these communities occupy a small total volume of functional space, high values of FEve indicate that species are evenly distributed within the functional trait space, using the resources available, and consequently, being highly productive. FDiv showed high values along the gradient (higher than 0.5), not exhibiting any clear pattern with latitude. High FDiv might be related to communities with a low competition for resources (Mason et al. 2005), where dominant species in the community present a high niche differentiation (Dimitriadis et al. 2012). However, the use of the relative frequency of the species, instead of species abundance or biomass, might affect both FEve and FDiv, and consequently, the results should be interpreted with caution. FEve and FDiv are based on the distribution of abundance in the volume of functional trait space (Villéger et al. 2008). Some authors have recognised differences in the FD measures depending on the use of abundance and biomass for FD estimations, which affect the interpretations whether the aim is to evaluate the environmental status of an ecosystem (e.g. Darr et al. 2014, Gusmao et al. 2016). Functional redundancy (FRed) was used as another measure of FD; this measure estimates the level of resilience of the benthic marine invertebrate communities (Micheli & Halpern 2005, Biggs et al. 2020). FRed was generally moderate throughout the latitudinal gradient. Thus, the benthic marine communities in Chile present certain levels of resilience and capacity to deal with and recover from perturbations or species loss, likely resulting in relatively stable communities and ecosystem functioning (Biggs et al. 2020).

6.3. Congruence between hotspots and complementarity between diversity measures

Previous macroecological studies have revealed a lack of congruence between hotspots based on functional compared to taxonomic measures; for example, in fishes (Stuart-Smith et al. 2013), marine mammals (Albouy et al. 2017), and sharks (Lucifora et al. 2011). This lack of congruence has led to more marine areas being considered important as conservation priorities. My results support this position, revealing low congruence between FD hotspots and those based on species richness and taxonomic diversity as well as a lack of congruence between different components of FD (Chapter 4). Reaching a high congruence among diversity hotspots based on different diversity aspects may not be considered an objective for conservation (Orme et al. 2005). A high congruence assumes that any measure of diversity can surrogate for any other diversity aspect (Orme et al. 2005). Thus, considering different diversity aspects would allow us for complete spatial planning for conservation purposes.

My research showed that the latitudinal band between 20° to 33° S represents an area where FD hotspots are located (e.g. nine hotspots; Chapter 4). This area has been considered as relevant for global conservation purposes by Myers et al. (2000) due to the high species diversity of marine mammals such as *Tursiops truncatus* (bottlenose dolphin), *Otaria flavescens* (Patagonian sea lion), and *Lontra felina* (marine otter), birds such as *Spheniscus* *humboldti* (the Humboldt penguin), and for Chilean endemic species of benthic invertebrates, such as *Concholepas concholepas* (Chilean abalone), and *Fissurella costata* (Keyhole limpet; Lenninger 2015). In addition, hotspots of FEve, FDiv and FRed were located in the Strait of Magellan and south of Tierra del Fuego, increasing the importance of this zone for Chilean biodiversity. My results support that these areas located toward the northern latitudes and poleward are important for Chilean biodiversity, and they should be priorities regarding conservation. For instance, northern latitudes need more attention due to the current interest of mining companies (e.g. La Dominga) in areas around 30° S. This mining project may cause severe damage to this area, which as was said before is an important diversity hotspot of global importance. On the other hand, there is a growing interest in expanding the salmon aquaculture south of Tierra del Fuego (~54° S, Channels and Fjords ecoregion; Salgado et al. 2015). This area represents one of the most pristine in Chile because it is far from human population and industrial development. It is a hotspot of algae and marine mammals (Tognelli et al. 2005). Thus, I strongly believe my research could bring new information to systems responsible for protecting Chilean marine biodiversity.

The complementarity between FEve, FDiv and species richness (Chapter 4) agrees with previous studies of benthic invertebrate communities inhabiting an upwelling centre (Bon et al. 2021) and in a highly dynamic estuarine area (Zhong et al. 2020). Small communities composed of few species can be highly adapted to stressful environmental conditions (e.g. eutrophication and hypoxia; Bon et al. 2021), such as was observed towards the northern latitudes in the Humboldtian ecoregion (Chapters 3 and 4). Törnroos et al. (2015) determined that even small communities formed of a few species can be functionally diverse; while communities can be composed of a high number of species performing a small range of functional traits (Zhong et al. 2020). It appears to be the case in those communities located towards southern latitudes in the Araucanian ecoregion, where the species richness increases toward southern areas (Chapter 3), while the FEve goes to moderate values (Chapter 4); in this area, the presence of rivers increases, forming an estuarine zone. Thus, this research brings new information about how benthic communities in this coastal and estuarine zone might be less functionally diverse than communities toward the northern and southern latitudes.

FRic reached an asymptote with increased species richness (Chapter 4), mainly in communities inhabiting the Chiloense ecoregion where the species richness is higher compared to the rest of the ecoregions. The intrinsic functional redundancy present within communities can generate an asymptotic relationship between species richness and functional diversity (Petchey & Gaston 2002). When the species diversity is higher, new species included in the community may perform similar traits to the species already present; thus, moderate FRed is observed (Micheli & Halpern 2005, Cornwell et al. 2006, Chapter 4), and consequently, the volume of functional space will not increase (i.e. reduced to moderate FRic; Cornwell et al. 2006). Thus, habitat filtering processes could modulate these communities of benthic marine invertebrates. Here, the biotic and abiotic environmental features allow the coexistence of tolerant species (Cornwell et al. 2006). At the same time, through this process, the environmental conditions also exclude non-tolerant species (Cornwell et al. 2006). As a result, the range of functional traits performed by these benthic invertebrate communities may be limited to specific functions and combinations of biologically and ecologically possible traits.

6.4. Key environmental and anthropogenic drivers of benthic diversity

Within the Humboldt Current System (HCS) in the northern latitudes of Chile, factors associated with environmental stress such as natural eutrophication and low dissolved oxygen (characteristic of areas within upwelling systems) are key drivers influencing the benthic invertebrate communities (Chapter 5). Dissolved oxygen is the key abiotic factor influencing benthic invertebrate communities in the continental shelf and slope ~36° S in the HCS, with lower species richness associated with hypoxia (Palma et al. 2005). Within an Oxygen Minimum Zone in shallow coastal waters, Bon et al. (2021) showed that benthic functional diversity was mainly driven by organic matter, also associated with environmental stress. I agree with Bon et al. (2021) that habitat filtering is the primary ecological process controlling the benthic invertebrate communities in the upwelling system; thus, only taxa showing specific morphological (e.g. small body size) and physiological adaptations to environmental stress, driven by the reduced bottom-water oxygen, may inhabit and dominate these areas. As a result, these communities might present a reduced number of species due to the deleterious hypoxic effects (Gooday et al. 2010).

Throughout the Inner Sea of Chiloe (ISCh) and the Patagonian fjords system, primary productivity (PP) and hydrographic variability related to gradients of bottom temperature and salinity are key drivers influencing the patterns of benthic invertebrate communities (Chapter 5). Primary productivity drives benthic diversity due to its key role in marine food webs via pelagic-benthic coupling and the bottom-up effects (whereby lower trophic levels control the structure of the community of higher trophic level, consumers). This is particularly important in brackish waters (Menge et al. 2003, Dimitriadis et al. 2012), such as those located in the ISCh and Patagonian fjords system. The increase in solar radiation in the south of Chile during austral summer influences the primary productivity and the abundance of diatoms in the Chiloense ecoregion, indicating a more effective pelagic-benthic coupling and vertical flux of particulate organic carbon (González et al. 2010). At the same time, the microbial web (associations between microalgae and microorganisms) is responsible for nutrient regulation, C recycling and the transport of C to higher trophic levels or its sedimentation to deep waters (Montecino & Pizarro 2008). Thus, the microbial web might supply C, other essential elements, and nutrients to the benthic marine system, increasing the taxonomic and functional diversity of benthic invertebrate communities.

Thus, my research regarding identifying key environmental drivers at a regional scale support the locally already known findings described in previous small-scale research (e.g. Bon et al. 2021, Palma et al. 2005, Gallardo et al. 2004, Zapata-Hernández et al. 2016, Quiroga et al. 2016, Villalobos et al. 2021). In addition, it gives more information about how southern benthic marine invertebrate communities may be functionally adapted to conditions such as natural environmental stress and environmental gradients in temperature and salinity, and why some areas in the Chiloense ecoregion might be real hotspots of diversity and not simply sampling artefacts influenced by the higher sampling intensity.

Benthic communities will decrease or increase their abundance, species diversity and dominance of tolerant and sensitive species in response to environmental gradients driven by human activities, such as enrichment with organic matter (Pearson & Rosenberg 1978, Borja et al. 2000). The need quantifies such human impacts can be seen in the increase in the number of indicators used to estimate and describe environmental status, such as TOC (total organic carbon; e.g. Hyland et al. 2005), dissolved sulphides (e.g. Cranford et al. 2020), BI (Biotic Index; e.g. Borja et al. 2000), foraminifera (e.g. Schafer 2000), diversity indices (e.g. Ferrando et al. 2015), and BTA (Biological Traits analysis; e.g. Bremner et al. 2006).

A major anthropogenic stressor in Chile is aquaculture. In comparison with other human pressures such as mining, industrial, and coastal activities, aquaculture has a well-established regulatory framework. This establishes well-defined variables of sediment, water and benthos to be measured for the purpose of environmental assessment, including physical measures (e.g. pH, redox, organic matter) and benthic diversity measures (e.g. richness, abundance, biomass; SUBPESCA 2009, Exempt Resolution N° 3612/2009). However, benthic invertebrate diversity is not considered in threshold measures of acceptability, despite efforts to include biotic indicators such as AMBI (AZTI's Marine Biotic Index; Borja & Muxica 2005) in the current environmental regulation (e.g. SUBPESCA 2009, Exempt Resolution N° 3612/2009) (Appendix 6). Biotic indices have the advantage of summarising ecological information into a unique value to simplify the understanding of complex data (Borja et al. 2000), but applied research using AMBI has not revealed a perturbed status in the proximity to salmon farms located in the Aysén Fjords (Quiroga et al. 2013) and within artisanal and industrial mussel farms in the Reloncaví Sound (Pino et al. 2015); both areas part of the Channels and Fjords and Chiloense ecoregion, respectively. Thus, the environmental assessment of aquaculture in Chile seems to be highly complex, even using measures proven to be effective as environmental impact indicators such as AMBI (e.g. Borja et al. 2015). Moreover, changes in the functional structure have been recognised through underwater video recorders in benthic communities associated with mussels' farms and depending on the type of system used (artisanal vs industrial); for instance, changes in the body size and motility of species (Pino et al. 2015). These changes are not easily quantified using univariate, multivariate and biotic indices (e.g. Pino et al. 2015). A recent study carried out by Sanchis et al. (2021) determined changes in the feeding modes and ecological groups of polychaete communities with the distance from salmon farms located in the ISCh and north of the Aysén region (i.e. Chiloense ecoregion). Groups of polychaetes influenced by salmon aquaculture are characterised by burrowing sub-surface deposit feeders represented by the dominance of *Capitella capitata* (Sanchis et al. 2021). The functional changes were more representative of the environmental impact of aquaculture than the conventional measures based on the community approach or biogeochemistry of the sediments (Sanchis et al. 2021). Thus, changes in the functional structure in a community may be detected using functional diversity indices or the species traits composition (Darr et al. 2014). The consideration of functional structure may say more about the ecological and environmental status of benthic invertebrate communities affected by aquaculture pressure, and decision-makers could consider it part of the environmental regulation.

My analysis of the functional structure of benthic communities in relation to anthropogenic pressures showed that FRed responds to pressures such as human population density more than FEve does (Chapter 5). Contradictory responses from FD measures have been observed when they have been used to evaluate the effects of human pressures such as sewage on benthic marine invertebrate communities (e.g. Llanos et al. 2020, Gusmao et al. 2016). If the aim is to evaluate environmental impact using different FD indices, it is also essential to choose the correct index because they may respond in a different way to the same impact (Schleuter et al. 2010, Legras et al. 2018). Scale is also important; for example, in birds, Mirochnitchenko et al. (2021) demonstrated the spatial scale-of-effect-dependence in the relationship between anthropogenic pressure covariates (land cover or type of land use) and different diversity facets (e.g. phylogenetic, taxonomic and functional). Therefore, smaller spatial grid cells would be necessary to implement FD measures such as FRed in the environmental assessment of Chilean benthic ecosystems to capture local variability.

FRed peaked in areas not affected by aquaculture, because these areas do not present favourable oceanographic conditions for development of aquaculture (Chapter 4). Although my results suggested that aquaculture was not important for FRed (Chapter 5), Dimitriadis and Koutsoubas (2011) showed that FRed did reveal the gradual loss of rare species in areas under organic enrichment associated with fish farms. They argued that only tolerant and adapted species inhabit benthic ecosystems in sediments affected by aquaculture; thus, different species perform the same traits (Dimitriadis & Koutsoubas 2011). Therefore, fish farming may influence the benthic biodiversity and modify the functional diversity of benthic communities, affecting the ecosystem functioning of coastal areas (Dimitriadis & Koutsoubas 2011). For instance, nutrient enrichment has adverse effects on the ecosystems, such as the loss of key species involved in nutrient processing (Douglas et al. 2017) and consequently, the loss in ecosystem resilience and ecosystem functioning stability. Sensitive species, playing important roles in ecosystem functioning, might be replaced by tolerant species performing similar roles (Llanos et al. 2020). Thus, FRed could be used simultaneously with BTA to obtain a complete landscape of the ecological status of marine benthos affected by aquaculture. Although it would imply a significant effort, it could also bring some benefits, such as knowing the actual dimension that aquaculture has reached in the benthic communities.

According to my findings, PAs and TURFs tend to affect species richness. This does not guarantee that communities in pristine areas will be successful in the face of pollution. For example, Ferrando et al. (2015) observed the low resilience to oil spills of benthic invertebrate communities inhabiting a pristine zone in Caleta Valdés (Argentina). These communities have higher univariate and multivariate diversity indices; however, their functional structure is reduced under oil contamination, and their resilience capacity is limited to species adapted to environmental stress (Ferrando et al. 2015). I argue that PAs and TURFs in Chile have been centred on species richness, abundance, and biomass of economically important species such as *C. concholepas* (e.g. Gelcich et al. 2008b). However, their implementations have not considered the functional ecological costs for the whole community, even when the effects of interspecific competition have been documented (e.g. Castilla et al. 1998, Gelcich et al. 2008b).

6.5. Future directions

Better understanding the variability of biological traits between assemblages along the latitudinal gradient and how the functional structure is related to environmental drivers and anthropogenic pressures would be an interesting next step in this analysis. Biological trait analysis would allow us to recognise the variability in spatial structure among ecoregions or even within them, providing essential information regarding ecosystem functioning, recognising that changes in the ecosystem services are more linked to changes in functional diversity than only in the species loss (Berke et al. 2014). This could be linked to gradients in environmental variables and human activities determined as important in this research. These gradients could be used to estimate beta diversity (e.g. pairwise dissimilarities vs geographic distance; Antão et al. 2019) and functional beta diversity (i.e. "effective number of equally large assemblages with no shared species and all species in the assemblages being equally distinct"; Chao et al. 2019, page 1). Expanding my study to consider Beta diversity would allow us to differentiate between turnover (i.e. species replacement) and nestedness (i.e. species overlapping or species loss; e.g. Baselga et al. 2010, Antão et al. 2019) along these environmental and pressure gradients. It would also be relevant to understand in more detail the importance of the latitudinal band between 42° to 43° S for the benthic diversity, identifying the processes (e.g. ecological, environmental) associated with the environmental drivers and anthropogenic pressure, potentially at a finer spatial resolution.

An additional area for future research would be to perform temporal analyses. For example, northern ecosystems such as those located through the HCS are highly variable due to the upwelling centres. This variability can be seasonal (from 26° S towards southern latitudes; Thiel et al. 2007), with the ENSO (El Niño Southern Oscillation) driving some interannual variability to the HCS (Escribano et al. 2004). Thus, the environmental factors influencing species richness, taxonomic diversity, and benthic invertebrate communities' functional structure might also vary over time. However, gaps in temporal data (e.g. Chapter 2) do not allow us to perform temporal analysis. To achieve this aim, increasing the scope of the main databases (diversity, sediment and water, and human activity) will be essential. This would also allow reducing the grain size of the grid cells to account for local variations.

6.6. Concluding remarks

My research has shown the relevance of using new sources of benthic invertebrate data different from those already used in the past by academic research. Moreover, this is the first research in approximately two decades considering the entire latitudinal gradient of Chile and different aspects of diversity other than number of species. My findings support the importance of the Chiloense ecoregion as an area of high diversity of benthic marine invertebrates in terms of species richness, taxonomic diversity and functional diversity. Here, diversity is mainly driven by primary productivity. The Channels and Fjords ecoregion, on the other hand, is relevant for the taxonomic and functional diversity; here, diversity is driven by the hydrographic variability related to environmental gradients such as sea bottom temperature. Towards northern latitudes in the Humboldtian, Central Chile and Araucanian ecoregions, the benthic communities are mainly composed of lower species richness; however, these communities can also be functionally diverse. The diversity here is driven mainly by environmental stress, which reduces the number of species, but increases the range of functional traits to tolerate the environmental conditions. Through this research, I would like to contribute to the knowledge of benthic diversity in Chile and the Southern Hemisphere.

6.7. Supporting information

Appendix S6: List of projects carried out by S. L. Marin at the University Austral de Chile related to AMBI.

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8. Supporting Information

Appendix S1: Scientific papers and technical reports provided by CIMAR

Cañete, J. I., Osorio, C. & Huaquín, L. (2015). Nuevos registros de imposex en muricidos de la zona Austral de Sudamérica (Estrecho de Magallanes). *Ciencia Tecnología Marina*, 36, 82-90.

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Appendix S2: Full code used to generate the OBIS Chilean benthos dataset.

Species_diversity - New OBIS analysis for Chile

Tom Webb-Loreto Pino

14/11/2018

Load the required libraries

```
library(tidyverse)
library(worrms)
library(mregions)
library(robis)
library(sp)
```

Work with EEZ Chile and OBIS

Get the Chile Exclusive Economic Zone (EEZ) from marineregions.org

```
chile_eez <- mr_shp("MarineRegions:eez", maxFeatures = NULL, filter = "Chi
lean Exclusive Economic Zone")
```

Find its bounding box

```
bbox(chile_eez)
```

Get a checklist of all taxa in OBIS recorded within the bounding box of the Chile EEZ: (In theory we could query the actual Chile EEZ, but this polygon is too complex for the robis query)

```
chile_checklist <- checklist(geometry = "POLYGON ((-84 -60, -84 -18, -59 -
18, -59 -60, -84 -60))")
```

Filter to species-level and tidy up

```
chile_checklist <- chile_checklist %>% filter(rank_name == "Species") %>%
  select(id, valid_id, tname, worms_id, records, datasets, phylum, class,
order:genus) %>%
  as_tibble()
```

Get functional groups for these species using the get_worms_fgrp function (It could take some time)

```
spp_attr <- chile_checklist %>%
 group_by(worms_id) %>%
 do(get_worms_fgrp(AphiaID = .$worms_id))

spp_attr
```

Add adult functional group to the main OBIS checklist

```
chile_checklist <- left_join(chile_checklist, dplyr::select(spp_attr, worm
s_id, adult), by = "worms_id")

chile_checklist <- chile_checklist %>% rename(functional_group = adult)
```

Combine some benthic groups

```
chile_checklist <- chile_checklist %>% mutate(fg = case_when(
  functional_group %in% c("benthos", "macrobenthos") ~ "benthos",
  TRUE ~ functional_group))
```

How many benthos?

```
table(chile_checklist$fg)
```

Read data

Read total database

```
total_dv <- read_csv("./Data/01-Total_database_plus_ecoregion(13-11-18).cs
v")
```

Remove OBIS from here (we will re-add OBIS records later)

```
total_db <- total_db %>% filter(source != "OBIS")
```

Generate a species list from here:

```
all_spp <- total_db %>% dplyr::select(AphiaID, validated_name) %>% distinc
t()
```

Check if the species in the list are present in the OBIS database

```
sum(all_spp$AphiaID %in% chile_checklist$worms_id)
sum(!(all_spp$AphiaID %in% chile_checklist$worms_id))
```

Create a new variable in the chile checklist to flag species already in your other datasets:

```
chile_checklist <- chile_checklist %>% mutate(in_db = case_when(
  worms_id %in% total_db$AphiaID ~ TRUE,
  TRUE ~ FALSE))
```

Check functional groups

```
chile_checklist %>% filter(in_db == TRUE) %>% count(fg)
```

According to this, from the species in total_db from surveys other than OBIS, will be possible to get the number of benthos, fish, nekton, and no functional group

```
chile_checklist %>% filter(in_db == TRUE & fg != "benthos") %>% select(tna
me, worms_id, phylum, class, fg)
```

Check species in the database which do not have functional group information from WoRMS because they are from the rest of the sources of information

```
chile_checklist %>% filter(in_db == TRUE & is.na(fg)) %>% select(tname, wo
rms_id, phylum, class, fg) %>% #data.frame()
```

After a revision, species without functional group were categorised as benthos

```
chile_checklist <- chile_checklist %>% mutate(fg = case_when(
  in_db == TRUE ~ "benthos",
  TRUE ~ fg))
```

We can the restrict the data to benthos:

```
chile_benthos <- filter(chile_checklist, fg == "benthos")
```

This can now be used as the basis for querying OBIS for actual occurrence records for each of these species within the Chile bounding box, and assigning these points to the relevant ecoregion (or discarding if they fall outside the ecoregions)

Next steps:

1. Write a function that gets OBIS records within the Chile bbox for each of these species
2. Run across species and bind together the results into a single data frame
3. Get the polygons of the relevant ecoregions from mregions
4. Assign each occurrence point to an ecoregion, and discard points falling outside the ecoregions
5. ttdy and format the occurrence dataset to combine with the occurrences from the other data sources

Function to get occurrences within Chile for a given species

```
get_chile_occ <- function(sp_id,
                          chile_geo = "POLYGON ((-84 -60, -84 -18, -59 -18, -59 -60, -84 -60))",
                          fnames = c("species", "decimalLongitude", "decimalLatitude", "depth", "eventDate", #"yearcollected", "aphiaID")
){

  occurrence(obisid = sp_id, geometry = chile_geo, fields = fnames)

}
```

Test: Run for one species:

```
get_chile_occ(sp_id = chile_benthos$valid_id[1])
```

Run across species Note: this takes an hour to run

```
chile_obis_occs <- chile_benthos %>%
  group_by(valid_id) %>%
  do(get_chile_occ(sp_id = .$valid_id))
```

Export this data set so it can be loaded without re-running

```
write_csv(chile_obis_occs, "all chile benthos obis.csv")
```

Read the loaded data

```
chile_obis_occs <- read_csv("./Data/all chile benthos obis.csv")
```

Create a spatial version of the dataset

```
chile_obis_sp <- chile_obis_occs
coordinates(chile_obis_sp) <- ~ decimalLongitude + decimalLatitude
proj4string(chile_obis_sp) <- proj4string(chile_eez)
```

Convert to sf

```
chile_obis_sf <- st_as_sf(chile_obis_sp)
chile_eez_sf <- st_as_sf(chile_eez)
```

Run st_join to find which points fall within the chilean EEZ, and then filter the dataset to these

```
chile_obis <- st_join(chile_obis_sf, chile_eez_sf)
chile_obis <- chile_obis %>% filter(!is.na(geoname))
```

Read in MEOWs and re-run the st_join to get ecoregion IDs for all points. MEOWs downloaded from: https://www.worldwildlife.org/publications/marine-ecoregions-of-the-world-a-bioregionalization-of-coastal-and-shelf-areas

```
meow <- st_read("MEOW")
chile_obis <- st_join(chile_obis, meow)
```

Create a final dataset with the obis records and ecoregion

```
chile_obis_df <- chile_obis %>% st_set_geometry(NULL) %>%
  as_tibble() %>%
  dplyr::select(aphiaID, species:yearcollected, ECOREGION) %>%
  bind_cols(as_tibble(st_coordinates(chile_obis))) %>%
  rename(ecoregion = ECOREGION, decimalLongitude = X, decimalLatitude = Y)
```

It has 12094 records of 1668 benthic species

Write this as a csv

```
write_csv(chile_obis_df, "02-chile_benthos_obis_meow.csv")
```

Quick check that these points look sensible:

```
dev.new(height = 7, width = 3)
ggplot(chile_obis_df, aes(x = decimalLongitude, y = decimalLatitude)) + ge
om_point()
```

Check ecoregion assignments

```
chile_obis_df %>% count(ecoregion)
```

Work with OBIS to get taxa

```
obis <- read_csv("./Data/02-chile_benthos_obis_meow.csv")
```

Get unique species names to match species name in worms

```
unique_sp_obis <- obis %>%
  dplyr::select(species)

unique_sp_obis <- as.data.frame(unique(unique_sp_obis))

write.csv(unique_sp_obis, file = "obis.sp.csv")
```

Match species name Read species matched

```
match <- read_csv("./Data/obis.sp_matched.csv")

species_matched <- merge(match, obis, by.x = "ScientificName", by.y = "spe
cies", incomparables = NULL)

glimpse(species_matched)
```

Separate data

```
obis_dataset <- species_matched %>%
  separate(eventDate, c("year", "month", "day"), sep = "-") %>%
  separate(day, c("day", "other"), sep = "T") %>%
  filter(ecoregion != "Juan Fernandez and Desventuradas") #234 obs to JFD
```

Work with OBIS dataset

```
obis2 <- obis_dataset %>%
   remove some columns
   dplyr::select(-X, -Match.type, -ScientificName.1, -AphiaID_accepted, -K
ingdom,
                -Order, -Family, -other, - Genus, -Subgenus, -Species, -Su
bspecies, -aphiaID, -year) %>%
   generate new variables to be matched with the Chilean survey dataset
   mutate(station = "", station = as.character(station),
         n_ind = "", n_ind = as.numeric(n_ind),
         biomass = "", biomass = as.numeric(biomass),
         abundance = "", abundance = as.numeric(abundance),
         dredge = "", dredge = as.character(dredge),
         mesh = "", mesh = as.numeric(mesh),
         source = "OBIS") %>%
   change columns name
   rename(validated_name = ScientificName_accepted,
         species = ScientificName,
         year = yearcollected,
         long = decimalLongitude,
         lat = decimalLatitude,
         phylum = Phylum,
         class = Class) %>%
  filter(!phylum %in% c("Ciliophora", "Ochrophyta")) %>%
  remove fishes from total database
  filter(!AphiaID %in% c("215607", "280277", "272449", "280634", "279640",
"281324"))
```

Table S1. Metadata of attributes included in the main database (1846 to 2017) and in the final dataset (1991 to 2017), including the measurement units, the type of variable and a brief description of each attribute.

Attribute column	Unit	Variable	Description	Database / Dataset
cells		numeric	Number of the grid cell.	Dataset 1991 - 2017
x	Longitude - ESRI projection 102033	numeric	Centre point in the grid cell.	Dataset 1991 - 2017
y	Latitude - ESRI projection 102033	numeric	Centre point in the grid cell.	Dataset 1991 - 2017
coords.x1	Longitude - ESRI projection 102033	numeric	Geographical point of the occurrence.	Dataset 1991 - 2017
coords.x2	Latitude - ESRI projection 102033	numeric	Geographical point of the occurrence.	Dataset 1991 - 2017
species		character	Species name obtained from the dataset.	Database 1846 - 2017 Dataset 1991 - 2017
AphiaID		numeric	Code given to each species recorded in WoRMS. Each record has an unique AphiaID.	Database 1846 - 2017 Dataset 1991 - 2017
validated_name		character	Species name validated by WoRMS.	Database 1846 - 2017 Dataset 1991 - 2017
phylum		character	Phylum validated by WoRMS.	Database 1846 - 2017 Dataset 1991 - 2017
class		character	Class validated by WoRMS.	Database 1846 - 2017 Dataset 1991 - 2017
year		numeric	Year of sampling.	Database 1846 - 2017 Dataset 1991 - 2017
long	Decimal longitude - WGS84	numeric	Longitude.	Database 1846 - 2017 Dataset 1991 - 2017
lat	Decimal latitude - WGS84	numeric	Latitude.	Database 1846 - 2017 Dataset 1991 - 2017
source		character	Name of the dataset. It can take the name SERNAPESCA, IFOP, DIRECTEMAR, CIMAR, and OBIS.	Database 1846 - 2017 Dataset 1991 - 2017
station		character	Code obtained joining the year + longitude + latitude of each occurrence.	Database 1846 - 2017 (OBIS - CIMAR) Dataset 1991 - 2017 (All the dataset)
short_dist_km	kilometre	numeric	Distance from the coast.	Dataset 1991 - 2017

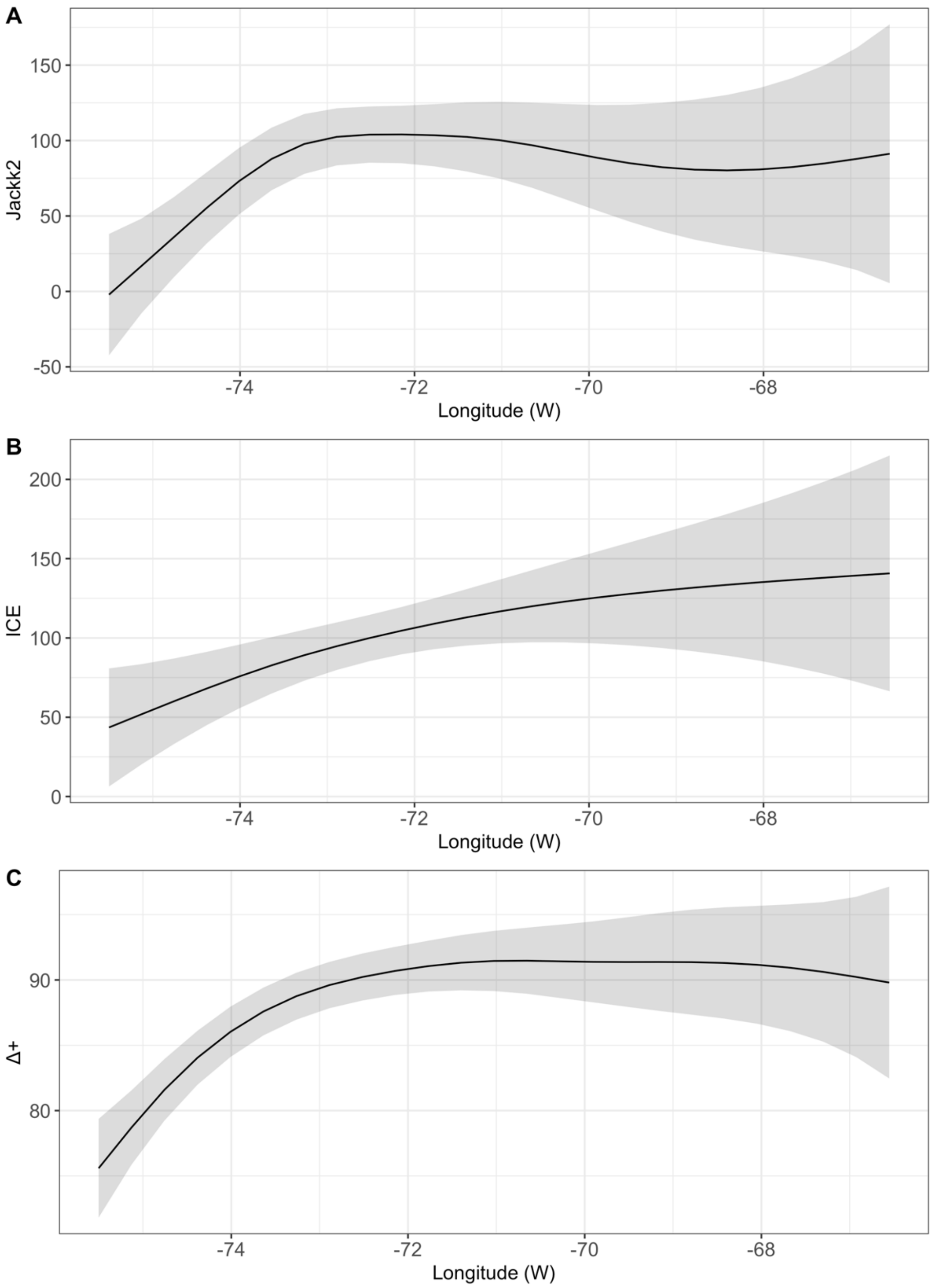

Figure S1. The relationship between longitude and A) Jackk 2 - Jackknife 2, B) ICE - Incidence based on coverage estimator, C) Δ^+ - Taxonomic distinctness. Blackline represents the fitted Generalised Additive Model (GAM), and the grey bits the interval confidence.

Appendix S3. List of references used to construct functional traits dataset used in Chapter 4

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Appendix S4: Metadata biological traits database

Link available from ORDA: https://doi.org/10.15131/shef.data.19195967

Appendix S5: Biological traits database

Link available from ORDA: https://doi.org/10.15131/shef.data.19195967

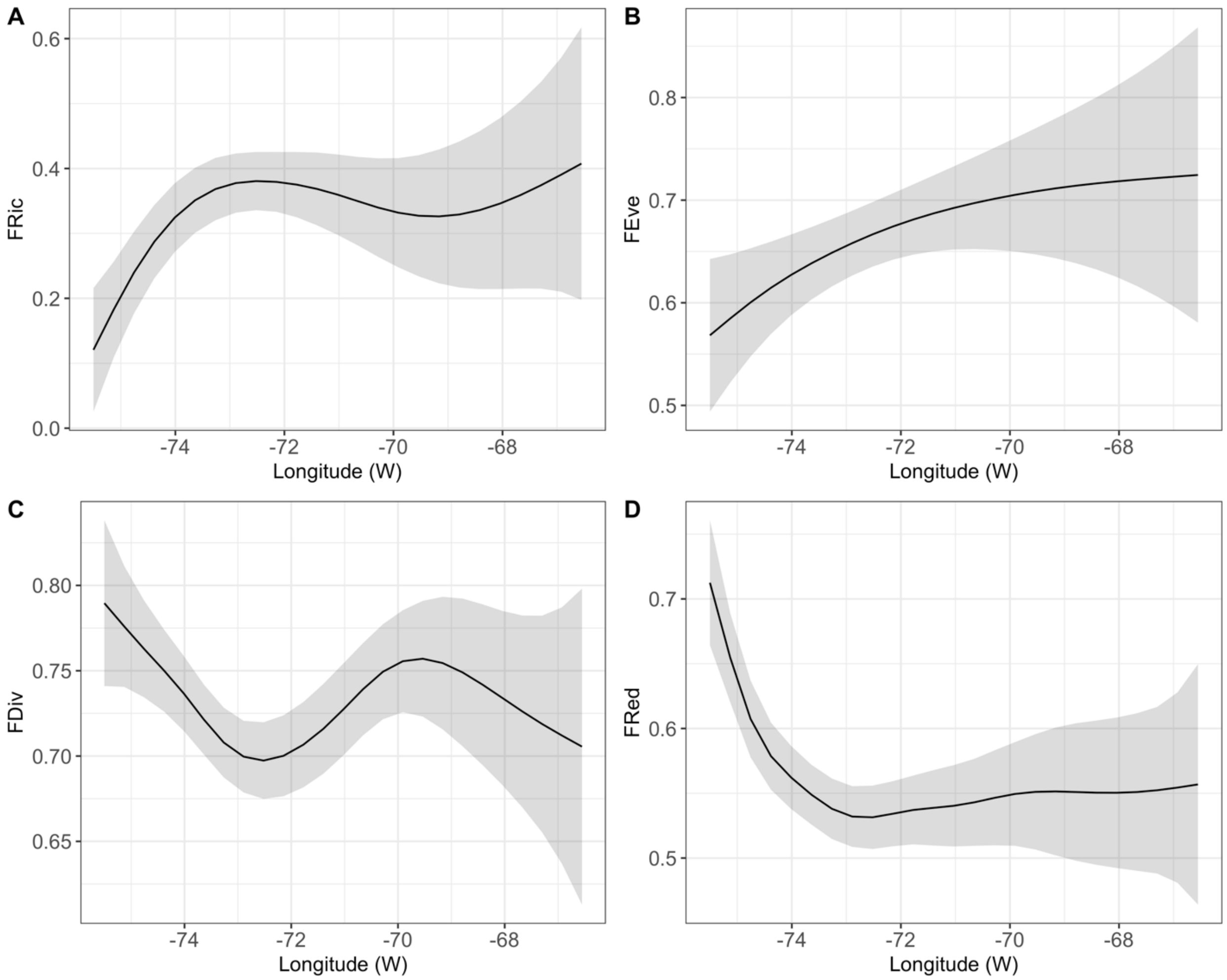

Figure S2. The relationship between longitude and A) FRic - Functional richness, B) FEve - Functional evenness, C) FDiv - Functional divergence, and D) FRed - Functional redundancy. Black line represents the fitted Generalised Additive Model (GAM), and the grey bits the interval confidence.

Table S2. Details of the sediment and water column variables considered to be potential environmental drivers of Chilean benthic diversity. Expected relationship indicates whether a direct or indirect relationship is expected between the environmental driver and benthic diversity, with further details of the expected relationship provided in the final column. These variables were not considered in the model due to the high (|*r*| > 0.7) correlation with variables in table 5 (Compiled by author).

Covariate and variable name	Unit	Matrix	Time coverage	Type of data	Data source	Expected relationship	Importance notes
Sand	%	Sediment	1995 - 2017	Average / Time period	SERNAPESCA IFOP DIRECTEMAR CIMAR	Direct - Species, taxonomic and functional diversity (FD) increase with the increase of grain size, and also with the increase of habitat heterogeneity (Ellingsen & Gray 2002, Mastrototaro et al. 2008).	Granulometry is related to **environmental / habitat heterogeneity.** ● Important driver of beta and gamma diversity of benthic invertebrates in soft bottoms (e.g. Ellingsen & Gray 2002, Mastrototaro et al. 2008). ● Beta and gamma diversity increase with the increment of habitat heterogeneity driven by the granulometry (Ellingsen & Gray 2002). ● Communities from muddy bottoms, also rich in organic matter, were less diverse in species richness than those inhabiting coarse sediments and higher bottom heterogeneity (Mastrototaro et al. 2008).
pH	Measure of the acidity in the sediments	Sediment	1995 - 2017	Average / Time period	SERNAPESCA IFOP DIRECTEMAR CIMAR	Direct - Species richness and taxonomic diversity decrease with the decrease of pH. Unknown in terms of FD measures.	pH of the sediments is related with **acidification** and **environmental stress** due to its relationship with Redox (Hargrave 2010). ● Species behaviour related with life habitat, bioturbation (e.g. burrow residence period, and irrigation) and species diversity are important for pH levels (Zhu et al. 2006). ● Nitrate formation, reduction of oxygen are related to low levels of pH (Zhu et al. 2006). ● pH is lower under net-pens in salmon farms than in non-farm areas (Hargrave 2010). ● Some variations in functional structure of benthic invertebrate communities is observed in

Covariate and variable name	Unit	Matrix	Time coverage	Type of data	Data source	Expected relationship	Importance notes
							relationship with burrowing (e.g. Zhu et al. 2006, Waldbusser et al. 2004).
Redox	mV	Sediment	1995 - 2017	Average / Time period	SERNAPESCA IFOP DIRECTEMAR CIMAR	Direct - Species richness decreases with the decreases of redox potential (Brooks et al. 2001).	Redox of sediment is related to **environmental stress**. ● The redox cascade is recognised under hypoxic and anoxic levels of oxygen, heterotrophic microbes decompose the excess of OM using processes of anaerobic respiration, including nitrate, manganese, iron, and sulphate reduction. ● Significant differences between farms and control sites were observed in the potential redox of the water-sediment interface (Soto & Norambuena 2004).
Temperature	°C	Sediment	1995 - 2017	Average / Time period	SERNAPESCA IFOP DIRECTEMAR CIMAR	Indirect - Species richness decreases with a gradient of OM (Mastrototaro et al. 2008, Hyland et al. 2005). Taxonomic diversity decreases with the increase of OM content. FD (e.g. FEve) decreases with the increase of OM content (Bon et al. 2021).	● The higher temperature of the sediments contributes to the organic matter decomposition (Patterson et al. 1989). ● Relationship with diversity would be similar to those observed for OM.

Covariate and variable name	Unit	Matrix	Time coverage	Type of data	Data source	Expected relationship	Importance notes
Mean Chlorophyll concentration [Chl]	mg/m^3	Maximum bottom depth in the water column	2000 - 2014	Average / Time period	Bio-ORACLE	Direct - Species, taxonomic and FD increase with the growth of chlorophyll a (e.g. Cusson et al. 2007, Zhong et al. 2020). Direct - Species, taxonomic and FD increase with the growth of net PP of Carbon (e.g. Zapata-Hernández et al. 2016).	Chlorophyll-a and mean net primary productivity of Carbon are related to **Primary Productivity** (PP). ● Species richness and Shannon-Wiener diversity were influenced by gradients of primary productivity (e.g. Canadian Arctic Archipelago, Cusson et al. 2007). ● High diversity of taxa in (including invertebrates, bony fishes, rays and sharks) were related to the benthic food webs supported by the Carbon originated from surface phytoplankton (Zapata-Hernández et al. (2016).
Mean sea surface temperature (SST)	℃	Water column	2002 - 2009	Average / Time period	Bio-ORACLE	Direct - Species, taxonomic and FD increase with the increase of SBT (e.g. Tittensor et al. 2010, Rivadeneira et al. 2011).	● SST is described as the unique environmental factor influencing the diversity patterns of marine taxa (e.g. fishes, tuna, sharks, cetaceans, corals, and foraminifera, among others) at global scale (e.g. Tittensor et al. 2010). ● However, SST was not the main factor influencing the species diversity of benthic marine molluscs in Chile (e.g. Valdovinos et al. 2003), but it increased the performance of some taxa such as peracarida (e.g. Rivadeneira et al. 2011). ● Boyce et al. (2015) indicated that SST was the determinant factor explaining the spatial patterns and the structure of the trophic dynamics across marine ecosystems at large scale in the oceanic and continental shelf of the North Hemisphere. The authors argued that cold-water ecosystems are mostly controlled by consumer species.

Covariate and variable name	Unit	Matrix	Time coverage	Type of data	Data source	Expected relationship	Importance notes
Mean Salinity	PSS	Water column	1961 - 2009	Data Interpolating Variational Analysis (532,377 data points)	Bio-ORACLE	Indirect - Diversity decreases with increasing salinity.	● Freshwater inputs from rivers have an impact on coastal ecosystems, influencing the distributions of coastal species (Snelgrove 1998). ● Villalobos et al. (2021) observed that species richness, evenness and diversity of macrobenthic species peaked at high salinity (> 27 psu) at relatively shallow waters (5 to 21 m of depth) in the Inner Sea of Chiloe (Chile). ● However, the recognized hypothesis says that diversity decreases with salinity (Törnroos & Bonsdorff 2012).
Mean Bottom Sea Water Salinity (B Salinity)	PSS	Maximum bottom depth in the water column	2000 - 2014	Average / Time period	Bio-ORACLE		
Mean phosphate concentration [B Phosphate]	mol/m^3	Maximum bottom depth in the water column	2000 - 2014	Average / Time period	Bio-ORACLE	Indirect - Species richness decreases with a gradient of nutrients. Taxonomic diversity decreases with the increase of nutrients. FD (e.g. FEve) decreases with the increase in eutrophicated environments (Bon et al. 2021).	● Natural and anthropogenic eutrophication have their origin in the increase of nutrients availability such as nitrogen and phosphorus in the system. ● Eutrophication can be related to upwelling, or be facilitated by the discharge from estuaries and rivers nearby to human activities (e.g. agriculture, mining, cities, which can provoke an excessive growth of phytoplankton (Levin et al. 2009). ● Anthropogenic eutrophication also can include the organic enrichment of the water column and seabed due to the nitrogen and phosphorus released to the environment through the excretion, faeces, and uneaten food due to salmon aquaculture (Soto & Norambuena 2004, Niklitschek et al. 2013, Quinones et al. 2019).
Mean Carbon phytoplankton concentration [C phyto]	$umol/m^3$	Maximum bottom depth in the water	2000 - 2014	Average / Time period	Bio-ORACLE	Direct - Species, taxonomic and functional diversity increase with the	Chl-a and mean net primary productivity of Carbon are related to **Primary Productivity** (PP). ● Species richness and Shannon-Wiener diversity were influenced by gradients of primary

Covariate and variable name	Unit	Matrix	Time coverage	Type of data	Data source	Expected relationship	Importance notes
		column				growth of net PP of Carbon (e.g. Zapata-Hernández et al. 2016).	productivity (e.g. Canadian Arctic Archipelago, Cusson et al. 2007). ● High diversity of taxa in (invertebrates, bony fishes, rays and sharks) were related to the benthic food webs supported by the C originated from surface phytoplankton (Zapata-Hernández et al. (2016).

Table S3. Details of the human activities considered to be potential drivers of Chilean benthic diversity. Expected relationship indicates whether a direct or indirect relationship is expected between the human activities and benthic diversity, with further details of the expected relationship provided in the final column. These variables were not considered in the model due to the high ($|r| > 0.7$) correlation with variables in table 6 (Compiled by author).

Activity	Covariate and variable name	Unit (by grid cell)	Matrix	Time coverage	Data source	Expected relationship	Importance
Aquaculture	Total salmon area	km^2	Sea	1980 - 2019	SERNAPESCA	Indirect- Species diversity due to decrease with the increase in OM (Villalobos et al. 2021). Direct- Increases in distance from aquaculture farms will increase the biotic parameters (e.g. species richness; Kalantzi & Karakassis 2006, Borja et al. 2009).	● **Aquaculture** provokes anthropogenic gradients of disturbance, affecting the physicochemical of the sediment, benthic macrofaunal community composition and net benthic ecosystem functioning (Godbold & Solan 2009). ● The habitat degradation, due to the excessive accumulation of OM under salmon farms located in areas influenced by natural and anthropic eutrophication, also has revealed that the low quality of organic matter of the sediments is related to a low species diversity of benthic marine invertebrates in areas under high aquaculture pressure (e.g. Northern Patagonian Fjords; Villalobos et al. 2021). ● Anthropogenic eutrophication also can include the organic enrichment of the water column and seabed due to the nitrogen and phosphorus released to the environment through the excretion, faeces, and uneaten food due to salmon aquaculture (Soto & Norambuena 2004, Niklitschek et al. 2013, Quinones et al. 2019).
	Total mussel area	km^2					
	df mollusc aquaculture	km					
	Mean focal aquaculture area / Average by neighbourhood	km^2					
Small harbours	Mean focal small harbours / Average by neighbourhood	number	Sea/Earth	Updated August 2019	SERNAPESCA	Indirect - The fishing activity related to small harbours will impact benthic	● Benthic fisheries impact the population of coastal and marine invertebrates directly, for example, through the overfishing of sea urchins

Activity	Covariate and variable name	Unit (by grid cell)	Matrix	Time coverage	Data source	Expected relationship	Importance
						invertebrate communities and decrease their populations. Proximity to small harbours might impact benthic communities.	(e.g. *L. albus* and *A. dufresnii*) and mussels (Chilean abalone, *C. concholepas*). ● Benthic fisheries at a small scale do not provoke damages in the habitat of non-target species because it is done through diving (Gelcich et al. 2008b).
Trading ports	Total number of trading ports df trading ports Mean focal trading port / Average by neighbourhood	number km number	Sea/Earth		Laboratory of geography (UFRO)	Indirect - the proximity to trading ports has a negative impact on species richness.	● The expected impact of these ports is related to oil spills, the discharge of sewage from industrial and mercantile ships, and cruises.
Landings by port	Total landings by ports	Tons	Sea/Earth	2018	Laboratory of geography (UFRO)	Unknown	● **Landings by port** included those captured by artisanal and industrial fisheries as well landings by aquaculture.
Mining	Total number of mines	number	Earth	Unknown	Laboratory of geography (UFRO)	Indirect - The increase in the number of mining and the related tailings, decrease the species, taxonomic and functional diversity of	● Lancellotti and Stotz (2004) argued that although extractive activity of **Mining** occurs in land, its effects also may be observed in the coast, where there are mineral deposits. ● Mining is not subject to proper environmental legislation with the aim to protect the coastal and marine ecosystems from mining discharges, even when the effects on marine communities have been evidenced (e.g. Castilla 1983).

Activity	Covariate and variable name	Unit (by grid cell)	Matrix	Time coverage	Data source	Expected relationship	Importance
	df iron mining df copper mining	km km				benthic invertebrates.	● Mining activity and mining tailing have effects on biological diversity, decreasing the diversity of species of marine invertebrates (Castilla 1983; Ramirez et al. 2005, Fariña & Castilla 2001, Rodríguez et al. 2021), reducing the number of taxa and densities of meiofauna (Lee & Correa 2005), affecting the trophic structure of benthic communities, being mostly represented by deposit feeders (e.g. *Lumbrineris bifilaris* and *Diastylis tongoyensis*; Lancellotti & Stotz 2004), and decreasing the populations of sessile species on rocky intertidal communities (Fariña & Castilla 2001).
Protected areas	Total number of PA Mean focal PA / Average by neighbourhood	number number	Sea/Earth	Updated August 2019	World Database on Protected Areas	Direct - Large area of PAs, and the proximity to PAs have a positive impact on species richness, taxonomic distinctness, and FD.	● The species response may also depend on their life-history traits and the ability to dispersion larvae in juvenile and adult stages (Micheli et al. 2004).
TURFs	Total number of TURFs Mean focal TURFs / Average by neighbourhood	number number	Sea/Earth		SERNAPESCA	Direct - the proximity to TURFs has a positive impact on species richness (Gelcich et al. 2008b), taxonomic distinctness, and FD.	● TURFs positively impact the recovery of benthic target-species populations strongly overexploited in the past, such as the gastropod *C. concholepas* (Gelcich et al. 2008b). ● An increase in species abundances, body size, and recruitment of benthic invertebrates is observed inside these areas (Castilla et al. 1998, Gelcich et al. 2008b).

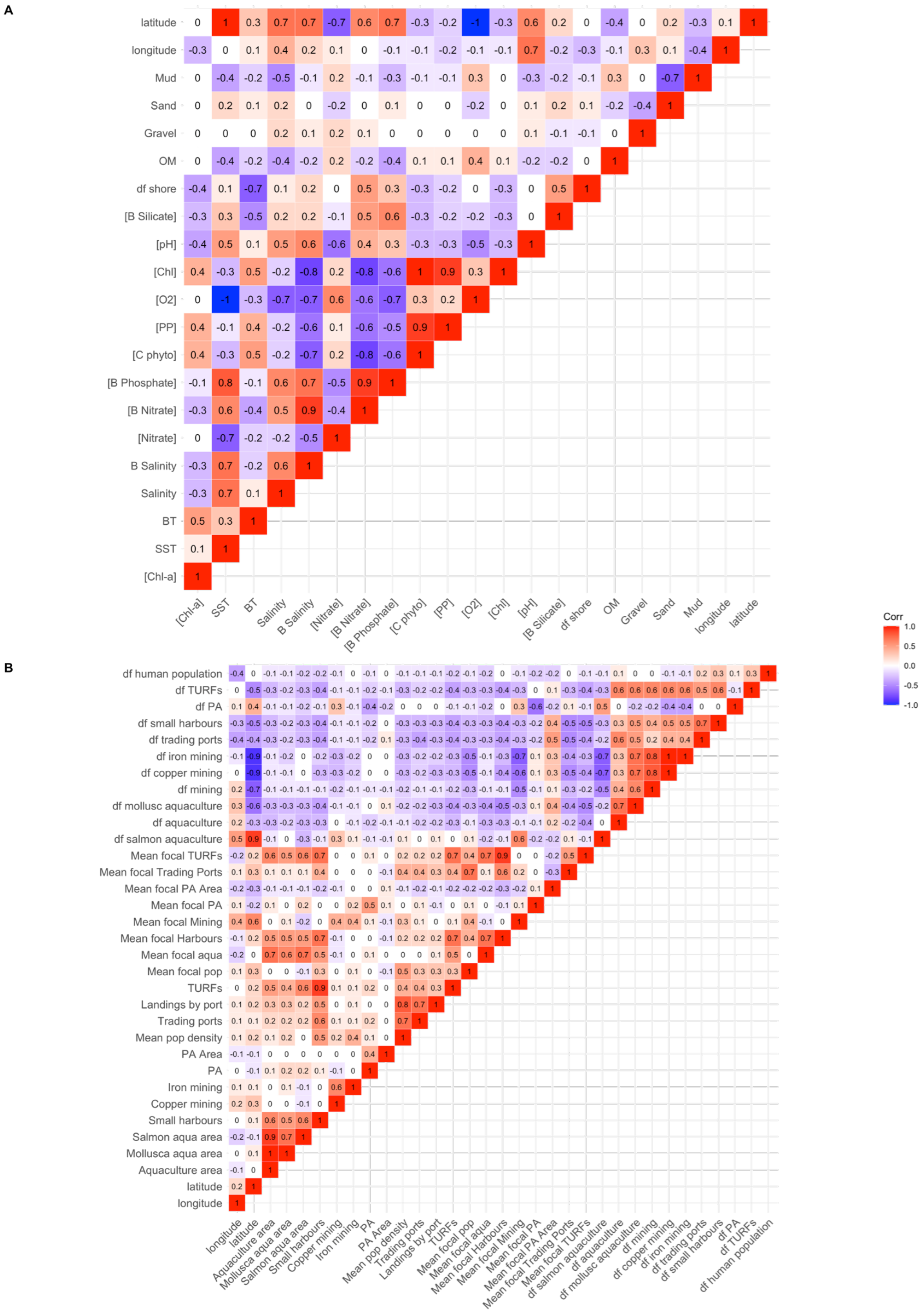

Figure S3. Pearson correlation between A) environmental variables and B) human activities.

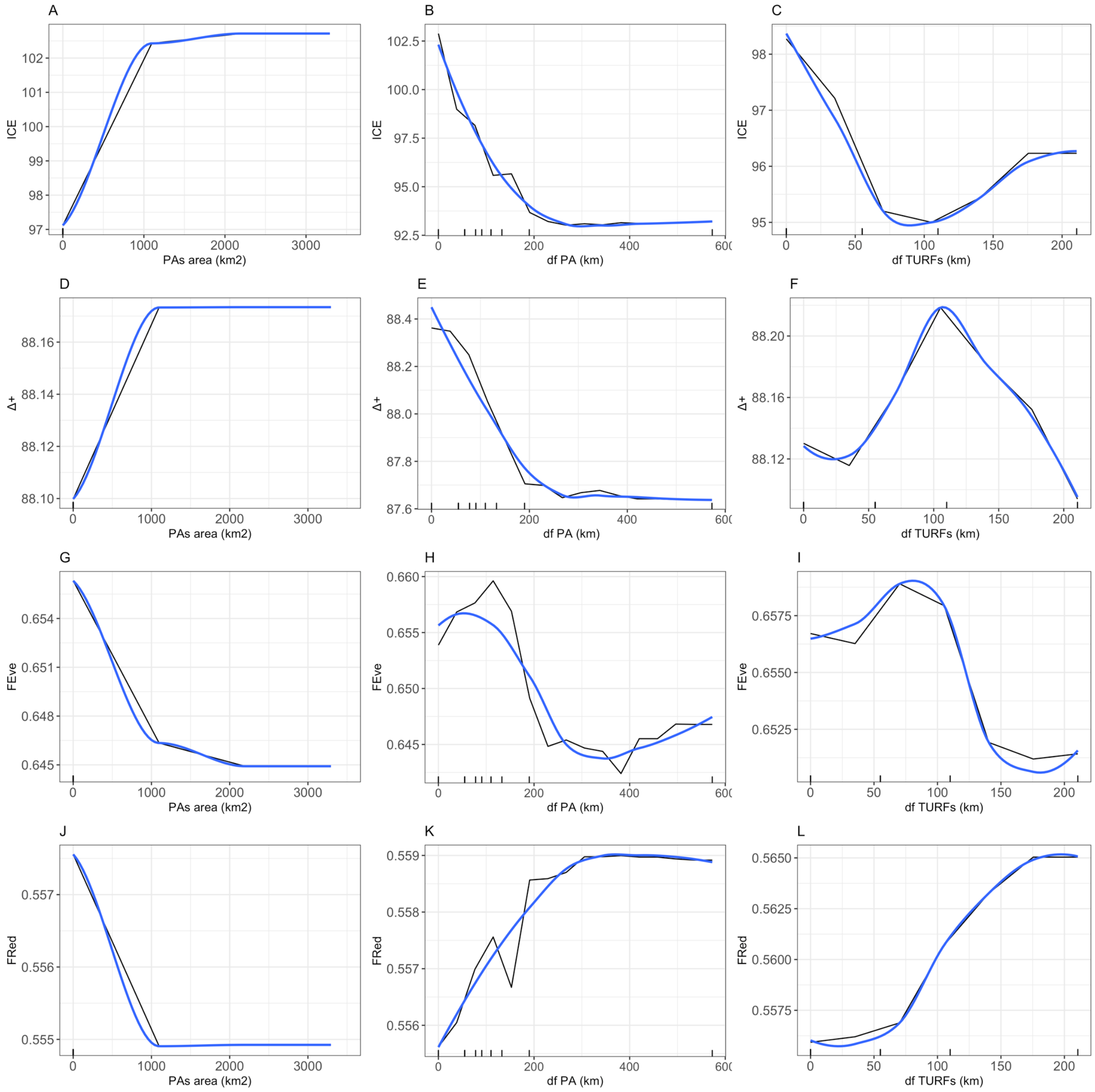

Figure S4. Partial dependence plots showing the model predictions (black lines) for the four diversity metrics: A, B, C) Incidence Coverage - Based Estimator (ICE); D, E, F) Taxonomic Distinctness (Δ^{+}); G, H, I) Functional Evenness (FEve); J, K, L) and Functional Redundancy (FRed) in relationship with measures of conservation such as Protected Area - PA (Terrestrial + Marine Protected Areas) and Territorial Use Rights for Fisheries - TURFs (TURFs + MEABR), in terms of the total PAs area, and the distance from (df) PA and TURFs. The blue line represents the smoothness of the model prediction.

Appendix S6: List of projects carried out by S. L. Marin at the University Austral de Chile related to AMBI.

Marin, S. L. (2022). Validation of a public-private environmental management model for AMBI biotic index incorporation (AZTI Marine Biotic Index) in the monitoring and environmental assessment of aquaculture projects related to soft bottom subtidal ecosystems in Chile. Fondef IT.

Marin, S. L. (2016). Information survey on soft-bottom subtidal benthic communities and characterization of their environmental condition using biological indices (AMBI) and physical and chemical variables in the southern zone (1st stage). Levantamiento de información de las comunidades bentónicas submareales de fondos blandos y caracterización de su condición ambiental usando índices biológicos (AMBI) y variables físicas y químicas en la zona sur (1ra etapa). Proyecto FIPA N°2016-02, ID 4728 _53_ LQ16.

Marin, S. L. (2014). Benthic macrofauna register and biological indices implementation for environmental assessment of subtidal benthic communities. Elaboración de un catastro de macrofauna bentónica y la aplicación de índices biológicos para la evaluación ambiental de las comunidades bentónicas submareales. Subsecretaría de Pesca y Acuicultura. 4728-50-LP13. 2013-2014.

Marin, S. L. (2013). Institutional management model design for AMBI implementation, "AZTI Marine Biotic Index" in the national aquaculture industry. Diseño de un modelo de gestión institucional para la implementación del AMBI, "AZTI Marine Biotic Index" en la industria acuícola nacional. Proyecto FIC Los Lagos (Fondo para la Innovación y Competitividad Regional). Código BIP 30128372-0. 2012-2013.

Marin S. L. (2013). Environmental Monitoring Proposal for the Mussel Farming Industry. Propuesta de Monitoreo Ambiental para la Industria Mitilicultora. Proyecto FIC Los Lagos (Fondo para la Innovación y Competitividad Regional). Código BIB 30115222-0. 2011-2013.

Marin S. L. (2012). Management tools for the salmonid feeding process leading to improvement of biological conversion factor, final product quality and environmental sustainability. Continuidad del Proyecto Herramienta para la gestión del proceso alimentario de salmónidos conducente al mejoramiento del factor de conversión biológica, calidad del producto final y sustentabilidad ambiental. Proyecto INNOVA CORFO. Código 05CT6PPT-21. 2011-2012.