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RESEARCH ARTICLE

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Limited complementarity of functional and taxonomic diversity in Chilean benthic marine invertebrates

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Abstract

Aim: Patterns of benthic biodiversity at the macroecological scale remain poorly characterised throughout the Chilean latitudinal gradient, in part due to the lack of integrated databases, uneven sampling effort, and the use of species richness alone to quantify biodiversity. Different diversity measures, encompassing taxonomic and functional components, may give us extra information on biodiversity relevant to conservation planning and management. Thus, evaluating the spatial complementarity of these measures is essential.

Location: Coast and continental shelf of Chile.

Methods: The latitudinal gradient of Chile was divided into five ecoregions according to the Marine Ecosystems of the World classification. Using a 55 × 55 km equal area grid, we estimated the incidence coverage-based estimator (ICE), taxonomic distinctness (Δ^+) and three measures of functional diversity: functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv). For each measure, we described spatial patterns, identified hotspots, evaluated hotspot congruence and evaluated complementarity between measures.

Results: Diversity patterns varied between ecoregions and over the latitudinal gradient. ICE and Δ^+ peaked in the Chiloense and Channels and Fjords ecoregions. Δ^+ and FRic present a similar pattern at mid-latitudes. FEve showed a contrary pattern, principally with FRic. Areas with high numbers of hotspots differed spatially according to each metric, and three latitudinal bands were observed. ICE, Δ^+ and FRic were positively correlated, but the hotspot overlap at the grid cell level was more limited.

Main Conclusions: The complementarity between taxonomic and functional diversity measures is limited when we observe the overlap between grid cells representing hotspots. However, some regions are consistently identified as highly diverse, with the Magellanic Province (Chiloense and Channels and Fjords ecoregions) being the most important for the richness, taxonomic and functional diversity of benthos. Confirmation of the importance of this region can help prioritise conservation efforts.

KEYWORDS
benthic marine invertebrates, benthos, biodiversity, functional diversity, functional evenness, functional richness, non-parametric measures, spatial distribution, taxonomic distinctness

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1 | INTRODUCTION

Benthic invertebrates are a dominant component of marine benthic ecosystems, with high diversity in terms of taxonomy, ecology and life histories (Gray & Elliott, 2009; Krumhansl et al., 2016). They contribute to a range of ecosystem functions, which include dynamic processes such as bioturbation, and ecosystem services such as food web regulation, supporting higher trophic levels as secondary producers, contributing to the biogeochemical cycles, waste material recycling and capture of hazardous substances (Cooper et al., 2008; Gray & Elliott, 2009), increasing benthic–pelagic coupling (Stief, 2013) and being economically and nutritionally important for humans (Snelgrove, 1998). They are also sensitive to a range of environmental stressors (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 assessments (Muniz et al., 2005). Understanding how the diversity of marine benthic invertebrates varies in space at a regional scale, including the location of hotspots of diversity, is therefore important for marine spatial planning, including for fisheries management (Santora et al., 2017) and the establishment of Marine Protected Areas (Bundy et al., 2017). At large spatial scales, there is mixed evidence of a general latitudinal gradient in benthic biodiversity; for example, in the Arctic Continental Shelf of Canada (Cusson et al., 2007), in the Atlantic Ocean (Macpherson, 2002), off the United States West Coast (Piacenza et al., 2015) and in the North Atlantic (Renaud et al., 2009). Instead, diversity patterns are more strongly related to environmental heterogeneity in factors including depth, seabed characteristics and productivity (e.g. Ellingsen & Gray, 2002; Grebmeier et al., 2015; Piacenza et al., 2015; Thompson et al., 2021), as well as to levels of threat from human activities and climate change (e.g. Duarte et al., 2020; Snelgrove, 2001; Thompson et al., 2021).

Chilean coastal waters are particularly interesting for the study of macroecological patterns in benthic species distributions. They span approximately 4200 km, encompassing 39° of latitude (18°30″ to 57°30″ S; Fernández et al., 2000), forming an ecogeographical gradient with significant variation in temperature, salinity, oxygen, solar radiation and primary productivity, all of which are potential factors driving benthic community structure. The Marine Ecosystems of the World classification (MEOW; Spalding et al., 2007) represents the Chilean coast and continental shelf in two provinces and five ecoregions (Figure 1), with limits based on Chilean research developed by Camus (2001), Fernández et al. (2000) and Ojeda et al. (2000). The first province, the Warm Temperate Southeastern Pacific (from 18.5° to 39° S), is represented by the Humboldtian, Central Chile and Araucanian ecoregions (Figure 1). This province is the area along the Humboldt Current System (HCS) where oxygen minimum zones (OMZs) are present (Thiel et al., 2007). El Niño Southern Oscillation (ENSO) events add interannual variability to the HCS (Escribano et al., 2004) and complicate predictions of ecological processes towards the northern latitudes of Chile (Thiel et al., 2007), driving oceanographic changes such as the intrusion into coastal areas of

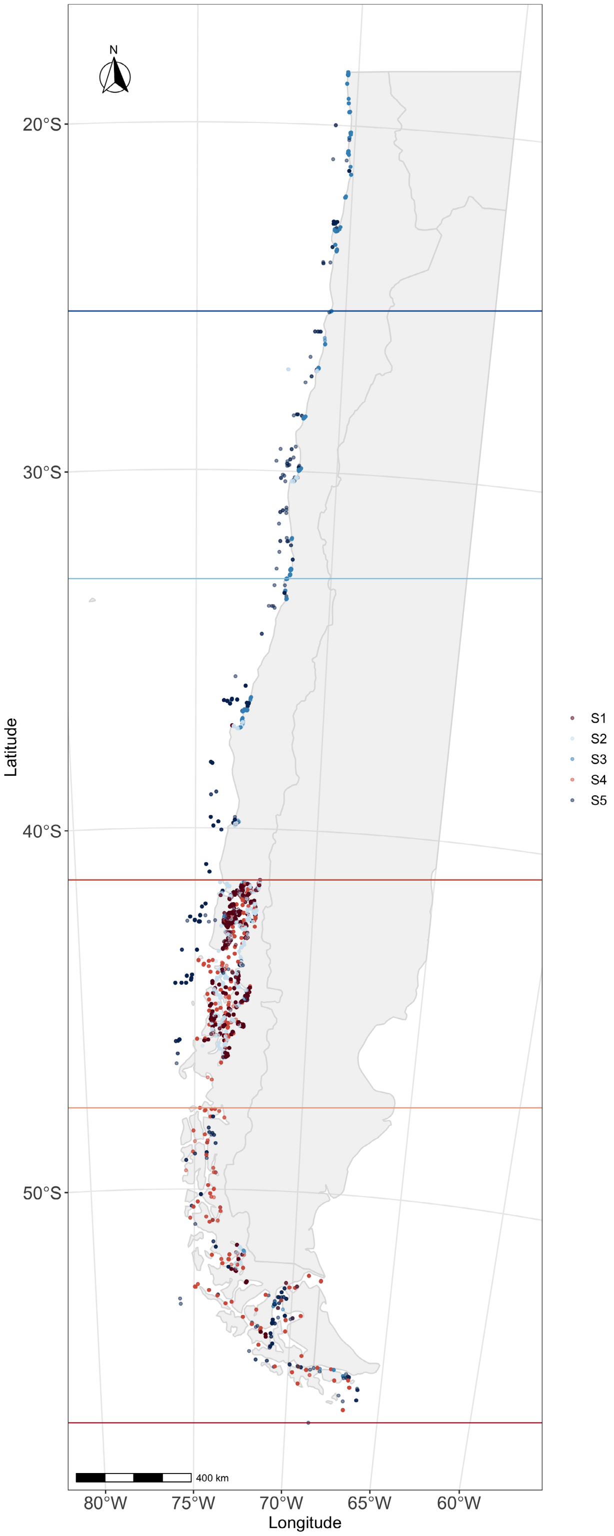

FIGURE 1 Distribution of the occurrences for the five sources of information along the Chilean latitudinal gradient for the period 1991–2017. The five ecoregion's limits and their respective provinces are represented by the lines: Humboldtian, Central Chile, Araucanian, Chiloense and Channels and Fjords ecoregion. Each ecoregion is assigned to one of the two provinces: Warm Temperate Southeastern (WTS) Pacific province and Magellanic Province. Latitude and longitude were projected as Albers Equal Area Conic (ESRI projection 102033).

warmer oceanic water, causing a decrease in the biomass of primary producers, and a positive sea surface temperature anomaly along the Chilean coast (Escribano et al., 2004). Freshwater inputs vary from only two main freshwater inputs from rivers in the extremely arid Humboldtian and Central Chile ecoregions to many rivers and estuaries towards southern latitudes in the Araucanian ecoregion from 35° to 39° S.

The second province, the Magellanic (from 41.5° to 56° S), is divided into two ecoregions: the Chiloense and the Channels and Fjords (Figure 1). This province is composed of numerous islands, fjords, gulfs and basins (Pantoja et al., 2011; Quiñones et al., 2019), is one of the largest estuarine regions (Iriarte et al., 2010), one of the most productive areas in the world (Betti et al., 2021) and has high concentrations of anthropogenic activities including aquaculture, fisheries and tourism (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), generating micro-environments (Aracena et al., 2011) and consequently a heterogeneous or mosaic environment with the capacity of maintaining high biodiversity (Iriarte et al., 2010).

This high diversity of ecoregions results in Chilean marine and coastal ecosystems supporting the world's largest capture fishery (Peruvian anchoveta, *Engraulis ringens*; FAO, 2022). Significant benthic fisheries also exist, which 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. In addition, because the centres of the human population in Chile are coastal, associated activities typically impact coastal ecosystems. These impacts include deposits from copper and iron mining in the northern zone (Lancellotti & Stotz, 2004) and nutrient enrichment resulting from salmon and mussel aquaculture in the channel and fjord systems in the southern zone (Iriarte et al., 2010; Mayr et al., 2015).

Overall, the highest diversity of benthic macroinvertebrate species has been observed south of 42° S (Fernández et al., 2000), specifically in the Inner Sea of Chiloe (at around 42° S; Valdovinos et al., 2003). This pattern is not universally observed, and other researchers have found the highest species diversity south of 52° S (e.g. Cañete et al., 2012; Gambi & Mariani, 1999; Rivadeneira et al., 2010), due to the diversity of biotopes and the high environmental heterogeneity. 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. However, since 2000, there has been little progress, and subsequent studies have been limited in terms of the factors examined (e.g. 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., 2010). Mollusca, Annelida and Crustacea are the best-represented taxa according to the most complete benthic invertebrate species data compilations in Chile (e.g., Lancellotti & Vasquez, 2000). Patterns of diversity appear to differ between these groups, with the diversity of polychaetes and molluscs peaking between 39° and 41° S (e.g. Hernández et al., 2005; Lancellotti & Vasquez, 2000; Valdovinos et al., 2003) and between 51° and 53° S in soft bottom sediments, whereas the diversity of peracarida increases poleward (Rivadeneira et al., 2010). The species richness of herbivores, on the other hand, peaks between 30 and 32° S, decreasing towards northern and southern latitudes on rocky shores (Rivadeneira et al., 2002).

An additional shortcoming of previous studies is that they rely on species richness to quantify diversity patterns. While species richness remains the simplest and most frequently used measure of biodiversity (Johnston & Roberts, 2009), it is highly influenced by sampling effort, and the highest species richness will be observed in localities that are most intensively surveyed (Clarke et al., 2007; Clarke & Lidgard, 2000; Miloslavich et al., 2011). In general, differences in sampling effort have hampered the identification of species distribution patterns throughout the Chilean latitudinal gradient (e.g. Häussermann, 2006; Lancellotti & Vasquez, 2000; Valdovinos et al., 2003), and the overall diversity gradient of benthic invertebrate species from north to south (e.g. Hernández et al., 2005; Ibáñez et al., 2009) might be influenced as much by differences in sampling effort (northern latitudes have historically been less well sampled than latitudes south of 39° S) as by real changes in the taxonomic composition and functional structure of benthic communities of marine invertebrates. One clear example of this sampling bias is the creation, since 1995, of an entire research programme to explore the Fjords system through Marine Investigation Cruises in Remote Areas from 41° to 56° S (CIMAR; Silva & Palma, 2006). A similarly extensive research programme does not exist for the northern latitudes. At the same time, 42° to 43° S has also been more intensively sampled than other areas of Chile, in part because it is thought to be a diversity hotspot (Fernández et al., 2000), as well as due to monitoring associated with the increase in aquaculture strongly developed in the area. For instance, two environmental survey programmes related to aquaculture have been carried out since 2001 by the Chilean National Fisheries Service (known in Spanish as SERNAPESCA) and since 2012 by the Fisheries Development Institute of Chile (known in Spanish as IFOP). Both programmes cover the latitudinal gradient where this activity is developed (27° to 54° S); however, the number of sampling sites is directly proportional to the number of farms registered. Of the total of 3256 aquaculture farms registered in SUBPESCA (2023), 66% occur in the latitudinal band between 39° and 45° S, and so this area is also one of the most intensively sampled.

A range of different approaches have been developed to compensate for the effect of varied sampling efforts on estimated species richness (e.g. Chao et al., 2014; Chao & Jost, 2012; Colwell et al., 2012). Typically, these involve methods to rarefy and/or extrapolate species richness to a standardised sample size (Branco et al., 2018). They may also account for the fact that rare species are more difficult to detect than common species and that the number of rare species in a sample carries useful information about the number of undiscovered species (e.g. Branco et al., 2018; Chao & Chiu, 2016; Colwell & Coddington, 1994; Magurran, 2004). An example of such a measure is the incidence-based coverage estimator (ICE; Chao & Lee, 1992), which separates species based on their frequency of incidence within sampling units (Chao & Chiu, 2016; Magurran, 2004). However, these measures of diversity neglect information on species identity and how the role of species in a community may vary along an environmental gradient (Cadotte et al., 2011; McGill et al., 2006). A simple way to address this is to use taxonomic identity. Clarke and Warwick (1998) defined taxonomic distinctness as the average taxonomic relatedness of all species within a community. More formally, taxonomic distinctness is the average distance between all the species pairs in a community, where interspecies distance is the number of taxonomic 'steps' linking a species to any other, used to approximate a phylogenetic tree (Clarke & Warwick, 1999). To the extent that taxonomic distinctness is an effective proxy of phylogenetic (i.e., evolutionary) diversity (e.g. Rivadeneira et al., 2010), it may explain more about the key mechanisms determining ecosystem functioning than species richness alone (Srivastava et al., 2012).

A more direct way to quantify the differences in species roles within an ecosystem is to consider their functional traits (Ricotta & Moretti, 2011; Villéger et al., 2010), defined as the biological attributes influencing the performance of the organisms (Bremner et al., 2003; Violle et al., 2007). The traits of species can be combined into indices of functional diversity (FD), which in turn can be decomposed into three main components: functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv; Mouchet et al., 2010; Villéger et al., 2008). Each component represents how the species in a community fill functional trait space (Schleuter et al., 2010; Villéger et al., 2008). A high FRic indicates that the volume of functional trait space occupied by the species in a community is large; thus, species with more extreme traits occupy a larger volume of functional trait space (Villéger et al., 2008). High FEve indicates a more even distribution of species in functional space, which may be associated with better use of available resources and more productive communities (Mason et al., 2005). High FDiv may indicate communities with low competition for resources (Mason et al., 2005). While FEve and FDiv are independent of species richness (Mason et al., 2005; Villéger et al., 2008), species richness is expected to be related to FRic (Mason et al., 2008). Because the three components of FD may have different responses to the same perturbation (Legras et al., 2018; Schleuter et al., 2010), considering FD in this multifaceted way is useful for observing the real impact of perturbations on biotic communities (Villéger et al., 2010), including their consequences for 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. species richness, taxonomic and/or phylogenetic diversity) remains scarce (Hultgren et al., 2021), and few studies test whether areas of high species diversity are also functional hotspots (Törnroos et al., 2015). This is important 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; Pardo et al., 2016). Thus, estimating congruence between hotspots of different dimensions of diversity is a first step to formulating more complete conservation policies. At the same time, 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 (Dimitriadis & Koutsoubas, 2011). Although historically, diversity priority areas have been defined by the high concentration of endemic species, high species diversity and areas with high vulnerability to species loss (Myers et al., 2000), new hotspot definitions have been included as spatial planning tools, e.g. hotspots of multiple trophic levels to conserve fisheries (e.g., Santora et al., 2017) and hotspots of functional groups to define Marine Protected Areas (e.g., Bundy et al., 2017). Thus, identifying the location of FD hotspots in the latitudinal gradient of Chile may provide new information to be used in conservation planning.

In this study, we evaluate simultaneously spatial patterns of benthic diversity quantified using species richness, taxonomic diversity and functional diversity along the natural latitudinal gradient of Chile. We hypothesise that these diversity measures have different latitudinal patterns and, consequently, that there is limited complementarity among the diversity hotspots identified by the different metrics. To test this, we compiled a new database from three Chilean environmental surveys and one research cruise, together with species occurrence records from the Ocean Biodiversity Information System (OBIS, 2022), for the Chilean coastline and continental shelf. We divided the Chilean continental shelf into the five ecoregions described by MEOW (Spalding et al., 2007). Using a 55 × 55 km equal area grid, we estimated taxonomic diversity through the nonparametric measure ICE and taxonomic distinctness. In addition, we compiled a new database of quantitative and qualitative (response and effect) biological traits and used these to estimate functional diversity using the three components of FD, FRic, FEve and FDiv metrics in benthic marine invertebrate communities. Using this new data compilation, we first describe spatial patterns of species richness (ICE), taxonomic distinctness and functional diversity throughout the Chilean coastal and continental shelf environments. Then, we identify hotspots and evaluate their congruence. Finally, we assess spatial complementarity in diversity as estimated by species richness, taxonomic distinctness and functional diversity.

2 | METHODS

2.1 | Benthic biodiversity database

We constructed an integrated and georeferenced database of benthic marine invertebrates, hereafter 'benthos', of Chile from five sources of information: three environmental monitoring surveys of human activities associated with coastal areas and aquaculture in Chile (S1, S2 and S3), supplemented with research data from cruises of marine investigation in the Austral Zone of Chile (S4), and data from OBIS (the Ocean Biodiversity Information System, S5), a global database of standardised and georeferenced information on the occurrences of marine species (OBIS, 2022). Because not all constituent datasets included information on biomass or abundance, we recorded species occurrences only, which will also be more robust to variation in sampling methodology. We used only occurrences identified at the species level, and we excluded records flagged as juveniles and parasitic species. Taxonomic names were standardised across datasets using the World Register of Marine Species (WoRMS Editorial Board, 2023), via the online Taxon Match tool (http://www.marinespecies.org/aphia.php?p=match). None of the four Chilean sources of information had previously contributed invertebrate data to OBIS; consequently, the main database did not include duplicated information.

Any aggregated database has biases that could affect biodiversity estimations. For example, different data sources used different sampling devices (e.g. Van Veen grabs, box cores, Aggasiz trawls and diving; Table S1). Moreover, this sampling information was often unknown for occurrences from OBIS and S4. In addition, some records did not identify the size of the mesh used in sieving organisms from the sediment. Therefore, all organisms in the database were classified as benthos, with no further subdivision into groups. This georeferenced database, like other similar databases, has the issue of imperfect detectability, i.e., lack of the capacity to differentiate between a true absence (a species is not present in an area) and a pseudo-absence (the species is present in an area, but it was undetected) (Edgar et al., 2016). We, therefore, employed methods to account for incomplete sampling (see below).

The data were gridded into equal-area grid cells of 55 × 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 an ecoregion following the Marine Ecoregions of the World (MEOW) classification (Spalding et al., 2007) (Figure 1).

2.2 | Biological trait database

Thirty-five trait modalities, divided into eight biological traits, were selected to describe the ecology and life history of the 762 species of benthos (Table 1). Firstly, we focused on response traits including adult motility, feeding method, maximum body size, reproductive mode, sexual differentiation, larval development (direct and indirect) and development mode (benthic or pelagic). These response traits will respond to the natural variability in the environment (Díaz & Cabido, 2001) across Chile's long latitudinal gradient, for instance, current systems, temperature, salinity and oxygen level. As a complementary trait, we included the effect trait 'ecosystem engineering' (EE). The EE trait modalities were categorised according to the type of bioturbation, whereby the activity of organisms causes physical changes in abiotic and biotic materials, controlling directly or indirectly the availability of resources for other organisms (Jones et al., 1994). The presence of

TABLE 1 Biological traits and their categories.

Traits	Modalities
MBS: Maximum body size (mm)	≤2.5
	2.6–5
	5.1–10
	10.1–20
	20.1–50
	50.1–80
	80.1–100
	≥101
EE: Ecosystem engineering	Biodiffuser
	Upward conveyor
	Downward conveyor
	Regenerator
	Blind-ended ventilation
	Open-ended ventilation
	Reef forming
AM: Adult motility	None
	Low
	Crawler
	Burrower
	High
FM: Feeding method	Predator
	Suspension feeder
	Filter feeder
	Deposit feeder
	Scavenger
ED: Early development	Direct
	Indirect
DM: Development mode	Benthic
	Pelagic
RM: Reproductive mode	Asexual
	Sexual
SD: Sexual differentiation	Gonochoristic
	Synchronous hermaphrodite
	Sequential hermaphrodite
	Hermaphrodite

EE species in an environment may have consequences for nutrient cycling and the rate of exchange of oxygen between sediment and water. Thus, response traits are related to the variation of benthic FD along the natural environmental gradient, and effect traits will capture differences in FD driven by ecosystem processes. Full details about the chosen traits are given in the metadata at Pino (2022).

Information for each trait was obtained mostly from primary sources such as scientific papers and thesis and secondary sources such as books and open source databases, including WoRMS (http://www.marinespecies.org; WoRMS Editorial Board, 2023), Biotic (https://www.marlin.ac.uk/biotic/; MarLIN, 2006) and Polytraits (http://polytraits.lifewatchgreece.eu; Faulwetter et al., 2014). A complete list of references for literature resources is available in Appendix S1. Trait information was collected at the lowest possible taxonomic level, with priority given to data at the species and genus level. The family level was also considered when information from species and genus was not possible to capture, and then professional judgement was used after a deep understanding of the specific family.

A species-by-traits matrix was created using the fuzzy coding approach, 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 (Chevenet et al., 1994). The affinity scores were standardised as frequency distributions by species (Beauchard et al., 2017; Chevenet et al., 1994). Thus, per species, the sum of the modalities of one trait was equal to 1. Its aim was to give the same weight to each species and each trait in the analyses (Van Der Linden et al., 2012) and show full affinity for a modality. The biological trait dataset is available under CC BY 4.0 at Pino (2022).

2.3 | Biodiversity metrics

We used a suite of complementary metrics to quantify and determine matches in spatial patterns in the taxonomic and functional diversity of Chilean benthic invertebrates.

2.3.1 | Incidence coverage-based estimator

Species richness by grid cell was estimated using the incidence coverage-based estimator (ICE; Chao & Lee, 1992). Estimating ICE requires the incidence-based frequency (i.e. the number of times that one individual species was found in a grid cell), 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). We used the cut-off value of 10 as recommended by Chao and Chiu (2016). ICE was obtained using the function ChaoSpecies() in the 'SpadeR' (Chao & Chiu, 2016; Chao et al., 2016) in R (R Core Team, 2021; version 4.1.2).

2.3.2 | Taxonomic distinctness

Taxonomic diversity was estimated using taxonomic distinctness (Clarke & Warwick, 1998) and calculated per grid cell based on the taxonomic hierarchy (i.e. phylum, class, order, family, genus), which was used to calculate pairwise taxonomic distances between each species using the taxa2dist() function in the 'vegan' package (Oksanen et al., 2020). Branch lengths were generated using the default process in the function, where the successive classification levels are divided into equal steps. This was then used to calculate the taxonomic distinctness (Δ^+) per grid cell, using taxondive() in 'vegan' (Oksanen et al., 2020).

2.3.3 | Functional diversity

Functional diversity (FD) was measured using three indices: functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv). A species-by-grid cell matrix using relative frequency was constructed to estimate FEve and FDiv and using presence-absence to estimate FRic. As the biological traits considered in the analyses included both continuous (e.g., maximum body size) and discrete traits (e.g., development mode: benthic or pelagic), we obtained a Gower's distance matrix on the 'species-by-traits matrix' using the function gowdis() in the 'FD' package (Laliberté et al., 2014; Laliberté & Legendre, 2010) in R. The Gower's distance matrix and a species by grid cell matrix were included in the function dbFD(), used to estimate the three FD indices in the 'FD' package. Each index was constrained between 0 and 1.

2.4 | Latitudinal trends in biodiversity

ICE, Δ^+ and FD measures were analysed as a smoothed function of the latitude and the longitude of each grid cell using generalised additive models (GAMs) of the form Diversity measure ~ s(latitude) + s(longitude). Latitude and longitude were included as separate smooth terms, with latitude representing 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 fitted using the 'mgcv' package (Wood, 2017) in R. The F test statistic and its significance, the R^2 and the effective degrees of freedom (edf—an indication of the extent of nonlinearity of the fitted smooth) for each smooth term were all extracted from the model.

2.5 | Hotspots and congruence between biodiversity metrics

Hotspots were determined and mapped as the 10% most diverse grid cells based on each diversity measure. As the definition of hotspots is not strict (e.g., Balletto et al., 2010; Ceballos & Ehrlich, 2006; Thompson et al., 2021), for determining hotspots as the 10%, we considered the total number of 91 grid cells with information on diversity indices along the 39° latitude, the size of each grid cell ($55 \times 55\,\text{km}^2$) and the differences among grid cells per ecoregion (Humboldtian, Central Chile and Araucanian ecoregions, each with 10 grid cells, and 24 and 37 grid cells for the Channels and Fjords and Chiloense ecoregions, respectively).

Venn diagrams were used to observe congruence and complementarity between hotspots identified using the different diversity measures. The diagrams were built with the function ggvenn() in the 'ggvenn' package (Yan & Yan, 2021). To describe the similarity between measures, Pearson coefficients of correlation between species richness (ICE, Incidence Coverage-based Estimator), taxonomic diversity (Δ^+ Taxonomic Distinctness) and the FD measures (FRic and FDiv) were calculated in R.

3 | RESULTS

3.1 | Benthic biodiversity database

Our composite database included data from five geographically complementary sources, together covering the entire latitudinal gradient of Chile between 18° and 57°S (Figure 1; Table S1), with a total of 34,172 species occurrences (i.e. species present at a specific geographical location) acquired between 1991 and 2017 within 110 km from the coast of Chile. It includes occurrences and data on the eight target biological traits for 762 benthic marine invertebrate species, belonging to the phyla Mollusca, Annelida, Arthropoda, Foraminifera, Echinodermata, Porifera, Cnidaria, Bryozoa, Brachiopoda and Nemertea (available under CC BY 4.0 at Pino, 2022).

3.2 | Latitudinal trends in biodiversity

Latitudinal trends in the two taxonomic and three FD metrics are shown in Figure 2. ICE peaked at around 42° and after 52°S, corresponding to the Chiloense and Channels and Fjords ecoregions (Figure 2a; GAM: $F = 6.7$, edf $= 3$, $p < .001$, $R^2 = .2$). Δ^+ peaked at around 42°S in the Chiloense ecoregion and increased poleward after 52°S in the Channels and Fjords ecoregion (Figure 2b; GAM: $F = 5.2$, edf $= 3$, $p = .003$, $R^2 = .4$). FRic peaked at mid-latitudes from 30° to 43°S, corresponding to the Central Chile, Araucanian and Chiloense ecoregions (Figure 2c; GAM: $F = 2.4$, edf $= 3$, $p < .001$, $R^2 = .3$). Lower values of ICE, Δ^+ and FRic were observed in the northern latitudes in the Humboldtian ecoregion and the latitudinal band between 48° and 50°S in the Channels and Fjords ecoregion (Figure 2a–c). FEve peaked in the Humboldtian and poleward after 52°S in the Channels and Fjords ecoregion, and decreased in mid-latitudes in the Araucanian and Chiloense ecoregions (Figure 2d; GAM: $F = 3$, edf $= 2$, $p = .02$, $R^2 = .3$). There was no significant relationship between FDiv and latitude (Figure 2e; GAM: $F = 1.2$, edf $= 1$, $p = .194$, $R^2 = .0$).

3.3 | Hotspots and congruence between biodiversity metrics

Hotspots were defined as the nine grid cells with the highest value for each diversity measure. Seven of nine ICE hotspots were located in the latitudinal band between 42° and 46°S (Figure 3a). Eight of nine Δ^+ hotspots were located between 52° and 56°S (Figure 3b). Seven of nine FRic hotspots were mainly observed between 42° and 46°S, and three were located between 28° and 33°S (Figure 3c). Five of the nine FEve hotspots were located between 48° and 55°S, and two between 20° and 25°S (Figure 3d). Four of nine FDiv hotspots were located between 42° and 46°, and four of nine between 48° and 56°S (Figure 3e).

One hotspot was congruent between ICE and Δ^+, and four hotspots were congruent between ICE and FRic (Figure 4a). Five hotspots were congruent between FEve and Δ^+ (Figure 4b). Two hotspots were congruent between FEve and FDiv (Figure 4d).

FRic was significantly and positively correlated to ICE (Figure S1A; $r = .5$, $p < .001$) and to Δ^+ (Figure S1B; $r = .6$, $p < .001$). FEve was negatively correlated to ICE (Figure S1C; $r = -.2$, $p = .05$). FEve was positively and significantly correlated to Δ^+ (Figure S1D; $r = .3$, $p < .001$). FDiv was uncorrelated with ICE (Figure S1E; $r = 0$, $p = .8$) and Δ^+ (Figure S1F; $r = 0$, $p = .8$). FRic was uncorrelated with FEve (Figure S2A; $r = 0$, $p = .7$). FRic was negatively correlated with FDiv (Figure S2B; $r = -.2$, $p < .05$). FEve and FDiv were uncorrelated (Figure S2C; $r = 0$, $p = .5$). ICE was significantly and positively correlated with Δ^+ (Figure S3; $r = .4$, $p < .001$).

4 | DISCUSSION

4.1 | Latitudinal trends in biodiversity

Our 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. Both taxonomic richness metrics (ICE and Δ^+) peaked at around 42°S in the Chiloense ecoregion and poleward in the Channels and Fjords ecoregion (Figure 2a,b). There is similarity with some functional diversity metrics too: Δ^+ and FRic both increase from the Central Chile ecoregion towards the Araucanian and Chiloense ecoregions (Figure 2b,c), while ICE and FRic show similar latitudinal trends in the Chiloense ecoregion (Figure 2a,c). To some extent, these similarities are expected, given that FRic is influenced by species richness (Mason et al., 2005); however, relationships are not inevitable; for instance, Δ^+ is formally independent of species richness (Clarke & Warwick, 1998). Overall, our results provide further support for the importance of the diversity of latitudes between 42° and 43°S, an area that has been defined as highly

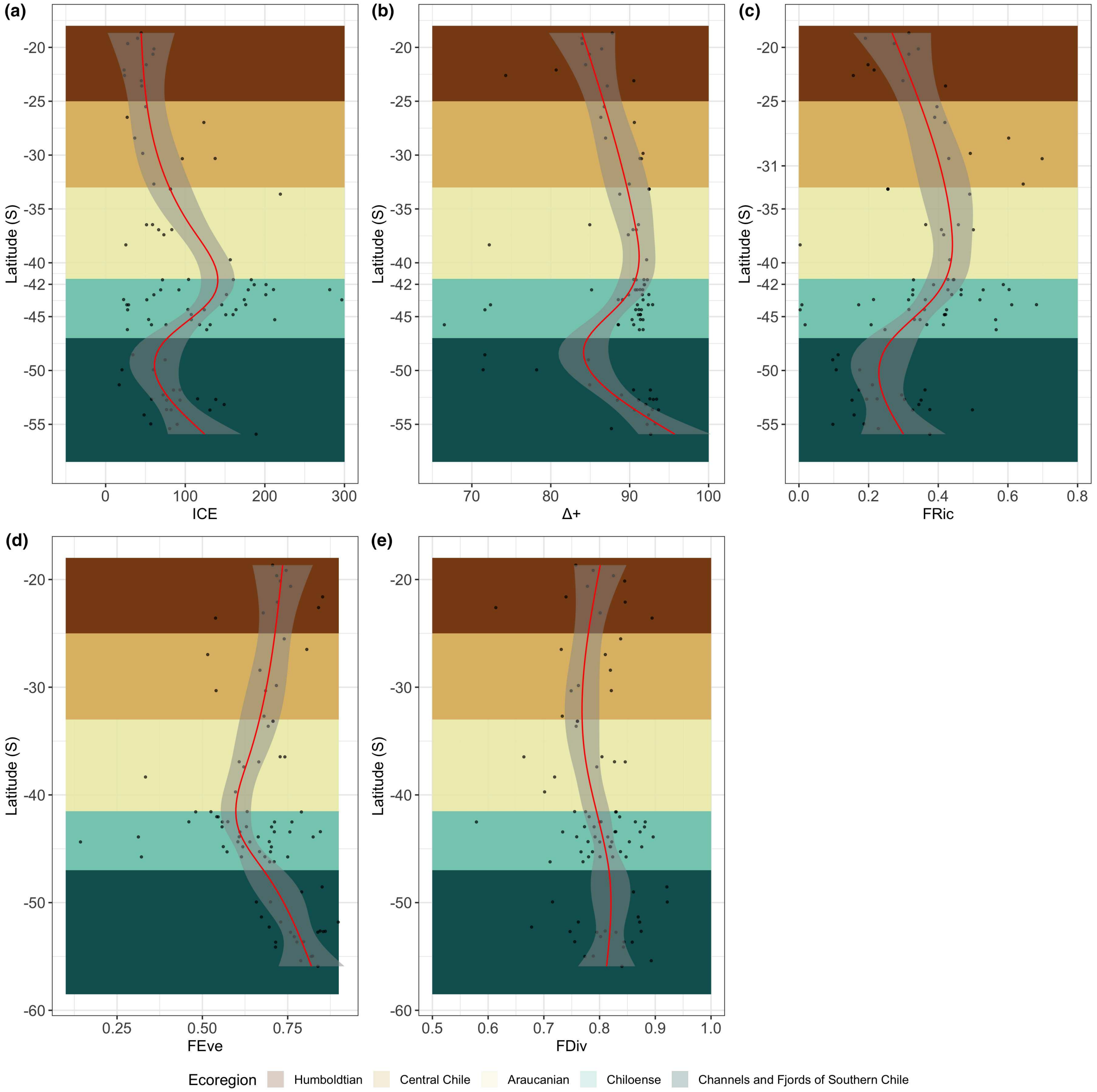

FIGURE 2 The relationship between latitude and (a) ICE—Incidence Coverage-based Estimator, (b) Δ^+—Taxonomic distinctness, (c) FRic—Functional richness, (d) FEve—Functional evenness, and (e) FDiv—Functional divergence. Red line represents the fitted generalised additive model (GAM), with the confidence interval in grey. Dot points represent the values for each taxonomic and diversity metrics.

biodiverse for benthic invertebrates in Chile (e.g., Camus, 2001; Fernández et al., 2000; Häussermann, 2006; Hernández et al., 2005; Villalobos et al., 2021; Zapata-Hernández et al., 2016). Our results show that this finding is robust to different diversity measures, including those that control for sampling effort. However, more complete datasets, with more similar sampling efforts across the entire gradient of Chile, will be needed to fully resolve the debate around how differences in sampling among ecoregions influence estimates of benthic diversity in Chile.

We find different latitudinal patterns for the three FD indices (Figure 2c–e; and no correlation between them, Figure S2), supporting recommendations to measure each component of functional diversity independently and simultaneously (Legras et al., 2018; Schleuter et al., 2010) because they capture different aspects of FD (Mason et al., 2005). FEve showed a contrary pattern to FRic (Figure 2c,d), while FDiv was not consistently related to latitude (Figure 2e). Similar poleward patterns with latitude for FEve and contrary patterns with functional richness have

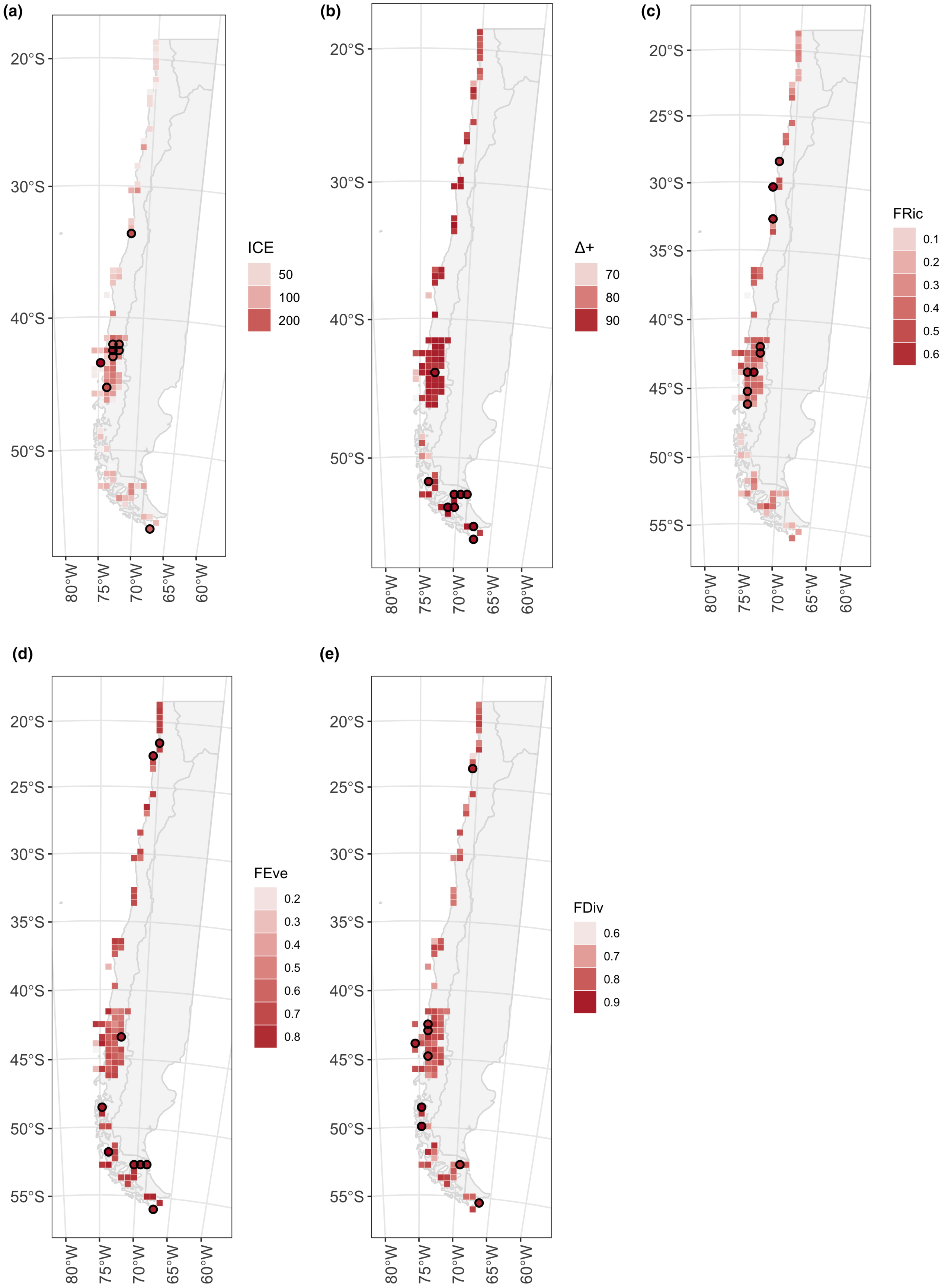

FIGURE 3 Gridded map showing the spatial distribution of each functional diversity metric and the hotspots (defined as the 10% most diverse area for each metric, nine grid cells), indicated through the black circles. (a) ICE—Incidence Coverage-based Estimator, (b) Δ^{+}—Taxonomic distinctness, (c) FRic—Functional richness, (d) FEve—Functional evenness, and (e) FDiv—Functional divergence. Grid cells equal to 55 × 55 km. Latitude and longitude were projected as Albers Equal Area Conic (ESRI projection 102033).

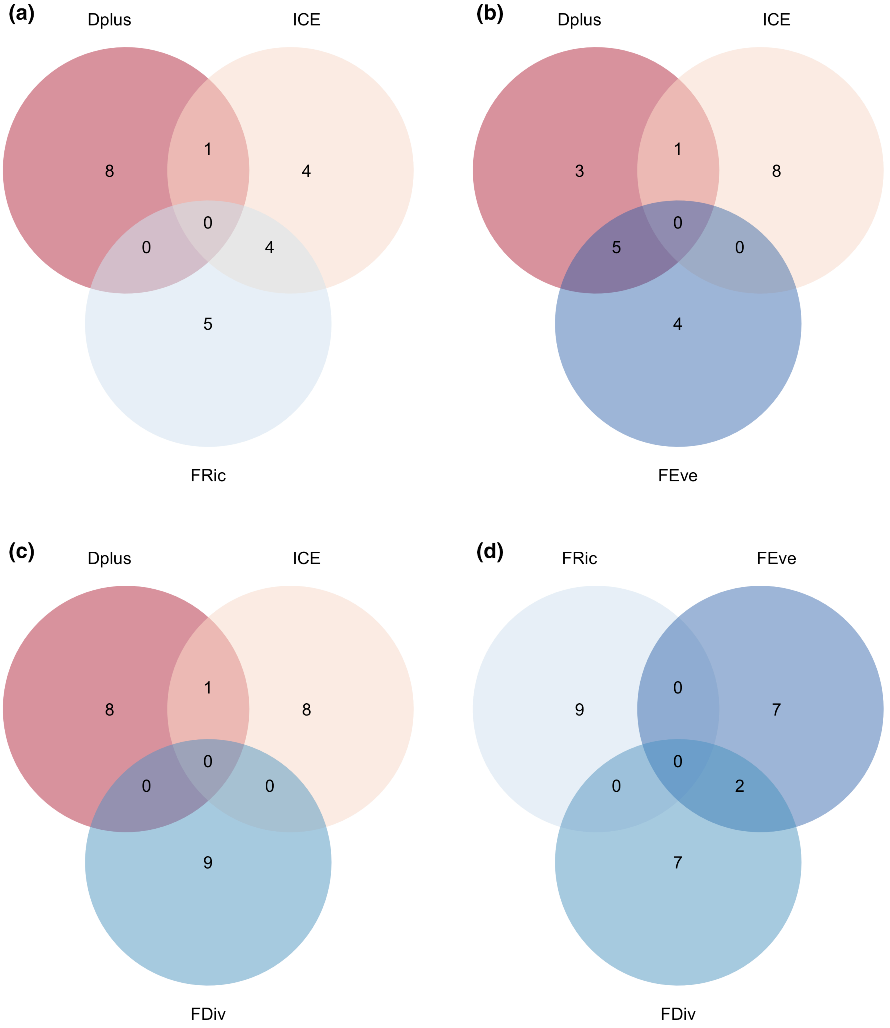

FIGURE 4 (a) Congruence between hotspots of taxonomic diversity Dplus (Taxonomic distinctness), richness ICE (Incidence Coverage-based Estimator) and functional richness (FRic); (b) congruence between hotspots of taxonomic diversity Dplus, richness ICE and FEve (Functional Evenness); (c) congruence between hotspots of taxonomic diversity Dplus, richness ICE and FDiv (Functional Divergence), and (d) congruence between hotspots of FRic, FEve and FDiv.

previously been observed in benthic marine invertebrate communities in both hemispheres (e.g. Berke et al., 2014; Edie et al., 2018; Schumm et al., 2019). Our findings provide further evidence that there may be general global patterns in FEve in benthic communities, and further investigating functional diversity at high latitudes would be a useful focus for future research. Trends in FEve at northern latitudes in Chile (Humboldtian ecoregion) may also provide new impetus to understand the benthic diversity in this area. Benthic diversity in the Warm Temperate Southeastern Pacific Province (Humboldtian, Central Chile and Araucanian ecoregions) has received less attention than the Magellanic Province (Chiloense ecoregion, Central Chile ecoregions), in part because it has been described as poor in species richness (e.g., Carrasco & Moreno, 2006). However, there is evidence that the environmental features and stress conditions such as upwelling centres and OMZs in the area are influencing the functional diversity of their benthic communities (e.g., Bon et al., 2021; Pacheco et al., 2011). Bon et al. (2021) described benthic marine invertebrate communities in the boundaries of the Humboldtian ecoregion inhabiting an upwelling system (23° S) as being composed of a lower number of species, with low to moderate values of FRic, high values of FDiv and moderate to high values of FEve. Specific biological traits present in these communities may indicate adaptations to tolerate the environmental conditions found there (Bon et al., 2021; Pacheco et al., 2011).

In the Humboldtian ecoregion and from 48° to 50° S in the Channels and Fjords, we found lower values of ICE, Δ^+ and FRic, moderate to high values of FEve and high FDiv (Figure 2). This may be driven by benthic marine invertebrates inhabiting these areas responding to the high environmental stress (e.g. OMZs, upwelling systems, ENSO periods in the north and freshwater inputs in the south), leading to communities composed of low numbers of species, occupying small volumes of functional space (low FRic), but highly adapted to the environmental conditions, effectively exploiting available resources (moderate to high FEve) and with little competition for resources (high FDiv; Mason et al., 2005). However, further research focused on defining environmental drivers influencing the benthic communities and identifying the specific biological trait profiles in these ecoregions is needed to determine how different facets of diversity are modulated by environmental filtering.

4.2 | Hotspots and congruence between biodiversity metrics

Areas with high numbers of hotspots differed spatially according to each metric (Figure 3). A first latitudinal band between 42° and 46° S located in the Chiloense ecoregion has the highest number of ICE and FRic hotspots (Figure 3a,c). Δ^+ and FEve hotspots were located in a second latitudinal band towards higher latitudes, south of 48° in the Channels and Fjords ecoregion (Figure 3b,d). FDiv hotspots were mostly distributed between 42° and 56° S (Figure 3e). Finally, a third area is represented by individual hotspots of ICE, FRic and FEve located towards northern latitudes between 22° annnd 33° S, part of the Humboldtian and Central Chile ecoregions.

The first latitudinal band in the Chiloense ecoregion has been widely described as a hotspot of diversity for specific benthic taxa, including Echinodermata and Demospongiae (Lancellotti & Vasquez, 2000), Anthozoa (Häussermann, 2006) and Polychaetes (Hernández et al., 2005). Fernández et al. (2000) argued that the high diversity of marine invertebrates in the area is related to the high endemism of species. Camus (2001) attributed the high species diversity to the transitional zone at 41° to 43° S, where species from zones of higher diversity could advance towards northern coastal areas due to the similarity in environmental features (Montiel et al., 2005). Moreover, these latitudes have highly heterogeneous coastal morphology (Häussermann, 2006), and the influence of the Antarctic circumpolar current divergence into the Humboldt Current and Cape Horn Current creates a high diversity of biotopes forming different habitats available to more diverse benthic communities (Hernández et al., 2005). For example, the presence of ecosystem engineering taxa 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 substrate availability, providing habitats for different taxa (Villalobos et al., 2021; Zapata-Hernández et al., 2016). Spring–summer phytoplankton blooms driving flows of carbon towards the benthos may also support the diversity of taxa, including invertebrates, bony fishes, rays and sharks (Zapata-Hernández et al., 2016).

Hotspots of Δ^+ and FEve were mainly located in the subantarctic ecosystem towards higher latitudes, south of 48° S, in the Channels and Fjords ecoregion, which is highly complex and diverse in habitats and species (Gambi & Mariani, 1999; Montiel et al., 2011). Hotspots of species diversity have previously been observed between 51° and 53° S for polychaetes (Hernández et al., 2005) and at 54° S for Prosobranchia (Cape Horn; Valdovinos et al., 2003) and peracarida (Rivadeneira et al., 2010). Poleward latitudes also represent hotspots of species richness for other species groups, including reptiles, fishes, invertebrates, marine mammals and macroalgae (Fernández et al., 2000; Miloslavich et al., 2011; Santelices & Marquet, 1998). Using Δ^+ as a proxy for phylogenetic diversity, Rivadeneira et al. (2010) related the highest Δ^+ of peracarids in southern Chilean latitudes to the accumulation of older clades, and a higher speciation rate towards southern latitudes of the Pacific Ocean. The authors also proposed that Southern Chile might be a source of evolutionary novelties. Through our findings regarding Δ^+, we support the observation by Rivadeneira et al. (2010); in addition, we argue poleward latitudes may also be a source of functional novelties, where benthic communities evolved to perform a diversity of biological adaptations in front of environmental features.

The individual hotspots of ICE, FRic, FEve and FDiv present in the latitudinal band between 22° and 33° S are located in or near important centres of upwelling in the Humboldt Current System, associated with high levels of nutrients, and high primary productivity, sustaining important pelagic fisheries (e.g. *Engraulis ringens* (anchoveta) and *Trachurus murphy* (jurel); Thiel et al., 2007). This area also has a high diversity of marine mammals, reptiles, fishes and invertebrates (Miloslavich et al., 2011), and was considered by Myers et al. (2000) as a priority for conservation purposes due to its importance for 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 (Fernández et al., 2000). Our findings provide further evidence of the importance of these northern ecosystems—sometimes neglected due to a focus on southern Chilean marine ecosystems—for the marine taxonomic and functional biodiversity of benthic invertebrates.

Relatively few grid cells were identified as hotspots by multiple diversity metrics (Figure 4), with five FEve and Δ^+ hotspots overlapping, as well as four FRic and ICE hotspots. The fact that FD revealed different hotspots from traditional taxonomic measures is in line with work on other taxa, including marine mammals (Albouy et al., 2017), fishes (Stuart-Smith et al., 2013) and sharks (Lucifora et al., 2011). According to Orme et al. (2005), the lack of congruence among hotspots has implications for their use in conservation. In particular, a lack of congruence means that any single measure of diversity cannot be used as a surrogate for diversity in general, and considering different metrics of diversity allows for more holistic spatial planning. This could include, for example, ecoregional conservation planning (e.g., Jorquera-Jaramillo et al., 2012; WWF Chile, 2011), considering the unique environmental, ecological and functional features of different regions.

According to the National Biodiversity Strategy 2017–2030 (Ministry of Environment of Chile, 2018), priority sites for conservation purposes include those areas identified as representative ecosystems of ecological uniqueness. At the ecoregional scale, conservation prioritisation may focus on maintaining the evolutionary and ecological processes generating and sustaining biodiversity, as well as on large habitats resilient and tolerant to long-term and long-scale perturbations (Vila et al., 2022). Our findings are aligned with both definitions, and they may help to identify new areas for conservation purposes, including new hotspots of FD, which might represent zones of 'ecological uniqueness' and representatives of communities inhabiting natural environmental stress, where the diversity of biological traits sustaining ecosystems should be preserved. In particular, we recommend that future conservation prioritisation efforts in Chile focus on: (i) the upwelling system from 20° to 25° S in the Humboldtian ecoregion, an area already described as a priority for conservation for marine vertebrates by Tognelli et al. (2005); (ii) the area around 30° S in the Central Chile ecoregion (see also Myers et al. (2000) and Tognelli et al. (2005)); (iii) 42° to 46° S in the Chiloense ecoregion, where diversity hotspots for benthic invertebrates have previously been defined (Fernández et al., 2000), and where the WWF Chile (2011) has already designed a strategic conservation plan; and (iv) 48° to 50° S and poleward 52° S in the Channels and Fjords ecoregion, where our findings confirm previously identified benthic biodiversity hotspots (e.g., Fernández et al., 2000; Hernández et al., 2005; Miloslavich et al., 2011; Rivadeneira et al., 2010; Santelices & Marquet, 1998; Valdovinos et al., 2003). Smith et al. (2001) emphasised the importance of preserving the total range of populations along different habitats present in an environmental gradient, preserving at the same time the unique traits of these populations and their diversity of adaptive strategies. We agree with these authors that the conservation of entire regions, as recommended previously, is important for the maintenance and generation of biodiversity and facing environmental changes.

We recognise our integrated-georeferenced biodiversity database is not perfect. For example, even though datasets had complementary geographical coverage (Figure 1), some latitudes were better represented than others, with effort mainly distributed along coastal areas. However, all databases present biases concerning the records they include and exclude (Renaud et al., 2009), and issues of methodological differences between constituent datasets (Edgar et al., 2016) as well as imperfect and variable detectability between taxa also impact global databases such as OBIS (OBIS, 2022) and BioTIME (Dornelas et al., 2018). Integrated databases require researchers, government agencies and citizens to share, record, maintain and allow open access to their data. Combining structured and unstructured datasets (e.g. OBIS and local datasets; Thompson et al., 2021) does, however, enable us to obtain a more complete picture of benthic marine biodiversity in time and space. Furthermore, most of the data sources we used (S1–S4) have not been previously used in a study of similar spatial scope, and our work validates their use for research purposes. Our combined database, therefore, provides a pragmatic solution to examining the distribution of benthic diversity in Chile, making the best use of available data.

5 | CONCLUSIONS

Our analysis of a newly compiled, comprehensive dataset of the occurrences of marine benthic invertebrates throughout Chilean coastal and continental shelf ecosystems shows broad complementarity between some taxonomic and FD measures of the diversity of marine benthic invertebrates (in particular, ICE, Δ^+ and FRic), but much more limited complementarity between these and other measures (FEve and FDiv), and there is low overlap in diversity hotspots defined according to the different metrics. Overall, the Magellanic Province (Spalding et al., 2007), composed of the Chiloense and Channels and Fjords ecoregions, is the most important for benthic richness, taxonomic and functional diversity. These findings largely confirm previously documented distributional patterns for Chilean benthos (Fernández et al., 2000; Valdovinos et al., 2003), with no evidence for a simple poleward decrease in diversity; rather, diversity hotspots increase south of 42° S. However, northern latitudes also include important ecosystems and isolated diversity hotspots. These areas should be better represented through the development of local and regional studies and the generation of integrated databases. Importantly, focusing only on species richness would neglect different facets of diversity in less represented areas, such as the northern latitudes of Chile. These conclusions are strengthened by the more comprehensive dataset that we have assembled, reinforcing the importance of preserving, maintaining and sharing diversity data. Finally, the existence of different latitudinal patterns and hotspots between the different diversity metrics supports recommendations to measure each component of diversity independently and simultaneously for a complete picture of the spatial distribution of biodiversity (Legras et al., 2018; Mason et al., 2005; Schleuter et al., 2010).

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13835.

DATA AVAILABILITY STATEMENT

Data used in this study are available in online materials associated with Pino (2022) at https://doi.org/10.15131/shef.data.19195967.v2.

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BIOSKETCHES

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Author contributions: LP and TJW conceived the research question and developed the methodology. LP carried out the data curation, database construction, paper writing, and data analysis. TJW carried out continued revisions to the databases, data analysis and paper writing. Both authors worked on the discussion and conclusions.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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