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Emergent Relationships Between the Functional Diversity of Marine Planktonic Copepods and Ecosystem Functioning in the Global Ocean

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ABSTRACT

Copepods are a major group of the mesozooplankton and thus a key part of marine ecosystems worldwide. Their fitness and life strategies are determined by their functional traits which allow different species to exploit various ecological niches. The range of functional traits expressed in a community defines its functional diversity (FD), which can be used to investigate how communities utilize resources and shape ecosystem processes. However, the spatial patterns of copepod FD and their relation to ecosystem functioning remain poorly understood on a global scale. Here, we use estimates of copepod community composition derived from species distribution models in combination with functional traits and indicators of ecosystem functioning to investigate the distribution of multiple facets of copepod FD, their relationships with species richness and ecosystem processes. We also project how anthropogenic climate change will impact the facets of copepod FD. We find that the facets of FD respond to species richness with variable strength and directions: functional richness, divergence, and dispersion increase with species richness whereas functional evenness and trait dissimilarity decrease. We find that primary production, mesozooplankton biomass and carbon export efficiency decrease with species richness, functional richness, divergence and dispersion. This suggests that ecosystem functioning may be disproportionally influenced by the traits of a few dominant species in line with the mass ratio hypothesis. Furthermore, climate change is projected to promote trait homogenization globally, which may decrease mesozooplankton biomass and carbon export efficiency globally. The emergent covariance patterns between copepod FD and ecosystem functions we find here strongly call for better integrating FD measurements into field studies and across scales to understand the effects of changing zooplankton biodiversity on marine ecosystem functioning.

1 | Introduction

Plankton comprise myriads of floating microscopic organisms that shape the functioning of marine ecosystems (de Vargas et al. 2015). In the plankton, copepods are small crustaceans (i.e., usually 0.2–10 mm) that dominate mesozooplankton communities in terms of abundance and species diversity (Steinberg and Landry 2017; Brandão et al. 2021). They are pivotal players for the biologically driven transfer of carbon from the atmosphere to the deep ocean, a process known as the biological carbon pump (Turner 2015; Steinberg and Landry 2017). Copepods display a spectrum of functional traits and traits trade-offs allowing them to efficiently feed on motile and non-motile microplankton, marine snow, and even gelatinous macrozooplankton (Kiørboe 2011;

Takahashi et al. 2013; Brun et al. 2017). Functional traits are characteristics that control the fitness of organisms and determine their ability to feed, grow, and reproduce (Violle et al. 2007; Litchman et al. 2013). The range and composition of functional traits expressed in a community constitutes the functional dimension of biodiversity: functional diversity (FD; Mouillot et al. 2013). Copepod trait composition determines how mesozooplankton contribute to key functions of the biological carbon pump, such as phytoplankton grazing, secondary production, or the active export of organic carbon at depth (Henson et al. 2019; Brun, Stamieszkin, et al. 2019; Pinti et al. 2023). For instance, large copepods egest large and fast sinking carbon-rich pellets that promote export efficiency of particulate organic carbon to depth (Stamieszkin et al. 2015; Brun, Stamieszkin, et al. 2019). The efficiency of the biological carbon pump partly depends on the amount and the composition of sinking particles (Le Moigne et al. 2016; Nowicki et al. 2022) which are influenced by trait composition and thus copepod FD.

However, the FD patterns of marine copepods have seldomly been measured in situ and over large scales (Becker et al. 2021; Tang et al. 2022; Li et al. 2022) whereas taxonomic diversity patterns are relatively well documented (Rombouts et al. 2010); (Benedetti, Gruber, and Vogt 2023). The spatial distribution of mean trait values in copepod communities is not even in the global ocean, as certain trait combinations are more suitable than others given varying environmental conditions (Brun et al. 2016; van Someren Gréve et al. 2017; Prowe et al. 2019; Benedetti, Wydler, and Vogt 2023; Djeghri et al. 2023). For example, planktonic copepods display larger body sizes in cold-water environments (Campbell et al. 2021). Moreover, strategies that optimize the survival of early life stages, such as sac-spawning, tend to prevail in tropical oligotrophic gyres where cannibalism and carnivory are more prevalent (Kiørboe and Sabatini 1994; Woodd-Walker et al. 2002; Benedetti, Wydler, and Vogt 2023). Many species can display very similar trait combinations and thus perform similar functions, so changes in the number of species or their identity can be uncoupled from changes in FD (Hillebrand et al. 2017; Blowes et al. 2019). Because of functional redundancy, we anticipate that copepods will exhibit FD gradients that diverge from richness gradients, similar to the patterns observed for numerous other marine clades, from reef fishes (Mouillot et al. 2014; McLean et al. 2021; Ferrari et al. 2023), corals (McWilliam et al. 2018), bivalves (Edie et al. 2018) to marine mammals (Albouy et al. 2017; Pimiento et al. 2020). Such studies showed that even speciose communities can be vulnerable to functional loss if functions are only carried by few species in said community (Mouillot et al. 2014; McWilliam et al. 2018; McLean et al. 2021).

Our limited understanding of zooplankton FD distribution limits our capacity to predict how changes in biodiversity affect ecosystem functions across ecosystems (Cardinale et al. 2012). This is a major aspect to address in the context of climate change since the richness and composition of zooplankton will likely be reshuffled (Beaugrand et al. 2015; Benedetti et al. 2021a). Global warming may elicit strong changes in community composition at high latitudes, as warmwater taxa migrate poleward and replace local coldwater taxa along the way (Benedetti et al. 2021a). Yet, it is unknown how such changes will affect zooplankton FD. Therefore, we need to answer the following questions: How do changes in copepod species richness relate to changes in trait diversity? Where are higher levels of zooplankton FD expressed worldwide? Do higher levels of FD promote ecosystem functions such as secondary production or carbon export?

Such ecosystem functions may be positively or negatively related to marine copepod FD and they may be scale-dependent (Chalmandrier et al. 2017; Gonzalez et al. 2020; Suárez-Castro et al. 2022). On the one hand, more speciose communities could harbor a wider range of functional traits (i.e., higher functional richness) enabling copepods to optimize the use of resources to be converted to biomass ("portfolio effect"; McCann 2000). As a result, copepod biomass may increase with species richness and functional richness. On the other hand, production could be mainly carried out by a few dominant species that outcompete less fit species in the community ("mass ratio hypothesis"; Grime 1998). As a result, copepod biomass could scale negatively with the richness of species and traits. If ecosystem functions such as carbon export are influenced by traits distinct from those governing secondary production, then the nature and intensity of their association with copepod FD may deviate from that observed with secondary production (Yan et al. 2023). FD is multi-faceted (Villéger et al. 2008), so these relationships could vary in strength and shape depending on the facet considered (Paquette and Messier 2011; Maureaud et al. 2019; Suárez-Castro et al. 2022). For instance, if the balance between trait combinations matters more to productivity than their absolute number, indices such a functional evenness or functional dispersion should correlate more strongly with ecosystem functions than functional richness (Brun, Zimmermann, et al. 2019; Le Bagousse-Pinguet et al. 2021). Because of functional redundancy, spatial gradients in trait composition may be decoupled from those in taxonomic richness and assemblages with very dissimilar trait composition (beta-FD; Villéger et al. 2011) may achieve similar levels of species richness (McLean et al. 2021; Suárez-Castro et al. 2022). Therefore, integrating beta-FD is crucial to explore the links between copepod diversity and ecosystem functions.

The relationships between copepod FD and ecosystem functions in the global ocean can be explored in two ways. First, direct measurements of ecosystem functions and fine-resolution diversity can be taken simultaneously to measure causal links between variables, using covariance coefficients or structural equation modelling (Gamfeldt et al. 2015; Lehtinen et al. 2017; Maureaud et al. 2019). Despite the substantial progress made in zooplankton field sampling (Lombard et al. 2019; Ratnarajah et al. 2023), such simultaneous and standardized measurements remain too sparse for global scale analyses. Choosing an indirect approach, we leverage the large number of species-level observations (Benedetti et al. 2021a, 2021b) and satellite-based or model-based indicators of ecosystem functioning to diagnose the emergent covariance between the various facets of copepod FD and ecosystem functions (Gamfeldt et al. 2015; Eriksson et al. 2023). We rely on functional trait data and global community matrices given by an ensemble of species distribution models (SDMs; Elith and Leathwick 2009) to estimate patterns of copepod FD for the contemporary and future ocean. Our approach allows to assess how decades of field observations answer the following questions: (i) How do the multiple facets of zooplankton FD relate to the global gradient of species richness on a mean annual scale (Stuart-Smith et al. 2013; Suárez-Castro et al. 2022)? (ii) What is the direction, shape, and strength of the emergent relationships between zooplankton FD and indicators of ecosystem functioning? And (iii) how will zooplankton FD patterns change in the future under anthropogenic climate change (Benedetti et al. 2021a)?

2 | Materials and Methods

2.1 | Copepod Community Matrices for the Contemporary and Future Ocean

We use community matrices that describe the species composition of copepod assemblages worldwide in combination with a functional trait table (see Section 2.2) to estimate multiple FD indices (see Section 2.3). These community matrices were generated by Benedetti, Wydler, and Vogt (2023) based on habitat projections generated by an ensemble of state-of-the art SDMs following the methodology of Benedetti et al. (2021a, 2021b). In short, SDMs were calibrated on a global monthly scale based on species-level presence data taken in the upper 500 m as compiled in the ZooBase dataset (Benedetti et al. 2021a, 2021b). For each species, presences were aggregated on a monthly 1°×1° ocean cell grid following the WGS84 spatial reference system and thinned according to a 100-km radius to remove observations that fell within the same monthly cell. For the 343 species displaying at least 50 different presences, background data were generated following the target-group approach of Phillips et al. (2009). Three types of SDMs spanning various levels of complexity were used to model the species' distributions and account for the main source of uncertainty in SDMs-based studies (Thuiller et al. 2019): generalized linear models (GLM), generalized additive models (GAM) and artificial neural networks (ANN). These SDMs were tuned to fit non-overfitting response curves that describe how each species' habitat suitability (ranging between 0 and 1) varies as a function of the environmental predictors included in the SDMs. Six environmental predictors were used: sea surface temperature (SST; WOA 2013v2), surface photosynthetically available irradiance (PAR), log-transformed surface nitrate concentrations (WOA 2013; Garcia et al. 2014), the excess of nitrate to phosphates relative to the Redfield ratio (N*; Sarmiento and Gruber 2006), the excess of silicate to nitrate relative to the Redfield ratio (Si*) and log-transformed surface chlorophyll-*a* concentration (SeaWiFS). These six predictors were chosen because: (i) they were not collinear at the scale of the occurrence data (Dormann et al. 2013); (ii) they ranked within the top predictors across all species, based on tests of relative importance ranks; (iii) these variables were available for describing the future state of the ocean based on an ensemble of earth system models (ESMs), thus allowing to perform ensemble projections and to evaluate the impact of climate change on FD. Previous work showed that this set of predictors robustly models global zooplankton diversity patterns, and that predictor choice is a minor source of projection uncertainty relative to SDM and ESM choice (Benedetti et al. 2021a, Benedetti, Wydler, and Vogt 2023). All three types of SDMs were calibrated 10 times on different random subsets of 80% the species-level datasets and evaluated against the remaining 20%. Ultimately, 303 copepod species (88% of the 343 initially considered) were robustly modeled and used to construct the species assemblages, one assemblage corresponding to one monthly 1°×1° ocean grid cell. Then, habitat suitability indices (HSI) were projected onto the 12 monthly climatologies of the predictors included in the 30 SDMs. Average monthly HSI was calculated for each type of SDMs and each species to build the ensemble members of contemporary copepod assemblage composition (see Benedetti, Wydler, and Vogt 2023 for a full description). Since the present HSI estimates are derived from occurrence data and not true species concentrations, they should not be interpreted as realized differences in abundances but as presence probabilities.

To estimate the impact of anthropogenic climate change on zooplankton FD, we estimated the composition of copepod assemblages for the future ocean. Future monthly fields of the six environmental predictors were obtained from the projections of five ESMs forced by the IPCC's RCP8.5 scenario from the MARine Ecosystem Model Intercomparison Project (MAREMIP; Sailley et al. 2013) and the Coupled Model Intercomparison Project 5 (CMIP5; Taylor et al. 2012). The future monthly climatologies were obtained from the ESM's projections over the 2012–2100 period and anomalies were computed by subtracting the values of the "baseline" period (2012–2031) to the values projected for the "end-of-century" period (2081–2100). To obtain the final climatologies of the six predictors for the future state of the surface ocean, those anomalies were added to the in situ climatologies used to calibrate the SDMs. The SDMs of the 303 copepod species modelled were then projected onto these future monthly climatologies for each of the ESM separately. This way, we estimate monthly species composition in the future global ocean based on mean species HSI derived from 15 ensemble members (three SDM types and five ESMs).

2.2 | Species Functional Traits and Functional Dissimilarity Matrix

Computing FD estimates requires information about the functional traits of the copepod species modeled. This dataset is fully described in Benedetti, Wydler, and Vogt (2023) and includes the following five functional traits based on the data available from the literature (Table S1): (i) Body size (quantitative continuous) estimated through average maximum female body size (adult stages only) in millimeter; body size is considered a master trait as it impacts all life functions, scales with most physiological rates and influences predator–prey interactions; (ii) trophic group (categorical) which gathers the species based on their preferred food sources to indicate their role in food-web dynamics (although we acknowledge that most marine planktonic copepods are omnivorous); (iii) feeding mode (categorical) which describes the various strategies copepods deploy to detect and capture their prey following Kiørboe (2011); (iv) myelination (binary) which indicates the presence or absence of a lipid-rich myelin sheath around the nerves which enables faster attack or evasive reactions and thus impact feeding and mortality rates (Lenz 2012); and (v) spawning mode (binary) which indicates whether the copepods release their eggs in open water after fertilization (free-spawning) or are carried by females in egg sacs or egg masses (sac-spawning). We underline that these functional trait values are representative of adult stages (i.e., not the nauplii) and correspond to mean values derived from field or lab observations of diverse copepod populations from around the world. The species' trophic groups and feeding modes were fuzzy coded to represent the fact that species can display several feeding modes and trophic groups. Therefore, the final functional trait table encompasses 10 trait dimensions and covers the 303 copepod species retained for the community matrices.

FD indices require a distance matrix that indicates the pairwise functional dissimilarity of copepod species based on their combinations of traits (Mouillot et al. 2013; Benedetti et al. 2016). To obtain the latter, we computed a Gower distance matrix based on the final functional trait table, as the Gower distance can accommodate continuous, binary and categorical traits. We used the *gawdis* R package (de Bello et al. 2021) as it enables us to specify which trait dimensions are fuzzy-coded and belong to the same trait category.

2.3 | Functional Diversity Indices

FD is a multifaceted concept embedding changes in composition within and between assemblages (Mason et al. 2005; Villéger et al. 2011). Consequently, we chose to compute indices that describe the following facets of FD: (i) How much of the total functional space is filled by the composition of each assemblage (functional richness), (ii) how the HSI and/or inferred presences/absences of species are distributed within the functional spaces (functional dispersion, evenness, or divergence), and (iii) how much assemblages overlap in functional space (beta-FD). The FD indices used here are summarized in Table 1 and an extensive description of their computation is given in the Supplementary Methods 1 in Supporting Information.

We computed Faith's index (Faith) as a proxy for functional richness using the Gower distance matrix described above as the functional dendrogram (Faith 1992). Standardized effect sizes of Faith (SES Faith) were calculated to study functional richness patterns that are not biased by differences in species richness (Schleuter et al. 2010). The SES Faith values and p-values indicate where functional richness is significantly higher or lower than the values dictated by species richness alone. SES Faith values <0 indicate that functional clustering occurs due to environmental filtering in the copepod assemblage, whereas values >0 indicate that functional overdispersion occurs (Mikryukov et al. 2023).

To evaluate facet (ii), we computed four complementary FD indices (Mason et al. 2005; Villéger et al. 2008): functional evenness (FEve), functional dispersion (FDis), Rao's quadratic entropy (Rao's Q), and functional divergence (FDiv). Following the guidelines of Mouillot et al. (2021), we calculated those FD indices based on the first four axes of a principal coordinate analysis (PCoA) as these retained a similar level of dissimilarity as the original Gower distance matrix (Figure S1). The position of the copepod species in the PCoA as well as the correlation of the functional traits modalities to the components of the PCoA are shown in Figure S2. Functional richness is more commonly quantified through the FRic index (Villéger et al. 2008) so we made sure that Faith provided similar functional richness patterns as standardized FRic values (Figure S3). We preferred Faith over FRic because it is less sensible to SDM choice and because FRic is only representative of changes in species composition occurring at the edges of the functional space.

To evaluate facet (iii), we compute pairwise beta-FD based on Jaccard's dissimilarity index and the functional dendrogram derived from the Gower distance matrix where each copepod species represents a tip of the dendrogram (Baselga 2010; Cardoso et al. 2014). Each pair of assemblages (A_i, A_j) shows a total trait dissimilarity that corresponds to the sum of the lengths of edges (i.e., species) that are unique to each assemblage-specific dendrogram (Cardoso et al. 2014). Trait dissimilarity can be partitioned into two additive components (Baselga 2010): replacement (hereby: trait turnover) and richness differences (hereby: trait nestedness). For every (A_i, A_j), Trait turnover corresponds to the substitution of branches exclusive to A_i by the other branches with the same total length that are exclusive to A_j. The remaining dissimilarity fraction (Trait nestedness) is equal to the absolute difference between the branch lengths of A_i and A_j (i.e., similar to differences in Faith). Trait dissimilarity values close to 1 indicate that two assemblages display functional dendrograms with very different number of non-overlapping branches. Since these indices are calculated for each community matrix, there are as many trait dissimilarity values as pairs of assemblages. Here, we retained the average values of trait dissimilarity, trait turnover, and trait nestedness. By doing so, we aim to test how environmental filtering structures potential trait composition on a global scale through the selection of niches and whether the traits expressed at high latitudes and upwelling systems are the same (nestedness) or very different (turnover) from those expressed in the tropics and oligotrophic regions. We deemed this method of estimating global copepod beta-FD better suited than comparing assemblages to closely located assemblages only considering the high connectivity of plankton populations at the scale of our study (Jönsson and Watson 2016).

The indices described in Table 1 were calculated for every monthly community matrix representative of the contemporary ($n=36$) and future ocean ($n=180$). We also computed monthly species richness based on the same community matrices to investigate how the facets of FD covary with taxonomic diversity and test if species-rich assemblages are more or less functionally diverse than species-poor assemblages (Stuart-Smith et al. 2013). Since the present species diversity and FD indices are based on community matrices derived from species-level HSI estimates and not realized species abundances, they should be viewed as indicators of potential community composition and thus potential realizations of FD.

2.4 | Proxies of Marine Ecosystem Functioning

We gathered variables describing the spatial patterns of primary production, secondary production, and particulate organic carbon (POC) export outside of the euphotic zone to explore their covariance with zooplankton functional diversity on a global mean annual scale. To assess the covariance of FD with productivity, we used the recent observation-based product of mean annual epipelagic mesozooplankton biomass (MESOZOO, in mmol C m^{-3}) of Clerc et al. (2023). MESOZOO was generated with a habitat modeling pipeline tailored for continuous

TABLE 1 | Summary of the metrics (name, meaning, underlying input data, methodology, and R packages used) used in the present study to estimate the various facets of marine copepod functional diversity (FD).

FD facet	Index	Meaning	Input data	HSI weighing?	Computation method	Main R packages used	References
(i) Functional richness (**fraction of the total functional space occupied by the species assemblage?**)	Faith's index (**Faith**)	Assemblages with higher Faith values are those where the present species represent more distant and more numerous branches on the total functional dendrogram (i.e., more functional volume filled by the assemblage)	Gower distance matrix (Section 2.1) + Community matrices with species' presence–absence data inferred from the species HSI (using the probability threshold that maximizes the agreement between observed and modeled distributions)	No	Sum of the lengths of all those branches of the functional dendrogram that are members of the corresponding minimum spanning path covered by the species constituting an assemblage	*gawdis* v.0.1.5 (de Bello et al. 2021) *picante* v.1.8.2 (Kembel et al. 2010) *ape* v.5.7–1 (Paradis and Schliep 2019)	Faith (1992) Schleuter et al. (2010)
	Standardized-effect-size of Faith (**SES Faith**)	SES Faith values <0 indicate that functional clustering (or functional convergence) occurs due to environmental filtering in the copepod assemblage whereas values >0 indicate that there is functional overdispersion		No	SES Faith were calculated by randomly reshuffling the tips of the functional dendrogram (i.e., the species names) 999 times. The 999 random Faith values provided a null distribution of Faith's index against which observed Faith's index values were compared. The ensuing global monthly SES Faith values and p-values indicate where functional richness is significantly higher or lower than the values dictated by species richness alone		

(Continues)

TABLE 1 | (Continued)

FD facet	Index	Meaning	Input data	HSI weighing?	Computation method	Main R packages used	References
(ii) Functional evenness, dispersion and divergence (**how is the functional space occupied by the species assemblage?**)	Functional evenness (**FEve**)	Higher FEve values indicate that species in the assemblage display similar HSI at equal distances between nearest neighbors in the functional space. Lower FEve values indicate the co-existence of scattered clouds of functional units	Multidimensional functional space obtained by projecting a Gower distance matrix (Section 2.1) into a principal coordinates analysis (PCoA) FD indices based on the first four axes of a PCoA (Figure S1)	Yes	FEve uses the HSI-weighted distances between all species pairs to calculate the minimum spanning tree that connects all said species in the multidimensional functional space (Villéger et al. 2008). Then, FEve measures the regularity of the branch lengths	*gawdis* v.0.1.5 (de Bello et al. 2021) *vegan* v.2.6–4 (Oksanen et al. 2022) *FD* v.1.0–12.3 (Laliberté et al. 2014)	Mason et al. (2005) Villéger et al. (2008) Laliberté and Legendre (2010) Schleuter et al. (2010) Mouillot et al. (2021)
	Functional dispersion (**FDis**) and Rao's quadratic entropy (**Rao's Q**)	FDis and Rao's Q estimate a similar facet of FD. Assemblages with higher FDis and Rao's Q values are those whose species are further away from each other and from the centroid in the functional space (i.e., more specialized species)			FDis measures the mean distance of the species to the centroid of the functional space occupied by the assemblage, using the species' HSI as weighs for the distances Rao's Q computes the variance of trait dissimilarity per species pairs (i.e., similar to a Simpson index) and weighs this variance by the product of the species' HSI		
	Functional divergence (**FDiv**)	Assemblages with higher FDiv values are characterized by higher HSI values at the vertices of their convex hull (i.e., more extreme traits values			FDiv defines the vertices and gravity center of a convex hull in functional space, based of the species present in the assemblage, and then measures the HSI-weighted deviances of each species present to the species' mean distance to that center of gravity		

(Continues)

TABLE 1 | (Continued)

FD facet	Index	Meaning	Input data	HSI weighing?	Computation method	Main R packages used	References
(iii) **Beta-FD** (How do assemblages overlap in functional space?)	Total trait dissimilarity based on Jaccard's dissimilarity index (**Trait dissimilarity**)	Trait dissimilarity values close to 1 indicate that two assemblages display functional dendrograms with very different number of branches that are non-overlapping	Same as Faith	No	Each pair of assemblages (A_i, A_j) shows a total trait dissimilarity that corresponds to the sum of the lengths of edges that are unique to each assemblage-specific dendrogram	*gawdis* v.0.1.5 (de Bello et al. 2021) *picante* v.1.8.2 (Kembel et al. 2010) *ape* v.5.7–1 (Paradis and Schliep 2019) *Phyloregion* v.1.0.8 (Daru et al. 2020)	Baselga (2010) Cardoso et al. (2014)
	Trait dissimilarity driven by turnover (i.e., replacement) (**Trait turnover**)	Trait turnover values close to 1 indicate that total trait dissimilarity is driven by the replacement of branches			For every (A_i, A_j), Trait turnover corresponds to the substitution of branches exclusive to A_i by the other branches with the same total length that are exclusive to A_j		
	Trait dissimilarity driven by nestedness (i.e., differences in trait richness) (**Trait nestedness**)	Trait nestedness values close to 1 indicate that total trait dissimilarity is driven by different number of branches, whatever their identity			Trait nestedness is equal to the absolute difference between the branch lengths of A_i and A_j		

target variables (Knecht et al. 2023) which was trained with the monthly mesozooplankton biomass fields from the MARine Ecosystem DATa (MAREDAT) (Moriarty and O'Brien 2013) in combination with monthly environmental predictors of mesozooplankton biomass (Clerc et al. 2024).

To assess the covariance of zooplankton FD with the productivity of phytoplankton, satellite-based ocean color data (GlobColour) were sourced from the Copernicus Marine Environment Monitoring Service (CMEMS; data.marine.copernicus.eu). We retrieved the level 4-merged monthly concentrations (in mg m^{-3}) of chlorophyll-*a* (CHL-A) and the associated CHL-A concentrations in diatoms (DIATO), dinoflagellates (DINO), haptophytes (HAPTO), green algae (GREEN), *Prochlorococcus* (PROCHL), and prokaryotes (PROKAR), on a 100-km resolution (Xi et al. 2021). We used the monthly fields for the 2003–2022 period not to be biased by years where some months are missing and to match the period for which global NPP estimates are available as well. As the difference between gross primary production and respiration, NPP indicates the rate of biomass accumulation by phytoplankton that is available to zooplankton grazers. We retrieved the standard vertically generalized production model (VGPM) product from the Ocean Productivity website (oregonstate.edu; Behrenfeld and Falkowski 1997). It provides surface NPP estimates based on MODIS observations for the 2002–2022 period, in mg C m^{-2} day^{-1}.

To assess how zooplankton FD relates to the particle size distribution of plankton cells and particles, we retrieved the slope of the power-law particle size distribution (SLOPE) measured from satellite ocean color observations (Kostadinov et al. 2009). SLOPE values increase with the contribution of small cells and particles to the planktonic size spectrum. The GlobColour data, NPP estimates, and SLOPE estimates were re-sampled on the same 1° grid cell as the functional diversity estimates and monthly climatologies were computed based on all the data available.

To assess the covariance of zooplankton functional diversity with the strength and functioning of the biological carbon pump, we further retrieved the model-based estimates of mean annual sinking POC flux (POC FLUX) and mean annual POC export at the base of the euphotic zone (FPOC) of DeVries and Weber (2017) converted to mg C m^{-2} day^{-1}. We used the NPP estimates given by the latter study to estimate the efficiency of POC export fluxes through the E-RATIO (FPOC/NPP) which represents the fraction of POC that is exported below the euphotic zone relative to the initial productivity level. In the analyses below, we retained the VGPM-based NPP estimates as it very similar to the product of DeVries and Weber (2017) (Figure S4). We compared the annual FPOC estimate to the more recent one of Clements et al. (2023) to ensure that the emergent patterns investigated in this study are robust to various large-scale estimates of POC export (Figure S5). The mean annual values of these indicator variables are shown in Figure S6.

2.5 | Analyses

All analyses were carried out in the R coding environment (R Core Team 2021). First, mean annual ensemble values of species richness and FD indices were computed based on all the monthly values available and then mapped to visualize the main spatial patterns of marine copepod diversity for the contemporary period. For SES Faith, the spatial distribution and frequency of significant p-values at a risk of alpha = 0.05 were examined to identify the regions of the global ocean where Faith differs significantly from null expectations. For beta-FD, we computed the ratio between trait turnover and trait dissimilarity to identify the regions where functional traits dissimilarity is driven by trait replacement (i.e., ratio > 0.5). Covariance between species richness and FD indices was evaluated through linear models and second-degree polynomials. We retained the models showing the largest proportion of explained variance (adjusted R^2) based on variance analysis (ANOVA). This way, we investigated how mean annual taxonomic richness influences copepod FD and unveiled which species-rich assemblages also correspond to functionally diverse ones, along more than just one facet of FD (Stuart-Smith et al. 2013; McWilliam et al. 2018). We expected latitude to modulate the relationship between species richness and FD (Stuart-Smith et al. 2013; Benedetti, Wydler, and Vogt 2023). Therefore, we integrated an interaction term between species richness and absolute latitude in the linear models to test whether latitude imposes a strong effect on the covariance between taxonomic diversity and FD. Covariance between Faith and beta-FD indices was also examined to test if: (i) functionally rich assemblages show lower trait dissimilarity because of the co-occurrence of functionally redundant taxa, and (ii) the global gradient in functional richness is driven by trait turnover or rather by trait nestedness.

Second, we studied the covariance of the mean annual values of the ecosystem functioning proxies described in Section 2.4 with our diversity estimates. The same regression-based approaches as above were used. Considering the multidimensionality of the dataset (23 variables), we focused on examining the emergent covariance of species richness and FD indices with MESOZOO and the indicators related to the biological carbon pump (NPP, POC FLUX, FPOC and E-RATIO). To explore the covariance of all variables together, we centered and scaled them to variance (i.e., *Z*-scores computation) and entered them into a principal component analysis (PCA). The ecosystem functioning proxies were used as quantitative supplementary variables and all of them were log10-transformed because they were skewed toward low values, except for SLOPE and MESOZOO. The *Z*-scores were displayed on a heat map to illustrate the covariance structure between the FD indices and the ecosystem functioning proxies.

Finally, we investigated how climate change may impact copepod FD in the future. To do so, we computed the differences between the values of the monthly diversity indices calculated for the end-of-century period and the values calculated for the contemporary period, for each matching combination of assemblages (e.g., future monthly GAM-based assemblages were compared to contemporary GAM-based assemblages). These differences were standardized to the contemporary values to be expressed in relative changes. Then, mean annual ensemble values of these relative changes were computed for each grid cell based on all ensemble members ($n = 180$). Prediction uncertainty was investigated to show where future changes in copepod FD are more or less sensitive to ensemble member choice. The intra-annual variability, SDM-specific variability and ESM-specific variability were quantified and mapped through the standard deviation associated with their mean values.

All mean annual fields of global contemporary copepod species richness and FD as well as their future changes are publicly available at https://zenodo.org/records/14765901 (Benedetti et al. 2025).

3 | Results

3.1 | Distribution of Mean Annual Copepod FD Within and Between Assemblages

Copepod species richness displays a classic latitudinal diversity gradient on a mean annual scale (Figure 1), as extensively documented in previous work already (Benedetti, Wydler, and Vogt 2023; Benedetti Gruber, and Vogt 2023). Richness increases from the poles to the equator, with peaks in the tropical oligotrophic gyres and the eastern Mediterranean Sea and dips in upwelling systems (Figure 1a). More interestingly, we unveil an emergent functional richness pattern that departs from the species richness gradient toward higher latitudes (> 60°; Figure 1b,c). Within the tropical band (0°–30°), the Faith pattern is very similar to the species richness gradient (Spearman's correlation coefficient = 0.94; $p < 0.001$), with peaks in the gyres and dips in upwelling systems. Average richness drops from 104.5 to 68.6 (−34.2%) when moving beyond the tropical band. Meanwhile, Faith shows a much weaker decrease (−2.5%) as annual mean Faith values > 2.8 remain frequent beyond the tropics, especially in the North Atlantic Ocean (Figure 1b). SES Faith patterns show the regions where functional richness is higher or lower than null expectations for equal species richness levels (Figure 1c). We unveil a clear latitudinal gradient in the sign and amplitude of SES Faith values supporting the view that environmental conditions are leading to functional clustering of copepod traits in the tropics by filtering out subsets of the functional space. Mean (± standard deviation) global SES Faith is equal to −1.23 (± 1.66), indicating that most of the ocean shows lower functional richness than null expectations. Indeed, negative mean annual SES Faith values are more widespread (62.5% of ocean cells) than positive ones; they go down to −5.18 and are concentrated in the tropical band. Meanwhile, positive SES Faith values are capped at 1.85% and 99% of these grid cells are located > 32° latitude. Inspecting the *p*-value distributions revealed that most of the negative SES Faith values observed in the tropics are significant, contrary to the positive ones which cannot be reliably separated from null expectations (Figure S7). This means that the tropics show functional richness levels that are significantly lower than what could be expected from taxonomic richness.

We unveil a global gradient in mean annual FEve that is opposite to the gradient in species richness and functional richness (Figure 1d). This means that the copepod assemblages located in the tropical gyres are characterized by scattered clouds of species in functional space whereas assemblages at higher latitudes show more regular distribution of HSI along trait dimensions. Lowest FEve values are found within the tropical gyres (0.34 ± 0.05) and are higher outside of the tropical band (0.55 ± 0.04) and in upwelling systems. Actually, the highest FEve values (> 0.5) are located in those transitional areas between the tropics and the high latitudes (around 40°–45°).

The global FDis pattern is very similar to the species richness pattern (correlation coefficient = 0.89; $p < 0.001$; Figure 1e). Regions showing higher FDis are characterized by copepod assemblages whose species are more spread out in functional space (i.e., co-occurrence of functionally dissimilar species). The highest mean annual FDis values (> 0.32) are also found in the tropical oligotrophic gyres and the eastern Mediterranean Sea and lower values are found beyond the tropics, especially in the North Pacific Ocean and the Atlantic sector of the Southern Ocean. The lowest values (< 0.29) are located near the coasts and in eastern boundary upwelling systems. As expected, FDis patterns are nearly identical to Rao's Q patterns as both indices estimate the same facet of FD (Table 1; Figure S7).

Mean annual FDiv also shows a latitudinal gradient (Figure 1f), but its values only range between 0.84 and 0.90 globally (0.88 ± 0.01). All FDiv values > 0.9 are located at latitudes < 30° and all values < 0.86 are located beyond 60°. However, mean FDiv does not show substantial variations within ($0.89 \pm 3.0 \times 10^{-3}$) and outside the tropical band (0.87 ± 0.01). This means that species HSI values tend to be higher for extreme functional trait values in tropical assemblages, but that extratropical assemblages can also show high HSI values at such extreme portions of the functional space.

The indices estimating facet (iii) of copepod FD highlight where the assemblages with the most dissimilar trait composition are located and whether such dissimilarity is driven by trait turnover or differences in trait richness (Figure 2). Globally, mean annual trait dissimilarity (Figure 2a) ranges from 0.24 to 0.47 (0.31 ± 0.06), meaning that no assemblage shows a completely dissimilar trait composition. Trait dissimilarity follows the opposite gradient to copepod species richness: It increases from the tropics (0.27 ± 0.03) to the poles (mean values > 60° = 0.39 ± 0.03). Its lowest values (< 0.25) are found in the oligotrophic gyres and its highest (> 0.40) are in the Southern Ocean, North Pacific Ocean and near coastal upwelling regions.

We find that mean annual trait dissimilarity is largely driven by trait turnover (Figure 2b–d). Globally, mean trait turnover follows the same gradient as trait dissimilarity (correlation coefficient = 0.97; $p < 0.001$). Mean trait nestedness is restricted to values < 0.10 (Figure 2c) everywhere except in regions of the North Pacific Ocean and in coastal upwelling regions. Trait nestedness reflects differences in trait richness, so it is logically opposite to Faith patterns (Figure 1b). The ratio of trait turnover to total trait dissimilarity confirms the dominance of trait turnover as a main driving process of functional dissimilarity as it is mostly > 0.5 globally (0.76 ± 0.04; Figure 2d). It shows that the contribution of trait turnover is highest (> 0.80) in the North Atlantic Ocean, the Arctic Ocean, and the Southern Ocean.

We here focus on mean annual patterns, but all indices show intra-annual variability which follows the amplitude of seasonal environmental variations seasonality, especially in terms of surface temperatures (Figure S9). The uncertainty in FD indices that is driven by the choice of the species distribution model is

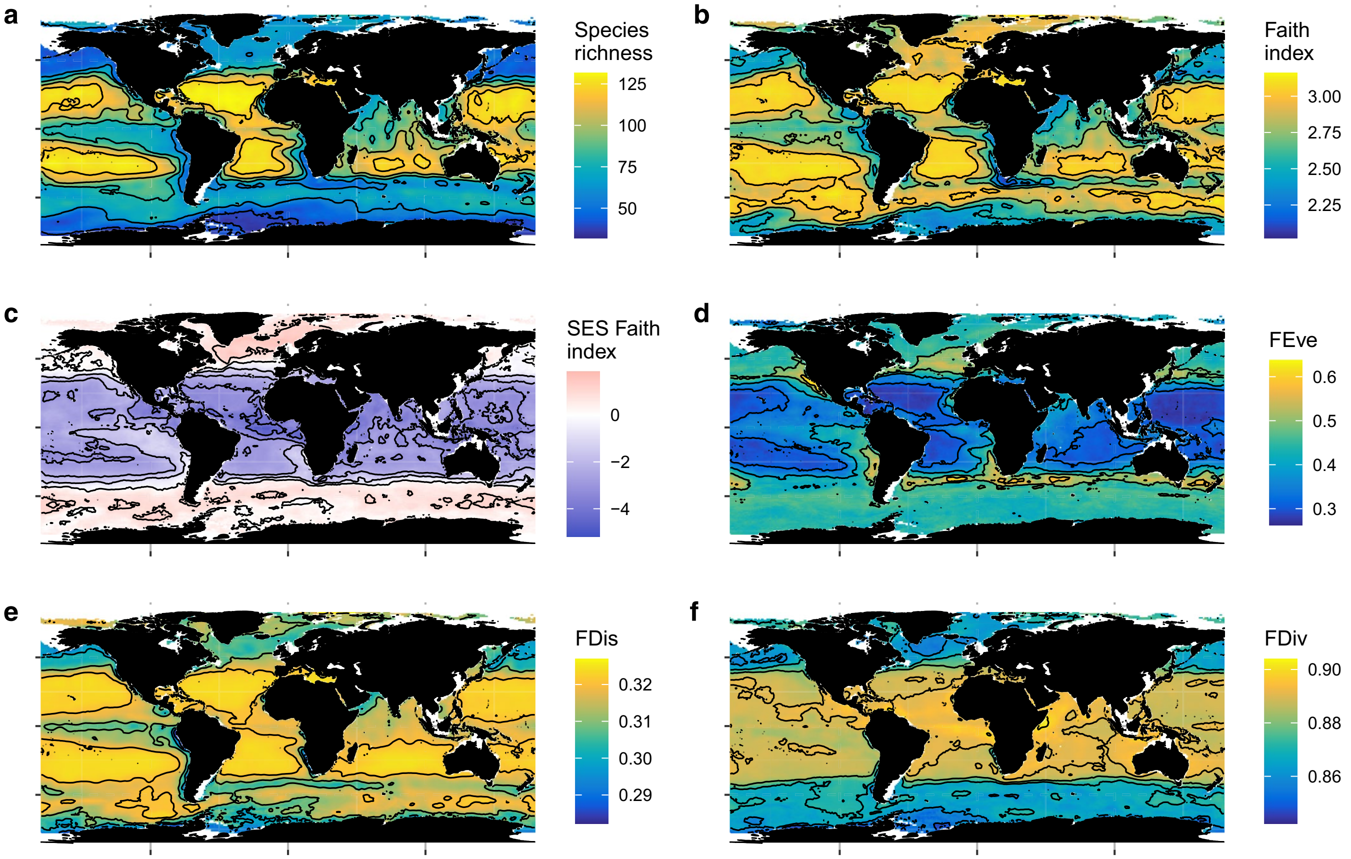

FIGURE 1 | Distribution of contemporary mean annual (a) species richness, (b) Faith index (Faith), (c) standardized effect sizes (SES) of Faith, (d) functional evenness (FEve), (e) functional dispersion (FDis), and (f) functional divergence (FDiv). Faith estimates functional richness. SES Faith measures the difference between observed Faith and null Faith estimates obtained from a randomly assembled community of the species same richness. Species richness and Faith were calculated on presence–absence data whereas FEve, FDis, and FDiv were weighed by habitat suitability indices ranging between 0 and 1 to better represent the distribution of habitat suitability in functional space. Mean annual values are derived from monthly values ($n = 12$) computed for assemblages whose species composition was modeled through three species distribution models. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

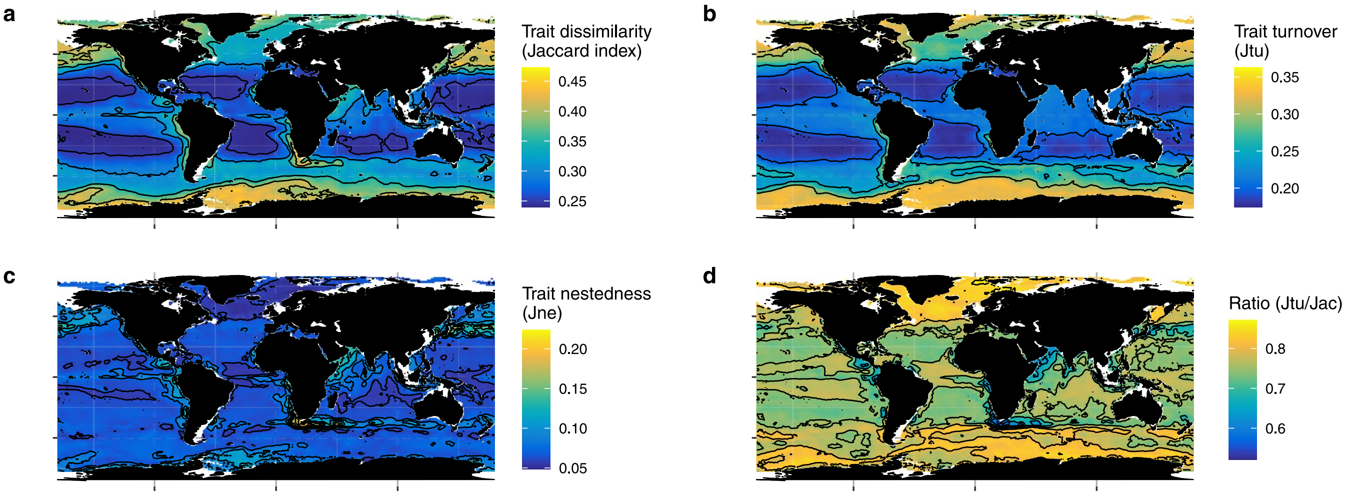

FIGURE 2 | Distribution of contemporary mean annual pairwise (a) total functional trait dissimilarity, (b) trait turnover, (c) trait nestedness, and (d) the ratio between trait turnover and total trait dissimilarity. The beta diversity indices were all computed on presence–absence data and were based on Jaccard's dissimilarity index. Mean annual values are derived from monthly values ($n = 12$) computed for assemblages whose species composition was modeled through three species distribution models. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

of the same order of magnitude as seasonal variations but tends to show a different spatial pattern (Figure S10): Model choice generates more uncertainties toward higher latitudes, especially in the Southern Ocean.

3.2 | Emergent Relationships Between Species Richness and FD

All FD facets show significant but varying responses to an increasing number of taxonomic units (Figure 3). We find that species-rich copepod assemblages are characterized by higher functional richness and more extreme trait values of functionally distant species compared to species-poor assemblages. Mean annual Faith, FDis, and FDiv show significant increases with richness of varying strength (R^2 ranging between 0.57 and 0.74; Figure 3a,d,e). Their relationship to species richness is best described by second-degree polynomials that unveil how the increase rate in Faith, FDis, and FDiv starts leveling off as richness increases. Based on the first derivative of the fitted polynomials, the rate of increase in Faith, FDis, and FDiv decreases by more than 50% beyond richness values > 80.

Mean annual SES Faith, FEve, and beta-FD indices show significant decreases of varying strength with species richness (R^2 ranging between 0.26 and 0.94; Figure 3b,c,f–h). We find that species-rich copepod assemblages are more clustered in functional space (i.e., lower SES Faith and lower trait dissimilarity) and are characterized by less regular and more extreme trait expression (i.e., lower FEve and higher FDis) than species-poor assemblages. The relationship of SES Faith and FEve to species richness is best described by a linear decrease whereas the relationships between the three beta-FD indices and species richness are best described by second-degree polynomials. Again, the latter unveils how the rate of decrease in trait dissimilarity and trait turnover levels off by 50% beyond richness values > 80. The polynomial fit is weakest for trait nestedness ($R^2 = 0.26$) and its rate of decrease with increasing richness is much weaker (from 0.10 to 0.06 only) than trait turnover. Overall, the decrease in trait turnover with increasing taxonomic richness indicates that: (i) species-poor assemblages display more dissimilar functional traits that are not found in species-rich assemblages; and (ii) increasing copepod richness in the tropics does not strongly affect trait dissimilarity because the newly added species often share similar trait combinations with those already present.

Figures 1–3 show that environmental factors associated with latitude have a potentially strong influence on the relationship between FD and species richness. To assess how strongly latitude modulates such covariance patterns, we include an interaction term between absolute latitude and richness in the linear and polynomial models above. We also perform covariance analysis (ANCOVA) to test if this interaction term improves the fit significantly. The strength of all covariance patterns varies significantly with latitude, but less so for FEve and trait turnover. Adding absolute latitude improves the models' fit (all ANCOVA tests return $p < 0.001$) with varying degrees depending on how strong the initial fit was. The adjusted R^2 increased by 53.5% for Faith, 45.8% for SES Faith, 37.0% for FEve, 7.0% for FDis, 26.9% for FDiv, 1.1% for trait dissimilarity, 9.4% for trait turnover and 93.8% for trait nestedness.

3.3 | Emergent Relationships Between FD and Indicators of Ecosystem Functioning

Next, we examine the covariance of species richness and FD with mean annual MESOZOO and a suite of ecosystem functioning indicators (Figure 4; Figure S11). Our analyses show that copepod species richness and FD are promoted under conditions of low primary production, but they do not favor the production of mesozooplankton biomass or POC export efficiency (Figure 4a). However, the latter two seem to be promoted when copepod assemblages display more dissimilar functional trait composition and more even trait expressions. MESOZOO and other indicators related to mean annual productivity and carbon export covary negatively with copepod richness and FD (Figure S11). Phytoplankton biomass (CHL-A), the biomass production of most phytoplankton functional types (DIATO, DINO, HAPTO and GREEN), and the efficiency of carbon export below the euphotic zone (E-RATIO) covary positively with the three beta-FD indices, SES Faith, and FEve, but they vary negatively with copepod species richness, Faith, FDis, and FDiv (Figure S11). Mean annual NPP, PROCHL, and indicators related to POC fluxes at depth show less marked patterns and mainly tend to covary negatively with Faith and SES Faith.

We focus on the most conspicuous patterns to test if copepod diversity has emergent positive or negative effects on zooplankton biomass production (Figure 4b–f). We find that emergent mesozooplankton production is lower in assemblages that display higher functional richness and more scattered species in functional space. Meanwhile, MESOZOO is favored in assemblages where trait expression is more balanced (i.e., higher FEve) and which show less common trait combinations (i.e., higher trait dissimilarity and turnover). Globally, MESOZOO decreases with species richness, Faith, FDis, and FDiv (Figure 4a,b,d,e) but increases with FEve and trait dissimilarity (and Trait turnover; Figure 4c,f). The strongest negative relationship was found for FDis ($R^2 = 0.62$) and the weakest for FDiv ($R^2 = 0.12$). The strongest positive relationship was found for trait dissimilarity ($R^2 = 0.48$). The strength of the covariance with MESOZOO varies significantly with latitude, but less so ($< 10\%$) for species richness, FEve and FDis. Indeed, including an interaction term between the diversity index and absolute latitude improved the fit of the linear models (all ANCOVA tests returned $p < 0.001$), but less strongly than in the previous case. The adjusted R^2 increased by 8.7% for species richness, 34.9% for Faith, 1.5% for FEve, 6.45% for FDis, 67.5% for FDiv, and 23.9% for trait dissimilarity. Finer regional patterns shown in Figure 4 are summarized in the Supplementary Results as well as in Figures S12 and S13.

3.4 | Changes in Copepod FD Under Global Change

We examine how copepod mean annual FD will change in the future as a function of climate change projections averaged over 180

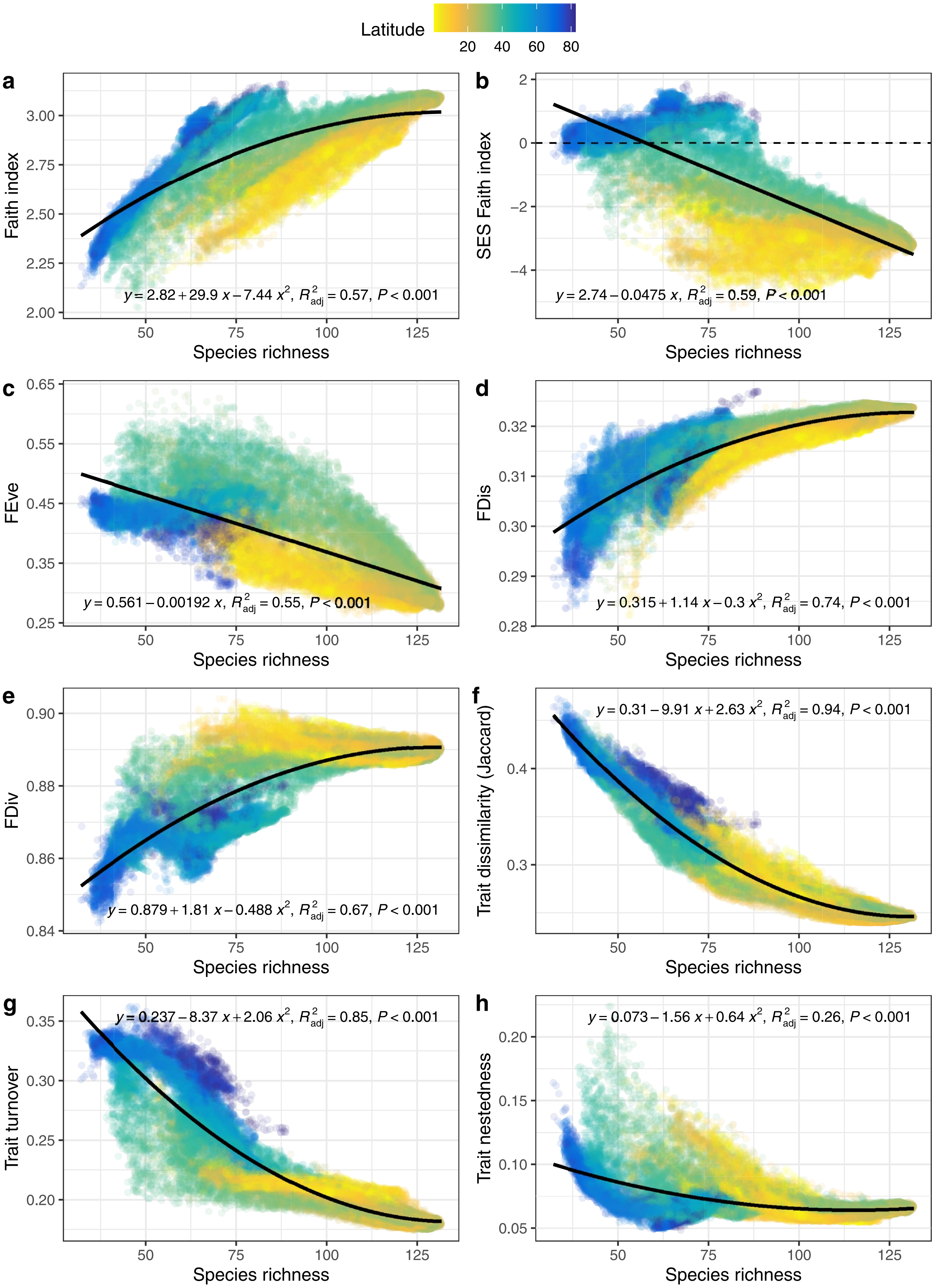

FIGURE 3 | Legend on next page.

FIGURE 3 | Emergent relationships between global mean annual values of copepod species richness and (a) Faith index (Faith), (b) standardized effect sizes (SES) of Faith, (c) functional evenness (FEve), (d) functional dispersion (FDis), (e) functional divergence (FDiv), (f) total functional trait dissimilarity, (g) trait turnover, and (h) trait nestedness. Mean annual values are derived from monthly values ($n=12$) computed for assemblages whose species composition was modeled through three species distribution models. Species richness, Faith, and functional beta diversity indices were based on presence–absence data whereas FEve, FDis, and FDiv were weighed by habitat suitability indices ranging between 0 and 1. Each point was colored as a function of absolute latitude to illustrate where spatial variations have the strongest effects. The statistics of the fitted regressions are given.

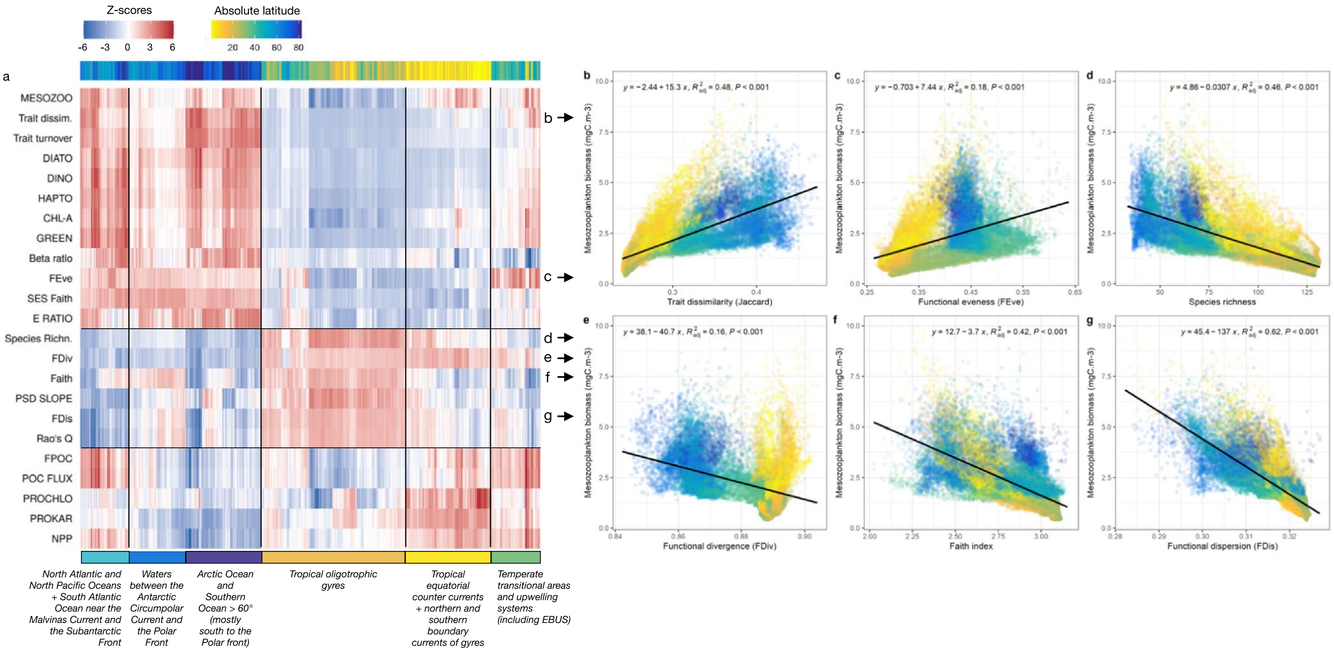

FIGURE 4 | Emergent relationships between global mean annual values of copepod diversity indices and indicator variables of ecosystem functioning based on the (a) *Z*-score profiles (number of standard deviations below or above the annual mean) showing where variables display higher (red) or lower (blue) values relative to the mean. We focus on the most conspicuous patterns enabling us to test the emergent relationships between zooplankton biomass production and (b) total trait dissimilarity, (c) functional evenness (FEve), (d) species richness, (e) functional divergence (FDiv), (f) Faith index (Faith), and (g) functional dispersion (FDis). Grid cells were colored as a function of absolute latitude to illustrate where spatial variations have the strongest effects. The sorting of the variables is based on the similarity of the spatial patterns of the *Z*-scores: Variables on the *Y*-axis are close if they show similar *Z*-scores patterns (according to Euclidean distances). The *X*-axis represents the ocean grid cells (i.e., space). The acronyms are given in Section 2.4, indicators of ecosystem functioning are given in capital letters. The contribution of trait nestedness is inversely proportional to the one of the Beta ratio so it was not shown here.

monthly ensemble members (Figure 5). On a global scale, our ensemble of SDMs predicts average relative increases in species richness (+6.0% ± 9.6; Figure 5a), Faith (+0.7% ± 2.6; Figure 5b), FDis (+0.3% ± 0.7; Figure 5d), FDiv (+0.1% ± 0.4; Figure 5e), but relative decreases in FEve (–2.4% ± 7.8; Figure S6). There is a marked spatial variability in the direction of changes in species richness and functional richness, as relative increases are offset by decreases in specific regions. Indeed, increases in richness are stronger at higher latitudes compared to the oligotrophic gyres (Kruskal–Wallis and post hoc pairwise Wilcoxon tests; Figure S14). Differences in Faith follow a similar spatial trend, but they range mostly between −10% and +10%. Future SES Faith values and their associated p-values show the same distribution as for contemporary ocean conditions (Figure S7), with negative SES Faith values prevailing in the tropical band, except in the coastal upwelling regions, and positive SES Faith values prevailing at high latitudes.

Future changes in FDiv only range ±5% and changes in FDis are even weaker (mostly < ±1.5%; Figure 5d,e). Therefore, these two facets of copepod FD are not severely affected by future changes in oceanic environmental conditions. Meanwhile, changes in FEve are more severe (±30%; Figure 5c) and show marked variations across regions. Copepod assemblages will tend to become more similar in terms of functional trait composition, especially in the northern hemisphere. Indeed, changes in trait dissimilarity are <0 nearly everywhere (Figure 5f). ΔTrait dissimilarity ranges between −5.5% (±3.0) in the tropics and −0.7% (±2.0) for latitudes > 60°. Again, changes in total trait dissimilarity are mainly driven by changes in trait turnover (correlation coefficient = 0.70, $p<0.001$; Figure 5f,g). The contribution of trait nestedness to trait dissimilarity will tend to increase in many regions, especially in the high latitudes of the northern hemisphere (Figure 5h).

The spatial distribution of the uncertainty of our projections in future copepod FD is shown in Figure S15 and are not homogeneous across FD indices. Regions showing weaker changes in future FD are those where ensemble members disagree the most on

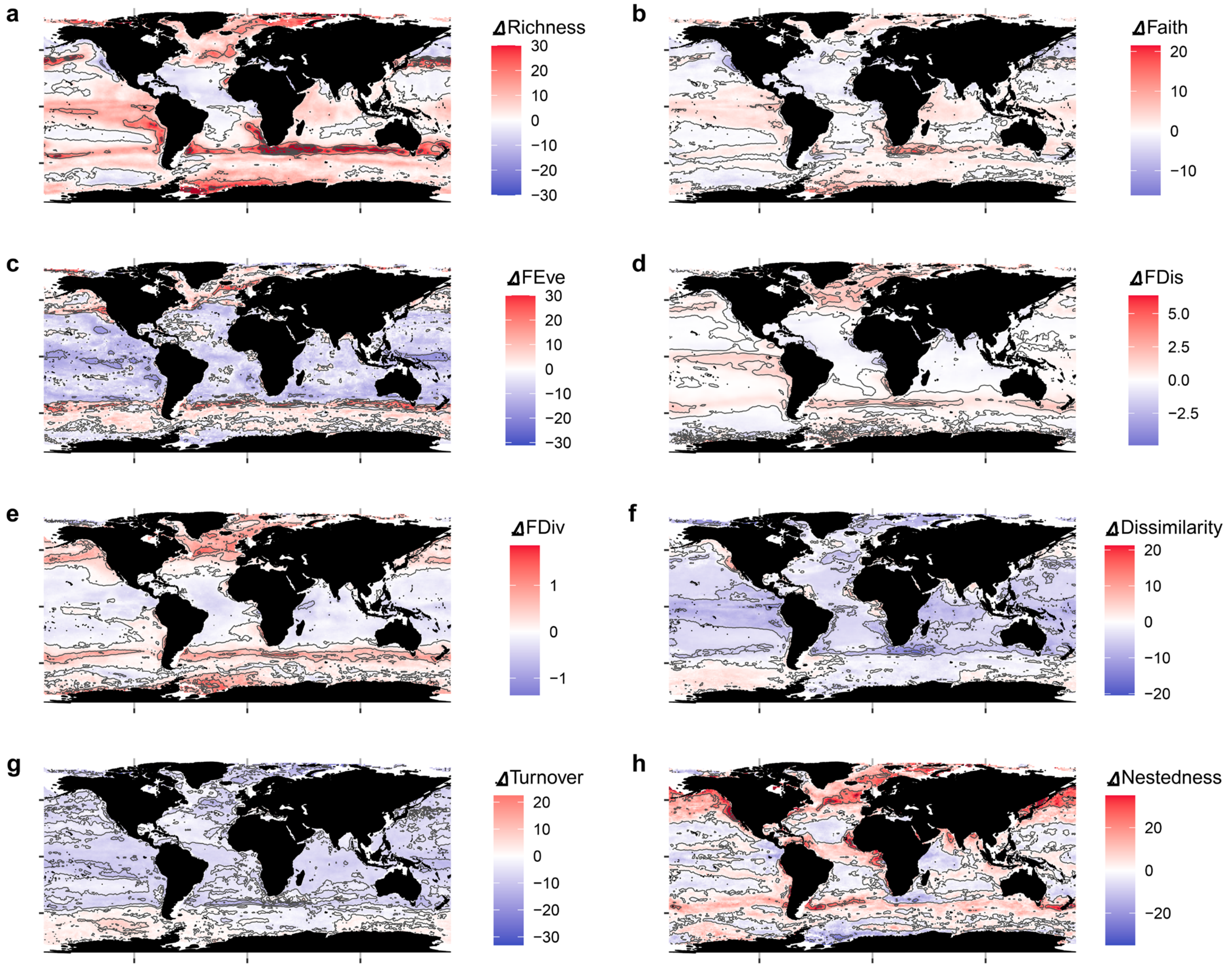

FIGURE 5 | Distribution of the relative differences (Δ, in %) in mean annual copepod (a) species richness, (b) Faith index (Faith), (c) functional evenness (FEve), (d) functional dispersion (FDis), (e) functional divergence (FDiv), (f) total trait dissimilarity, (g) trait turnover, and h) trait nestedness between the contemporary (2012–2031) and end-of-century (2081–2100) periods. End-of-century estimates were based on an ensemble of monthly values obtained for three species distribution models and five earth system models ($n = 180$). Species richness, Faith, and functional beta diversity indices were based on presence–absence data whereas FEve, FDis, and FDiv were weighed by habitat suitability indices ranging between 0 and 1. For (a), (c), and (h), values > 30% are plotted in a darker shade of red. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

the direction of these changes (Figure 5; Figure S16). Usually, less than 75% of ensemble members agreed on the direction of changes in annual diversity depending on the index (Figure S16). However, more than 50% of ensemble members always agreed on the direction of changes in FD across the globe. Previous work showed that this uncertainty is mainly driven by the choice of the SDM, followed by the choice of the ESM (Benedetti et al. 2021a, 2021b).

4 | Discussion

4.1 | Response of Copepod FD to the Global Species Richness Gradient

This is the first study to map marine copepod FD on a fully global scale and to investigate its covariance with taxonomic diversity and proxies of ecosystem functioning. First, we asked how multiple facets of copepod FD changed as a function of increasing taxonomic diversity on a mean annual scale. By doing so, we evaluated to what extent changes in richness translate into changes in FD for marine mesozooplankton. Functional richness, divergence, and dispersion increase with taxonomic diversity whereas functional evenness, trait dissimilarity, and turnover decrease (Figures 1, 2 and 3). These bivariate relationships show different directions, shapes, and strengths. Consequently, species richness should not be viewed as a reliable indicator of all facets of FD and is therefore not sufficient to document changes in zooplankton biodiversity in space and time (Hillebrand et al. 2017; Blowes et al. 2019). The intra-annual variability of our diversity indices is lower than 20% over large parts of the global ocean (i.e., relative standard deviation to mean annual conditions; Figure S9), suggesting that the patterns shown here on the annual scale are representative of the mean state. This first main result implies that field surveys should integrate the various facets of FD to exhaustively monitor zooplankton biodiversity.

The increase in functional richness with species richness is an emergent property that has been documented by previous field studies conducted on smaller scales for copepods (Becker et al. 2021; Tang et al. 2022; Li et al. 2022). We expected to confirm this pattern because our approach covers large environmental gradients that generate richness patterns through environmental filtering (e.g., warmwater taxa are sorted from cold-water taxa; Benedetti et al. 2021a, 2021b). As a result, speciose communities display larger species pools than non-speciose ones, allowing the emergence of more numerous trait combinations and thus higher functional richness (Mouchet et al. 2010; Chalmandrier et al. 2017; Suárez-Castro et al. 2022). This positive relationship was also observed across scales for several groups of marine ectotherms, from bivalves (Edie et al. 2018), corals (McWilliam et al. 2018) to tropical reef fishes (Stuart-Smith et al. 2013; Mouillot et al. 2014; Ferrari et al. 2023). Therefore, the increase of functional richness with species richness seems to be a universal property of marine ectotherms across scales.

More interestingly, previous studies also showed that the rate of increase of reef fish functional richness with taxonomic diversity varies with latitude (Stuart-Smith et al. 2013), a pattern observed here for marine copepods too (Figure 3a,d). Indeed, we find that high latitude systems show steeper increases in functional richness and dispersion than tropical ones. In other words, adding taxonomic units has a stronger effect on functional richness in cold species-poor assemblages than in warm species-rich ones. In a context of global change, cold-water communities will be progressively exposed to the intrusion of warmwater communities (Brun, Stamieszkin, et al. 2019; Benedetti et al. 2021a, 2021b). Therefore, our finding that the zooplankton FD is more sensitive to changes in richness in polar regions than in tropical regions further highlights how exposed polar communities are to future changes in climate and biodiversity (but see Section 4.3 for further discussion).

Tropical regions show weaker rates of changes in copepod FD with increasing richness as a result of functional clustering (or “niche convergence”; Mikryukov et al. 2023): the species progressively added in these assemblages display trait values that are already expressed, thus not increasing the coverage of the functional space. This is supported by the strong decrease in SES Faith with richness (Figures 1 and 3b) which shows how the most species-rich communities from the tropics display significantly lower functional richness than expected. Plus, the strong turnover in traits associated with the global species richness gradient (Figures 2 and 3) shows that some trait combinations are selected only under certain environmental conditions. We rely on models of abiotic habitats, so our zooplankton FD patterns reflect which trait combinations are more competitive than others under varying conditions of temperature and resource availability. Therefore, such functional clustering (i.e., SES Faith <0) emerges as a result of environmental filtering (Freschet et al. 2011; McLean et al. 2021).

Analyzing the maps of community-weighted traits underlying the present FD patterns (see Benedetti, Wydler, and Vogt 2023) as well as the structure of the multivariate functional space (Figure S2) allows to unveil which trait combinations are selected in warm oligotrophic conditions and then progressively replaced by other combinations toward colder and more productive habitats. High latitudes are characterized by higher proportions of larger myelinated current-feeding copepods (Campbell et al. 2021; Brandão et al. 2021). As a result, high latitudes harbor more dissimilar sets of traits (Figures 2, 3 and 4) that are not found in other regions (i.e., larger body sizes, more myelinated taxa and more current-feeding tactics that boost feeding rates; Benedetti, Wydler, and Vogt 2023). Meanwhile, the tropics show higher proportions of small amyelinated carnivorous copepods that rely on cruise-feeding or ambush-feeding tactics. We hypothesize that the copepod communities of these areas are characterized by higher levels of specialization likely driven by the strong competition for resources (de Bello et al. 2013; Kraft et al. 2015). This is supported by the fact that the tropical oligotrophic areas also show the increased levels of FDis and FDiv (Figures 3d,e and 5; Figure S11). These two FD indices identify communities characterized by “extreme” and dispersed trait values occurring at the edges of the overall functional space (Figure S2). Such trait values emerge under enhanced resource competition due to conditions of low food availability, where stress-tolerant species are better adapted to feed. Our results support this view as regions of strongest environmental filtering (i.e., SES Faith <0) and functional dispersion are characterized by conditions of low nutrient availability dominated by small phytoplankton (Figures S7 and S11).

According to this hypothesis, enhanced resource availability should relax the selection of traits due to environmental filtering and enable more balanced trait expression, leading to higher functional evenness in the zooplankton. Our present FEve estimates support this expectation. Contrary to FDis and FDiv, FEve decreases with species richness and the rate of functional clustering (Figure 3). FEve also increases with the turnover in trait composition but peaked right before the latter reaches its maximum (Figures 1, 2 and 4). Copepod FEve peaks in upwelling systems and the transitional areas connecting the warm tropical gyres to the colder high latitudes (Figure 4). Such regions display productive environmental conditions that allow a mixture of taxa from very dissimilar environments and functionally dissimilar communities throughout the year, which promotes balance between dissimilar traits. Further supporting our hypothesis, FEve is higher in those productive environments where multiple phytoplankton functional types co-exist throughout the year, either through asynchronous blooms or co-occurrence (Figure 5; Figure S11). According to our results, the increased concentration and variety of phytoplankton cells (i.e., enhanced resource availability) promotes more balanced trait expression, instead of favoring only a small subset of the zooplankton community.

4.2 | How May Zooplankton FD Influence Ecosystem Functioning?

We then examined the emergent relationships between copepod FD and multiple proxies of ecosystem functioning. By doing so, we tested whether communities with higher taxonomic and/or

FD optimize the use of resources to convert them to biomass ("portfolio effect"; McCann 2000). This hypothesis would be supported by positive relationships between our diversity estimates and productivity-related variables (i.e., MESOZOO, CHL-A, NPP, etc.). Conversely, if biomass production is mainly carried out by a few dominants whose traits are fitter under food replete conditions ("mass-ratio hypothesis"; Grime 1998), we would find a negative relationship between our FD estimates and productivity-related variables. The present MESOZOO estimate is largely derived from field observations of copepod biomass (Strömberg et al. 2009; Clerc et al. 2024), so focusing on copepods to explore the links between MESOZOO and FD is a reasonable assumption.

We found that indicators of primary production, mesozooplankton production, and POC export efficiency decrease with copepod species richness, functional richness, divergence, and dispersion (Figure 4; Figure S11), supporting the "mass-ratio hypothesis." The fact that trait dissimilarity due to turnover shows the opposite trend while decreasing with species richness (Figure 3) further supports this hypothesis: Less speciose communities, characterized by lower FD, are more productive and display traits that are not found in speciose communities (Figure 4). Communities with fewer species characterized by larger body sizes and a higher prevalence of omnivorous and herbivorous current feeders (Benedetti, Wydler, and Vogt 2023; Figure S2) are associated with higher mesozooplankton biomass production and more efficient POC export. These specific traits were shown to sustain more efficient grazing and carbon storage (Kiørboe 2011; Brun, Stamieszkin, et al. 2019) and to promote secondary production (Beaugrand et al. 2010; Brun, Stamieszkin, et al. 2019). The emergent negative patterns between FD and productivity and export efficiency could be driven by a few keystone species, such as the large-bodied Calanidae, whose traits enable larger and faster growth as well as more efficient particles fluxes outside of the euphotic zone, promoting "high production-high export" regimes (Stamieszkin et al. 2015; Jónasdóttir et al. 2015; Henson et al. 2019). Contrary to the diversity indices mentioned above, copepod FEve showed a positive relationship with phytoplankton biomass, MESOZOO and the E-RATIO (Figure 4; Figure S11). This implies that the balance in copepod functional trait composition, on top of high phytoplankton biomasses (Knecht et al. 2023; Clerc et al. 2023), could be key to promote mesozooplankton biomass (Maureaud et al. 2019; Le Bagousse-Pinguet et al. 2021). Yet, FEve is a weaker covariate of MESOZOO compared to species richness, Faith, and FDis (Figure 4c), so this facet of FD may be less important for regulating zooplankton productivity at the scale of our study.

We deem the findings above sensible as they reflect the outcome expected from our current understanding of copepod species traits and ecology. Nonetheless, we cannot draw causal mechanisms between copepod FD and the performance of the biological carbon pump based on our correlative approach. The ecosystem functions studied are driven by a complex interplay of biological and physical factors whose contributions vary in space and time and that we cannot here disentangle from the effects of zooplankton FD (van der Plas 2019; Boyd et al. 2019; Pinti et al. 2023). For instance, POC export efficiency also covaried positively with the contribution of large and mineralized phytoplankton to phytoplankton biomass (Figure S11). Such phytoplankton functional types are also known to favor and POC export efficiency (Tréguer et al. 2018; Henson et al. 2019; Nowicki et al. 2022). Nevertheless, our patterns can point toward the existence of interesting biodiversity–ecosystem functions' relationships that were undocumented globally.

We did not detect a significant covariance between copepod FD and estimates of NPP and POC fluxes (Figure 4; Figure S11). Copepod traits may contribute to regulating the relative amount of NPP that gets exported below the euphotic zone (i.e., E-RATIO), but absolute NPP and POC fluxes may depend more on other important physical and biological factors: the concentration and biomass of zooplankton groups with specific traits, the quantity of large mineralized phytoplankton, the concentration of heterotrophic bacteria, how species interact with one another, or strong mixing events that inject particles below the mixed layer (Henschke et al. 2016; Jaspers et al. 2023; Tréguer et al. 2018; Boyd et al. 2019; Henson et al. 2019; Nowicki et al. 2022). We also acknowledge that export dynamics may be uncoupled from changes in copepod traits in time and throughout the water column (Jónasdóttir et al. 2015; Steinberg and Landry 2017). For instance, members of the surface copepod community whose traits favor POC export can vertically migrate and excrete carbon-rich particles way below the euphotic zone, several months after their initial growth (Jónasdóttir et al. 2015; Pinti et al. 2023). Such processes may weaken the potential imprint of surface zooplankton FD on absolute POC fluxes that we tried to recover through our approach.

Our findings support the existence of mechanistic links between trait combinations and ecosystem functions, reinforcing the pressing need to integrate functional trait measurements in zooplankton field surveys (Ratnarajah et al. 2023). New imaging techniques can simultaneously measure body size, shape, feeding activity, and other relevant traits in an automatized fashion and at the scale of individuals (Orenstein et al. 2022). Through this process, the measurement of FD indices could also be integrated in field surveys to better assess the relative contribution of trait dimensions to services provided by zooplankton across scales, from production to ecosystem stability and resilience to environmental perturbations (Carmona et al. 2016; de Bello et al. 2021).

4.3 | How Will Anthropogenic Climate Change Reshuffle Zooplankton FD?

Global warming may force warmwater zooplankton to migrate poleward, leading to the replacement of polar communities by more tropical ones in time (Benedetti et al. 2021a, 2021b). The effect of these changes in richness in composition on zooplankton trait expression, and thus, ecosystem functioning remains poorly known. As high latitudes display particular trait combinations that are not found in lower latitudes (Figures 2 and 3), the compositional turnover associated with such poleward shifts could lower the functional dissimilarity of copepod communities, which would imply a global functional homogenization of zooplankton, a pattern already observed for fishes (Villéger et al. 2014; Magurran et al. 2015). To test this hypothesis, we explored the response of global copepod FD to anthropogenic climate change based on 180 future monthly projections according to the same ESM simulations as Benedetti et al. (2021a, 2021b).

We find that anthropogenic climate change will have a varied set of impacts on copepod biodiversity, with very weak effects on FDis and FDiv (i.e., Δ values < 5%) but stronger effects on species richness, Faith, FEve, and Trait dissimilarity (Figure 5; Figure S14). Most of the global ocean shows slight (< 10%) to strong (> 20%) projected increases in copepod species richness, which is in line with our previous projections (Benedetti et al. 2021a, 2021b). Since functional richness scales with species richness (Figure 3), regions that will undergo species gains also undergo gains in functions. Yet patterns of FDis, FDiv, and SES Faith (Figure S7) remain relatively unaffected under climate change, suggesting that environmental filtering will continue to act as a strong driver of trait expression in copepod communities (as discussed in Section 4.1). In the future, tropical systems will continue to host more speciose communities characterized by smaller carnivorous and omnivorous active and passive feeders better adapted to food-deplete conditions.

Future decreases in trait turnover are partially set-off by increases in nestedness but not strongly enough to maintain contemporary levels of functional dissimilarity. As a result, trait dissimilarity will decrease worldwide (Figure 5f–h), meaning that high latitude communities are projected to become more functionally even, weakening the global gradient in trait turnover (Figure 5c,f,g). Consequently, anthropogenic climate change may drive functional homogenization among copepod communities, with an increasing prevalence of "tropical traits" over time (Villéger et al. 2014; Magurran et al. 2015).

Based on the findings discussed in Section 4.2, what do our future projections in copepod FD imply for marine ecosystem functioning? Provided that mesozooplankton biomass and POC export efficiency are favored by the presence of certain trait combinations (i.e., large body size, myelination and current feeding) in communities of lower functional richness and higher evenness (Figures 3 and 4), our results suggest that anthropogenic climate change will re-organize copepod trait expression in a way that decreases mesozooplankton productivity and POC export efficiency. We did not find any significant relationships between copepod FD and the amount of organic carbon exported below the euphotic zone, precluding us from drawing conclusions regarding to this ecosystem function. Taken together, our results fall in line with the current view that ongoing and future spatial re-organization of marine biodiversity may threaten biomass production and export efficiency (Beaugrand et al. 2010; Lotze et al. 2019). Through bottom-up processes and trophic amplification, global warming will alter resource availability, causing changes in primary production that propagate up the food-web and eventually decrease the size and biomass of higher trophic levels (Kwiatkowski et al. 2020; Tittensor et al. 2021; Atkinson et al. 2024). We here show that future changes in zooplankton trait expression may contribute to lowering the productivity and the health of the oceans.

4.4 | Caveats

Our findings should be interpreted within the context of some key limitations that are inherent to a global correlative approach. One key limitation is that the availability of trait data and observations are often limited to adult stages (Brun et al. 2017); (Benedetti, Wydler, and Vogt 2023); (Pata and Hunt 2024). This bias toward adult stages implies that we underestimate the range of trait values (and thus functional richness patterns) expressed in true copepod communities where a large proportion of nauplii may occur. Those early life stages are smaller and display different morphologies and feeding strategies compared to adult stages (Kiørboe 2011; Pata and Hunt 2024). Therefore, intraspecies variability in functional traits due to local adaptations or ontogeny could not be taken into account (Carmona et al. 2016).

Similarly, the wide species pool necessary to explore emergent global FD patterns (~300 species) limits the number of functional traits available across all copepod species but see (Benedetti, Wydler, and Vogt 2023). Missing functional traits implies that we might miss key dimensions of copepod FD and thus underestimate its spatial gradients (Maire et al. 2015; Mouillot et al. 2021). Nonetheless, many functional traits scale allometrically with body size among zooplankton and other marine ectotherms (Andersen et al. 2016; Pata and Hunt 2024), especially those related to physiological rates (growth, respiration, ingestion or excretion; Kiørboe and Hirst 2014; Pata and Hunt 2024). Consequently, retaining body size as a continuous trait here may cover the interspecies variability in those traits. Copepods dominate mesozooplankton composition and concentration (Kiørboe 2011; Brandão et al. 2021; Drago et al. 2022); thus, we are confident that we cover significant dimensions of mesozooplankton FD. However, we did not account for the range of traits covered by other major meso- and macrozooplankton functional groups that show much larger body size, different body composition or alternative feeding strategies traits (i.e., krill, salps, jellyfishes, pteropods, foraminifera, or chaetognaths). The very recent trait synthesis of Pata and Hunt (2024) will allow the community to explore zooplankton FD dynamics in a more holistic fashion.

Our approach relies on occurrence-based modeling and HSI estimates bounded between 0 and 1. Consequently, we do not account for the differences in realized species abundance which span much larger range of values. As a result, the amplitude of the latitudinal gradients in FD indices accounting for HSI distribution in trait space (i.e., FDiv, FDis, FEve), as well as their future changes (Figure 5), are likely underestimated since species displaying very contrasted positions in trait space (Figure S2) also tend to show very strong differences in abundance between tropical oligotrophic gyres and more productive high latitudes (Becker et al. 2021; Brandão et al. 2021). In productive regions such as the poles, a few myelinated species with large body sizes (> 3 mm) and active current-feeding modes tend to dominate copepod biomass whereas other smaller ambush-feeding or cruise-feeding species contribute more marginally (Brandão et al. 2021; Drago et al. 2022). Therefore, integrating the species' abundances as weights in trait space may further accentuate the gradients in copepod FD between the poles and the tropics that we predict here based on potential community composition.

High latitudes showed higher uncertainty for species richness, functional richness, and FEve due to SDM choice compared to the tropics (Figure S10). This means that more observational research on zooplankton FD and ecosystem functioning is necessary in these regions to improve the accuracy of our estimates. As these diversity indices are more influenced by algorithm choice than intra-annual variability at latitudes > 60° (Figure S9), the trends shown here could become stronger with advancements in distribution modeling and the inclusion of more field observations of taxon-specific biomasses (Waldock et al. 2022; Lombard et al. 2019; Ratnarajah et al. 2023). Addressing this uncertainty is crucial since high latitude ecosystems are the most threatened by future warming (Benedetti et al. 2021a, 2021b).

5 | Conclusion

Our study suggests that zooplankton traits and FD depend on climate and resource availability and that changes in taxonomic diversity alone are insufficient to reveal the response of zooplankton biodiversity to changing environmental conditions (Hillebrand et al. 2017; Blowes et al. 2019). Various facets of zooplankton FD relate differently to phytoplankton productivity, zooplankton biomass, and biological carbon pump efficiency. Relationships between biodiversity and ecosystem functioning vary with the facets of biodiversity, echoing patterns in other terrestrial and marine systems (Chalmandrier et al. 2017; Le Bagousse-Pinguet et al. 2021). This calls for initiatives to better define what "biodiversity" is in the context of the marine microbiome and especially when diversity metrics are used in conservation and policy applications. Our future projections suggest climate warming will globally reshape marine biodiversity, potentially reducing productivity across trophic levels (Tittensor et al. 2021; Atkinson et al. 2024). Our copepod FD estimates align with field observations from smaller scales (Becker et al. 2021; Tang et al. 2022) and may serve as benchmarks for testing biodiversity hypotheses. We advocate integrating FD into field surveys to better track plankton biodiversity responses across scales and habitats (Ratnarajah et al. 2023). Historical and future oceanographic data, combined with functional traits, can further elucidate plankton functional diversity patterns (Pata and Hunt 2024). This will help ecosystem modelers assess the identity and number of traits and FD dimensions that are critical to model and monitor the response of marine ecosystems functioning to changes in plankton biodiversity (Kiørboe et al. 2018; Serra-Pompei et al. 2020).

Author Contributions

Fabio Benedetti: conceptualization, data curation, formal analysis, investigation, methodology, resources, software, supervision, validation, visualization, writing – original draft, writing – review and editing. **Jonas Wydler:** data curation, formal analysis, investigation, methodology, software, validation, visualization, writing – original draft, writing – review and editing. **Corentin Clerc:** data curation, resources, validation, writing – original draft, writing – review and editing. **Nielja Knecht:** methodology, resources, writing – original draft, writing – review and editing. **Meike Vogt:** funding acquisition, investigation, project administration, supervision, writing – original draft, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Zenodo at https://zenodo.org/records/14765901. The code supporting the findings of this study are openly available in Zenodo at https://zenodo.org/records/14747330 and GitHub at https://github.com/benfabio/Global-cOpepoD-functionaL-diversitY. Species occurrence data was obtained from Zenodo at https://zenodo.org/records/5101349. The sea surface temperature (SST) and surface nutrients (nitrates, phosphates and silicates) concentration data were obtained from the World Ocean Atlas 2013v2 at https://www.nodc.noaa.gov/OC5/woa13/woa13data.html. The surface photosynthetically available irradiance (PAR) and the surface chlorophyll a concentration data were obtained from the NASA Ocean Biology Distributed Active Archive Center (OB.DAAC) at https://oceandata.sci.gsfc.nasa.gov/l3/.

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Supporting Information

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