The marine annelid trait manifesto: A call to rethink functional traits for ecological and conservation research

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ABSTRACT

The Raunkiæran shortfall, defined as the scarcity of knowledge regarding species' attributes, represents one of the major obstacles for developing sound biodiversity conservation strategies and understanding ecological processes. In this context, despite the importance of marine annelids as dominant components of benthic ecosystems and key agents of marine ecosystem functioning, no comprehensive synthesis has centred their focus on the knowledge gaps related to their functional traits. To address this limitation, we conducted a systematic review to quantify the extent of Raunkiæran shortfalls related to marine annelids. Specifically, we investigated which traits have been measured, how they have been applied, whether trait selection is mechanistically aligned with ecological questions, the computational reproducibility of published studies, and the socio-cognitive structure underpinning the research field focusing on filling these knowledge gaps. As a result, feeding mode, body size, motility, and bioturbation emerged as the most frequently assessed traits, within a research agenda that has increasingly shifted from labor-intensive realized trait measurements toward the use of potential traits derived from databases and literature compilations to answer ecological questions. Bibliometric analyses revealed that this field is geographically structured, being dominated by North Atlantic research networks. Persistent challenges were identified, related to flaws in trait nomenclature standardization, lack of documentation of intraspecific trait variation, scarcity of demonstrations on mechanistic trait–fitness relationships, trait coding resolution disparities, and the lack of integration of a truly eco-evolutionary perspective on trait-based approaches. Collectively, our findings reveal that the field has matured into a sophisticated research domain but remains constrained by pervasive issues that hamper a proper understanding of benthic community assembly, ecosystem functioning, and conservation. In this sense, we point out future directions of research to overcome each of these challenges.

KEYWORDS: Biodiversity knowledge shortfalls; Annelida; Polychaeta; Marine Ecology; Functional Ecology; Global change

INTRODUCTION

There is a broad consensus that the quality and coverage of biodiversity data is limited, being one of the major issues hampering the development of suitable biological management and conservation policies (Diniz-Filho et al. 2013; Ladle & Hortal 2013; Hortal et al. 2015; Miatta et al. 2021). The emergence of this issue could be attributed to the interaction between the complex spatio-temporal dynamics of nature and the limited human capacity to cover it (Ladle & Hortal 2013; Hortal et al. 2015). As biodiversity declines at unprecedented rates worldwide, scientists increasingly seek to elucidate the mechanisms by which disturbances reshape community organization and influence ecosystem functioning. Advancing the surveying of biodiversity data, thus, is essential because biased, incomplete, or geographically unrepresentative biological information might compromise our ability to accurately describe eco-evolutionary patterns and predict how biodiversity will respond to environmental changes (Hortal et al. 2015).

A relatively novel research agenda has been developed to focus on identifying, quantifying, and discussing how to mitigate these gaps in biodiversity knowledge, referring them to specific, but interconnected, *shortfalls* (Diniz-Filho et al. 2013; Hortal et al. 2015; Rosado et al. 2016; de Bello et al. 2023; Gonçalves-Souza et al. 2023). Such shortfalls encompass major deficiencies in our understanding of the evolution, distribution and ecology of biological entities, being traditionally categorized into the main following domains: I) Linnean, II) Prestonian, III) Darwinian, IV) Wallacean, V) Raunkiæran, VI) Eltonian, and VII) Hutchinsonian (Hortal et al. 2015).

Among them, the Raunkiæran shortfall domain has received increasing attention because it highlights the persistent lack of knowledge regarding species' biological traits (Hortal et al. 2015; de Bello et al. 2023; Gonçalves-Souza et al. 2023). This growing focus reflects a longstanding effort to comprehend how the attributes of individual organisms mediate biotic interactions, species distribution patterns, and ultimately shape patterns of community assembly and ecosystem functioning (Gonçalves-Souza et al. 2023; de Bello et al. 2023). However, establishing these complex links is only possible through the measurement of species functional traits, as they capture distinct dimensions of a species' niche and, thus, mechanistically represent the relationship between individual form and ecological functioning (Violle et al. 2007; Kearney et al. 2021).

It is well established that functional traits provide baseline knowledge for research focusing on understanding how species couple with environmental conditions and how they influence ecosystem functioning (Lavorel & Garnier 2002; Violle et al. 2007; HilleRisLambers et al. 2012; de Bello et al. 2021a). Accordingly, they are commonly classified as “response traits”, which mediate species' responses to the environment, and “effect traits”, which determine their direct or indirect impacts on community structure and ecosystem processes (Lavorel & Garnier 2002). Moreover, they can be directly measured on individuals, being called “realized traits”, or derived from literature or database consulting, then referred to as “potential traits” (Martini et al. 2021). As biodiversity loss and environmental change continue to reshape ecosystems worldwide, both realized and potential trait-based approaches have become increasingly important for disentangling the complex interacting mechanisms underlying community assembly, for detecting patterns and consequences of functional

diversity changes on ecosystem functioning, and for establishing proper biodiversity conservation policies (McGill et al. 2006; HilleRisLambers et al. 2012; Münkemüller et al. 2020; Miatta et al. 2021; Rohr et al. 2025).

Even so, despite the relevance of trait-based ecology across several kingdoms of life to understanding natural eco-evolutionary processes, its conceptual foundations have been largely shaped by research on plant functional traits, with total publications outnumbering other groups of living beings (Villéger et al. 2017). Over the last decades, plant functional ecology has established a mature scientific framework supported by standardized measurement protocols, mechanistically informed trait definitions, robust conceptual foundations, and comprehensive databases (Díaz et al. 2016; Kattge et al. 2020; Carmona et al. 2025). In contrast, trait-based research in animals remains comparatively less developed, still limited by pervasive gaps (Cardoso et al. 2011; Moretti et al. 2017; Villéger et al. 2017; de Juan et al. 2022; Gonçalves-Souza et al. 2023; Beccari et al. 2024). Among them, important challenges related to methodological transparency have been extensively discussed, particularly concerning the computational reproducibility of published findings, emphasizing the need for transparency regarding the trait information that supports them (Powers et al. 2019; Keller et al. 2023; Gonçalves-Souza et al. 2023; Cooper et al. 2026). Addressing these challenges thus requires measuring traits of neglected groups, ensuring the accessibility of trait information, and providing detailed methodological documentation of analytical approaches that support the conclusions of published works (Gonçalves-Souza et al. 2023; Keller et al. 2023; Cooper et al. 2026).

Within marine benthic ecosystems, trait-based approaches have been extensively applied to explore mechanisms of community assembly and to quantify the contribution of macrofaunal communities to ecosystem functioning (Beauchard et al. 2017, 2022, 2023; Martins et al. 2024). However, the expansion of this research field has also revealed important conceptual and methodological challenges, particularly regarding the definition, measurement, and analysis of biological traits from multiple phyla and the lack of incorporation of species biological trait information into marine conservation planning (Beauchard et al. 2017; Miatta et al. 2021; de Juan et al. 2022; Martins et al. 2024). Consequently, an increasing number of reviews and critical syntheses have emerged to indicate the future directions of benthic trait-based ecology research, highlighting both its achievements and its unresolved limitations (Bremner et al. 2006b; Bremner et al. 2008; Beauchard et al. 2017; Lam-Gordillo et al. 2020; Miatta et al. 2021; de Juan et al. 2022; Beauchard et al. 2023; Martins et al. 2024).

The phylum Annelida is among the most ecologically influential components of marine benthic ecosystems, often dominating macrofaunal communities, driving key ecosystem processes, and also supporting fisheries activities worldwide (Cole et al. 2018; Rouse et al. 2022; Sato-Okoshi et al. 2022). Occupying virtually every marine habitat: from intertidal shores to abyssal plains, and from hard to soft-bottoms, annelids exhibit extraordinary variation in morphology, reproductive strategies, feeding modes, and behavioral patterns (Wilson 1991; Paiva et al. 2015; Jumars et al. 2015; Rouse et al. 2022; Reynolds et al. 2026). This exceptional functional diversification, combined with their broad environmental distribution and ecological prominence, points to annelids as particularly powerful model organisms for disentangling the processes underlying community assembly across environmental gradients in marine ecosystems. Indeed, annelid assemblages have been repeatedly used to reveal how benthic

communities assemble in both hard- and soft-bottoms from local to continental scales (e.g., Otegui et al. 2016; Wouters et al. 2018; Morais et al. 2019; Medeiros et al. 2021; Nogueira et al. 2023; Mendes et al. 2025, 2026; Reynolds et al. 2026).

Marine annelids are also considered a crucial group for evaluating both natural and anthropogenic impacts on marine benthic systems (Dean 2008; Pombo et al. 2020). Because of their close association with the substrate and broad range of life-history strategies, these organisms respond sensitively to environmental gradients and anthropogenic stressors (Giangrande et al. 2005; Dean 2008). Consequently, monitoring changes in population dynamics, species richness, and overall assemblage composition can provide clear indicators of disturbance, ranging from localized organic enrichment and metal contamination to major environmental disasters, such as the deposition of mining tailings, whose impacts can remain detectable years after the initial event (Nascimento et al. 2022). Furthermore, as key contributors to sediment bioturbation, nutrient cycling, and organic matter processing, changes in polychaete assemblages can directly translate into alterations in ecosystem functioning (Martins et al. 2024, 2026). Tracking such changes, then, allows researchers to investigate community assembly processes in depth, evaluate structural reorganization of benthic diversity driven by regional oceanographic variability, and assess the ecological footprint of environmental impacts across marine systems (Moritz et al. 2013; Monteiro et al. 2017; Mendes et al. 2025).

Nevertheless, despite their ecological importance and growing role in trait-based ecology within benthic systems, annelids remain largely overlooked in efforts to address the Raunkiæran shortfalls if compared with other groups of Metazoa (Gonçalves-Souza et al. 2023). Although recent reviews have summarized functional trait knowledge across several major animal groups (Cortéz-Gómez et al. 2015; Villéger et al. 2017; Lacher Jr et al. 2019), equivalent syntheses remain surprisingly scarce for Annelida (Fauchald & Jumars 1979; Faulwetter et al. 2014; Jumars et al. 2015; Otegui et al. 2016; Reynolds et al. 2026). As a result, fundamental questions regarding the extent and possible nuances of the Raunkiæran shortfalls affecting this phylum remain largely unexplored, limiting our ability to identify research priorities, strategically address persistent knowledge gaps, and advance a more predictive, reproducible, and comprehensive trait-based understanding of marine benthic ecology as a whole.

To address this issue, the aim of the present work is to elaborate a comprehensive review of the marine annelid functional ecology literature with the overarching goal of dissecting the Raunkiæran shortfalls associated with this ecologically important group in benthic systems, while simultaneously characterizing the cognitive and social organization of the research field focusing on this matter. Specifically, we asked: (1) which types of functional traits have been investigated; (2) how extensively and in what contexts these traits have been applied; (3) which ecological questions have been addressed and whether the selected traits are mechanistically aligned with the hypotheses under investigation; (4) to what extent published studies meet current standards of reproducibility and transparency; and (5) which network, cognitive, and thematic structures underpin the development of this research domain. Collectively, the first three questions provide a critical assessment of trait selection practices, conceptual paradigms, and persistent knowledge gaps (de Juan et al. 2020), whereas the latter two examine the field through a bibliometric lens, allowing us to uncover its underlying socio-

cognitive structure (Aria & Cuccurullo, 2017). By integrating these complementary perspectives, the present work provides a comprehensive diagnosis of the state of this research field and identifies key challenges and opportunities for advancing trait-based science for marine annelids.

METHODS

A systematic literature search was conducted in April 2026 using Scopus (all collections) and the Web of Science (WoS) Core Collection to identify scientific articles published between 1999 and 2026. The search period was defined to encompass the development of trait-based and functional approaches in annelid ecology while maintaining a consistent temporal window across the two databases (Gonçalves-Souza et al. 2023). In both databases, searches were conducted using the following Boolean expression in the "All fields" option: ALL = ("biological trait analysis" OR "BTA" OR "functional ecology" OR "functional diversity" OR "functional trait*") AND ALL = ("annelida" OR "polychaeta" OR "annelid*" OR "polychaet*"). The selected keyword boolean expression was adapted from the approach of Gonçalves-Souza et al. (2023). The Scopus search retrieved 5,086 records, whereas the WoS Core Collection search retrieved 217 records. The markedly different number of records between databases likely reflects differences in database coverage, indexing practices, search fields, and retrieval algorithms; therefore, the two searches were retained as complementary sources.

Records retrieved from both databases were exported and merged into a single bibliographic database, after which duplicate records were identified and removed based on their DOI's. The resulting dataframe underwent title and abstract screening according to predefined eligibility criteria. Studies were excluded when: they were conference abstracts, theses, reviews, or methodological papers focused on analytical approaches or functional diversity metrics; relied on trait surrogates (e.g., species richness as a proxy for functional diversity) without explicitly collating species-level traits; and used the term "functional trait" to describe molecular or tissue-level variation in histology, neurology, enzymology, pharmacology, or genetics without an explicit eco-evolutionary context. Studies focused exclusively on terrestrial or freshwater worms were also excluded. For studies involving multiple taxonomic groups, we retained those for which annelids were explicitly included. So, studies were considered eligible only when they (i) investigated at least one functional trait of an annelid taxon and (ii) used such trait information to address an ecological or evolutionary question. The final dataset comprised 321 studies, of which 209 (65.1%) were retrieved exclusively from Scopus, 44 (13.6%) exclusively from WoS, and 68 (21.3%) were indexed in both databases. This whole process was performed by a single author. For each included study, two main categories of information were extracted: the first characterized the extent of Raunkiæran shortfalls from a conceptual perspective (de Bello et al. 2023), whereas the second characterized the socio-cognitive structure of the research field from a scientometric perspective (Aria & Cuccurullo 2017).

On the Raunkiæran shortfalls

The dissection of Raunkiæran shortfalls extent answers the questions 1 to 3, and for this purpose, the following informations were extracted from the selected papers: a) cross-phyla resolution; b) species' traits nature and type; c) trait databases consulted; d) functional diversity operationalization approach; e) trait measurement momentum; f) thematic representation of the principal research area related to study question and its respective punctual focus; g) oceanic region, substrate type, and marine environments in which the study was produced. The cross-taxa resolution relates to the refinement level of the trait assessment approach, indicating whether the study lies within a multiple-phyla framework or focuses exclusively on annelids (Luza et al. 2022). Trait nature refers to the "Response vs Effect" framework (Lavorel & Garnier 2002), while trait type refers to the strategy of potential vs realized quantification approaches (Martini et al. 2021). As not all studies directly measure trait information on individuals (realized traits), but instead rely on the information present in available literature (potential traits), we mapped the trait databases consulted, whenever mentioned in the material and methods section or supplementary information.

The functional diversity operationalization approach concerns the quantification strategy of trait information, which could be related to multivariate approaches (e.g., RLQ, FCA, or PCA analyses) or functional diversity indexes. This is directly related to a second piece of information extracted, the trait measurement momentum, which refers to between-species trait variation (BTV) or intraspecific trait variation (ITV). The main study question area and thematic focus refer to the analysis of the study scope from broader and coarser perspectives, respectively. The study area was related to specific thematic agendas that were summarized as: behavioral ecology, community structure, ecophysiology, functional morphology, species impact assessment, trait compilation, and trophic ecology (Table 1). On the other hand, the study focus relates to detailed aspects that refine its thematic scope; these were: species life history responses to environmental changes, life history patterns descriptions, ecomorphological descriptions, responses to anthropogenic activities or natural environmental gradients, climate change simulation experiments, and biogeochemistry of the sediments.

Table 1. Summary of detected research questions principal thematic areas with their respective diagnostic scope.

Study question thematic area	Scope
Behavioural ecology	Studies that describe or model specific aspects of species life history that are reflected on its observed behavioural patterns (e.g., Vlaminck et al. 2023)
Community structure	Studies that capture trait diversity patterns in a given set of communities to answer ecological questions through distinct modelling approaches (e.g., Mendes et al. 2025)
Ecophysiology	Studies that explore or test individual level annelid physiological responses to environmental changes (e.g., Massamba-N'Siala et al. 2022)
Functional morphology	Studies that assess annelid morphology to adress some aspect of its response and/or effect in ecossystems (e.g., Otegui et al. 2024)

Species impact	Studies that quantify and/or model the overall influence of annelids in community and/or ecossystem level processes (e.g., Martins et al. 2026)
Trait compilation	Studies that compilate multiple fine measurements of species functional and life history traits within both a descriptive and/or comparative frameworks (e.g., Gambi & Cigliano 2006)
Trophic ecology	Studies that describe the trophic relationships of species within ecossystems to answer ecological questions through isotope analyses (e.g., Pérez-Posada et al. 2025)

Using this information, temporal shifts in the predominance of research trends were investigated through two approaches: multinomial regressions and binomial generalized linear models (GLM). Multinomial regressions were fitted to evaluate how study area and the relationship between trait selection and research questions varied as a function of year using the nnet R package (Venables & Ripley, 2002). The binomial GLM was used to model temporal changes in the two trait measurement approaches using the stats R package (R Core Team, 2026), also considering year as the predictor. For both modeling frameworks, an information-theoretic approach was implemented, whereby models were ranked based on the Akaike Information Criterion corrected for small sample sizes (AICc). Comparisons were made between each fitted model and its corresponding null model using the MuMIn R package (Burnham & Anderson, 2002; Bartoń, 2024). Models with $\Delta AICc > 10$ relative to the respective null model were considered to have substantially less support, indicating that temporal variation did not meaningfully improve model fit. Conversely, models with $\Delta AICc < 10$ relative to the null model were interpreted as providing satisfactory evidence for temporal shifts (Burnham & Anderson, 2002).

Subsequently, in order to visualize the multivariate connections of the information extracted from the selected papers and identify patterns in functional trait research, a Sankey diagram workflow was elaborated. This allows the systematic mapping of transitions between oceanic regions and their respective consulting patterns of trait databases, trait nature (response vs effect), study question thematic area, study focus, and functional diversity operationalization approach. The diagram was structured to visualize the logical progression from oceanic geographic origin to the final quantification of functional diversity that was applied to answer particular ecological questions, highlighting the most frequent methodological pathways in the literature.

Trait nomenclature was standardized following the framework of Beauchard et al. (2017), with minor adaptations for the peculiarities of the phylum Annelida (Table 2). The 4 most frequent traits were then selected to generate collector's and rarefaction curves using the *specaccum* function in the vegan R package (Oksanen et al. 2022). Other traits with a minimum frequency of 3 papers were also analyzed but are presented in the supplementary material. First, a chronological accumulation (collector's curve) was calculated, with data ordered by publication year. This allowed us to identify periods of stagnation or rapid measurements in the literature. Second, a sample-based rarefaction curve was calculated, using the "random" algorithm with 1.000 permutations. This curve represents how much new information on species traits is obtained per published article, independent of chronological bias. Both curves

were calculated separately for "direct measurements" and "literature consult" trait measurement approaches to compare the accumulation of "primary" (species-level measurements) vs. "secondary" functional trait information (deduced or inferred from databases for the same, or different congeneric species, and even from higher taxonomic levels).

Table 2. Summary of marine annelids functional traits extracted from the literature.

Fitness dimension	Functional traits retrieved	Usual representation	Nature	Mechanisms	Common ambiguities
REPRODUCTION	**Early development**	Modalities: Planktotrophic, lecithotrophic or direct development	Response traits, especially related to species life history	Recruitment success, demographic stability and resilience, dispersal potential, energy investment per reproductive event (Giangrande 1997; Llodra 2002; Beauchard et al. 2017)	Larval egg development/type, larval feeding type, larval mode, Offspring type, Pelagic larval duration, Reproductive technique, Developmental mechanism
	Egg/Propagule protection or Fate of ova	Modalities: Freespawning, internal brooding, tube brooding, gelatinous egg mass, egg capsules			Parental care, brooding strategy
	Reproductive frequency	Modalities: Continous, seasonal; Direct counts or distinct time intervals			Spawning frequency of the population, reproductive periods
	Age at sexual maturity	Direct counts or distinct time intervals			Age at first reproduction
	Sexual metamorphosis (Epitoky)	Modalities: Epigamy, schizogamy, absent			Epitoky, Reproductive transformation
	Fecundity	Direct counts or distinct classes of egg size and/or number per individual			Egg production, number of eggs, egg size, reproductive allocation
	Assexuality or Assexual reproduction	Modalities: assexual reproduction present or absent			Reproductive technique, clonal reproduction
	Factors triggering reproduction	Modalities: Lunar cycle, pheromones/ hormones, photoperiod, salinity, temperature			Spawning synchronization
	Sperm type and biology	Modalities: Ect-aquasperm, Ent-aquasperm, Introsperm			Sperm morphology, fertilization type
	Mode of reproduction	Modalities: Gonochoristic, sequentially hermaphrodite, simultaneous hermaphrodite, pelagic, short-pelagic, benthic			Reproductive strategy, reproductive behaviour
	Pattern of oogenesis	Modalities: Intraovarian extraovarian			-

	Propagule duration	Direct counts or distinct time intervals			Larval phase duration
	Life Span	Direct counts or distinct time intervals: short (<2 years), medium (2-4 years) or long (>4 years)			Life cycle duration, longevity
GROWTH	**Size**	Continuous measurements or distinct size classes or total number of chaetigers	Response and Effect traits	Vulnerability to environmental adversities, energy balance requirements, nutrient uptake, oxigen consuption rates (Jumars et al. 2015; Beauchard et al. 2017)	-
	Energy	Continuous measurements or distinct biomass/calories classes; Isotopic signatures and trophic transfer			
SURVIVAL	**Feeding mode**	Modalities: Carnivorous, herbivorous, scavenger, deposit-feeder (selective or non-selective), suspension-feeder		Resource acquisition strategy (Jumars et al. 2015)	Feeding strategy, diet, food preference, trophic position, primary food source, trophic group, feeding guild, feeding type
	Motility	Modalities: Sessile, discretely motile, motile; Direct observations of movement patterns		Expousure and vulnerability to environmental adversities, dispersal (Jumars et al. 2015; Beauchard et al. 2017)	Movement method, movement habit, living habit, degree of attachment to substrate, locomotion
	Morphology: Auxiliary foraging structures	Distinct categories: Pharynx armouring patterns, Phanryngeal morphology, Feeding palps, Radiolar or tentacular crowns	Response and Effect traits	Resource capture mechanisms, habitat exploration, environmental perception, biomechanical, respiratorial and sensorial support (Pagliosa 2005; Jumars et al. 2015; Otegui et al. 2016; Wouters et al. 2018; Mendes et al. 2025)	-
	Morphology: Body shape, mechanical, and sensorial support	Distinct categories: Parapodial lobes complexity, Chaetal configuration, Prostomial appendages, Parapodial appendages, Pygidial appendages, Body shape (vermiform, irregular, conical, or tube protected)			
	Morphology: Body Defense	Distinct categories: Tube material, body surface coverage			

	Morphology: Respiratory structures	Distinct categories: Branchiae regionalization, branchiae form, total surface area and volume			
	Habitat Ocupation Strategy: Substrate position	Modalities: Infauna, epifauna, interface; Intervals of sediment depth preference		Habitat preference, 3d or 4d habitat creation potential, nursery, refuge provision, foraging site behaviour (Beauchard et al. 2017)	Sediment position, living position, living habitat, depth zone, depth preference, substrate preference
	Habitat Ocupation Strategy: Substratum affinity	Distinct categories: Substrate type preferred, type of biogenic structure created			
	Bioturbation	Direct observations of burrowing behaviour or energy fluxes within the sediments; Modalities: Surficial modifiers, biodiffusors, regenerators, epifauna, upward and downward conveyors		Impact on sediment biogeochemistry, organic matter re-distribution, bioengineering (Kristensen et al. 2012; Queirós et al. 2013; Beauchard et al. 2017)	Sediment mixing, substrate modification
	Ecophysiological limits: salinity	Direct measurements of physiological responses, enzimatic activity, or organisms survivorship	Response traits	Species tolerance limits, resilience levels or avoidance patterns related to environmental changes, and the underlying physiological mechanisms structuring such responses	-
	Ecophysiological limits: temperature				
	Ecophysiological limits: oxidative stress				
	Ecophysiological limits: regeneration and growth				
	Biotic Interactions: interspecific	Direct observations or distinct categories		Ecological interactions that might modulate coexistence through organisms behaviour	
	Biotic Interactions: intraspecific				
	Bioluminescence			Defense against predators, intraspecific signaling, prey attraction (Verdes & Gruber 2017)	
	Structural robustness	Modalities: Fragile, Intermediate, Robust		Sensitivity to physical damage (Beauchard et al. 2017)	Fragility

On the social and cognitive structures of the research field

The second main field of information extracted from each paper refers to a bibliometric approach to assess the social and cognitive structures of the field (Aria & Cuccurullo, 2017),

thus answering questions 4 and 5. Firstly, to visualize the geopolitical distribution of authorship within the field, a world map was plotted representing the total number of publications from each author's country. Then, Bradford's law approach was applied to identify the literature sources that represent the core zone within this research field, obtained by ordering the published papers in relation to their citation impact (Bradford, 1934; Aria & Cuccurullo, 2017). The total and mean number of citations per year were also extracted from the dataset. Subsequently, each paper was classified into three modalities according to the computational reproducibility of its respective results: "none", "partial", or "complete" (Powers et al. 2019). Accordingly, "none" refers to papers that did not present any information necessary to fully or partially reproduce the results, "partial" represents papers that provided incomplete supporting information and/or dataset information, whereas "complete" represents papers that presented both supporting information and the respective dataset with all the necessary information to fully reproduce its results. To assess differences in reproducibility levels across modalities over the years, a multinomial regression model was fitted. Model selection was then performed by comparing its AICc to that of a null model, considering a ΔAICc > 10 as an indicator of a substantially better fit (Burnham & Anderson, 2002).

To explore the social and cognitive structures of the research field, three complementary approaches were employed: 1) collaboration network analysis of authors and institutions, 2) a co-word analysis, and 3) a thematic mapping of the field within pre-pandemic (<2020) and pandemic/post-pandemic (≥2020) periods. Both were based on metadata related to each paper extracted from the Scopus and WOS databases, including authorship, publication year, authors' institutional affiliations, authors' nationalities, keywords, total citations, source title, and publication title. In this sense, for the collaboration network analyses, the network nodes are the units of analysis (authors and institutions), whereas the links are the collaborations among each of those units (Aria & Cuccurullo, 2017). To explore the connections, network modularity was assessed using the Leiden cluster algorithm, which groups up to the 20 most relevant nodes into distinct communities that tend to work together (Aria & Cuccurullo, 2017; Traag et al. 2019). A node's size reflects the proportional weight, which is related to the total number of publications. Links represent network connectivity and are dashed or solid. Dashed links are "extra-community" collaborations. Solid links represent "intra-community" collaborations. In both cases, thickness represents collaboration strength between nodes; the thicker the link between a pair of nodes is, the more connections they have.

To ensure consistency in the following bibliometric analyses, all author keywords were standardized through a synonymizing procedure. Different spellings, plural/singular forms, abbreviations, and semantically equivalent expressions referring to the same concept were merged into a single standardized term. Specifically, the terms "benthic macrofauna", "benthos", "macrobenthos", "macrozoobenthos", "macrofaunal invertebrates", "macrofaunal communities", "macroinvertebrates", "macrobenthic invertebrates", and "macroinfauna" were unified as "macrofauna". Likewise, "benthic communitie(s)" and "benthic assemblage(s)" were standardized as "benthic community". Taxonomic terms were harmonized by merging "polychaete(s)" into Polychaeta, "annelid(s)" into Annelida, and "mollusk(s)" into "mollusk(s)". Keywords related to trait-based approaches were also standardized: "biological trait(s) analysis(es)", and "functional trait(s) analysis(es)" were grouped as "BTA" (the abbreviation for Biological Traits Analysis), whereas "functional trait(s)" were retained as

"functional trait" as they might denote a distinct logical structure. Methodological terms such as "RLQ analysis" and "fourth-corner analysis", "RLQ-fourth-corner analysis(es)" were standardized as "RLQ" and "fourthcorner". Additional standardizations included replacing "deep-sea" with "deep sea", "ecosystem engineer(s)" with "ecosystem engineer", "benthic functioning" and "ecosystem function" with "ecosystem functioning", "alpha diversity" and "beta diversity" into "alpha-diversity" and "beta-diversity", respectively. These standardizations reduced redundancy and improved the interpretability of keyword-based analyses.

Then, a co-word analysis was applied to produce a semantic map of keywords through a Multiple Correspondence Analysis (MCA) to dissect the current cognitive structure of the field. This technique was applied to a document-by-keyword matrix from surveyed literature, allowing terms to be represented within a two-dimensional Euclidean space that reflects distinct cognitive clusters within the research field (Aria & Cuccurullo, 2017). Finally, a thematic mapping analysis was implemented to compare the thematic evolution of the pre-pandemic (1999-2019) and post-pandemic (2020-2026) periods (Alkhammash, 2020). This analysis is represented by keyword co-occurrence network clusters associated with specific topics as bubbles, positioned according to Callon's centrality (x-axis) and density (y-axis) ranks (Callon et al, 1991; Aria & Cuccurullo, 2017). Accordingly, centrality indicates the extent of interaction with other clusters (i.e., thematic relevance within the research domain), whereas density reflects the subject's internal cohesion and development. Bubble size reflected keyword frequency within each cluster. Based on their position, clusters were classified as motor (high centrality and density), niche (high density, low centrality), emerging or declining (low centrality and density), and basic (high centrality, low density) themes (Aria & Cuccurullo, 2017).

RESULTS

The research field on marine annelid functional ecology exhibits a multifaceted methodological structure, as their functional traits have been employed to address a broad spectrum of scientific questions across distinct contexts, ranging from local-scale assessments of species impacts and/or their ecophysiological responses to large-scale investigations on community structural organization and ecosystem functioning. However, despite this complexity, the field is not unstructured. Discernible temporal patterns have emerged over the past two decades, revealing clear shifts in the predominance of specific methodological approaches, as well as in their underlying socio-cognitive structuring.

Dissecting the Raunkiæran shortfall

Overall, studies showed a variable cross-phyla scope (Fig S1A), combining approaches that incorporate trait measurements from multiple phyla (56%) or focus exclusively on Annelida (44%). The momentum of trait measurement (Fig S1B) and substrate types (Fig S1C) were unevenly distributed across modalities. Between-species trait variation (BTV) was the most explored (72%), whereas fewer studies reported or considered some extent of intraspecific variation (ITV) in their scope. Moreover, soft-bottoms were the primary substrate in which

annelid functional diversity has been investigated (79%; Fig S1C). Laboratory cosmos, intertidal (e.g., sandy beaches, tidal flats, etc.), and subtidal environments received relatively balanced attention, whereas deep-sea and lagoon systems were comparatively underrepresented (Fig. S1D).

Feeding mode, body size, motility, and bioturbation were the most frequently measured traits in the literature, whereas all remaining traits were assessed in less than 4% of the studies, particularly those associated with reproductive biology (Fig. S1E). Regarding trait types, potential traits were the most accessed, followed by realized traits (Fig. S2A). Qualitative (nominal trait categories) and semi-quantitative (binary and fuzzy) potential traits were more commonly employed to address ecological questions, with fuzzy coding emerging as a widely adopted approach (Fig. S2B). Feeding mode, motility, and body size also represented the traits measured for the greatest number of species across the surveyed studies, followed by bioturbation, which encompassed approximately half the total number of species assessed for the former traits (Fig. S2C). However, when species richness was partitioned according to trait measurement approach, realized traits yielded relatively similar numbers of measured species across these major traits, whereas potential trait information consistently resulted in substantially higher species richness (Fig. S3D). Moreover, most traits presented several nomenclatural ambiguities that were further summarized based on their biological meaning and relation with fitness dimensions (Table 2).

Publication numbers showed a consistent upward trend over time (Fig 1A), with a notable increase during the pandemic period (2020–2022). For instance, the number of publications doubled in 2021 compared to the previous peaks observed in 2018 and 2016 (Fig 1A). We detected substantial shifts in the robustness of trait selection, study areas, and trait measurement approaches adopted over time (Fig 1B–D). Studies providing strong justification for trait selection became less frequent, particularly during the pandemic period, while weak justifications persisted at low frequencies. In contrast, the absence of clear theoretical or hypothesis-driven support for trait selection increased, especially during the pandemic period (Fig 1B). Most research areas remained relatively stable through time, except for community functional structure, ecophysiology, and species impact (Fig 1C). Questions focusing on processes within the scope of the community functional structure exhibited a positive trend, whereas those focusing on species ecophysiology and impact declined (Fig 1C). Regarding trait measurement approaches, direct observations (realized traits) showed a decreasing trend, while reliance on literature and database sources (potential traits) increased (Fig 1D). Model selection results indicated that all three models (Fig 1B–D) outperformed their respective null models by more than 10 ΔAICc units, suggesting substantially better fit relative to null expectations (Table S1).

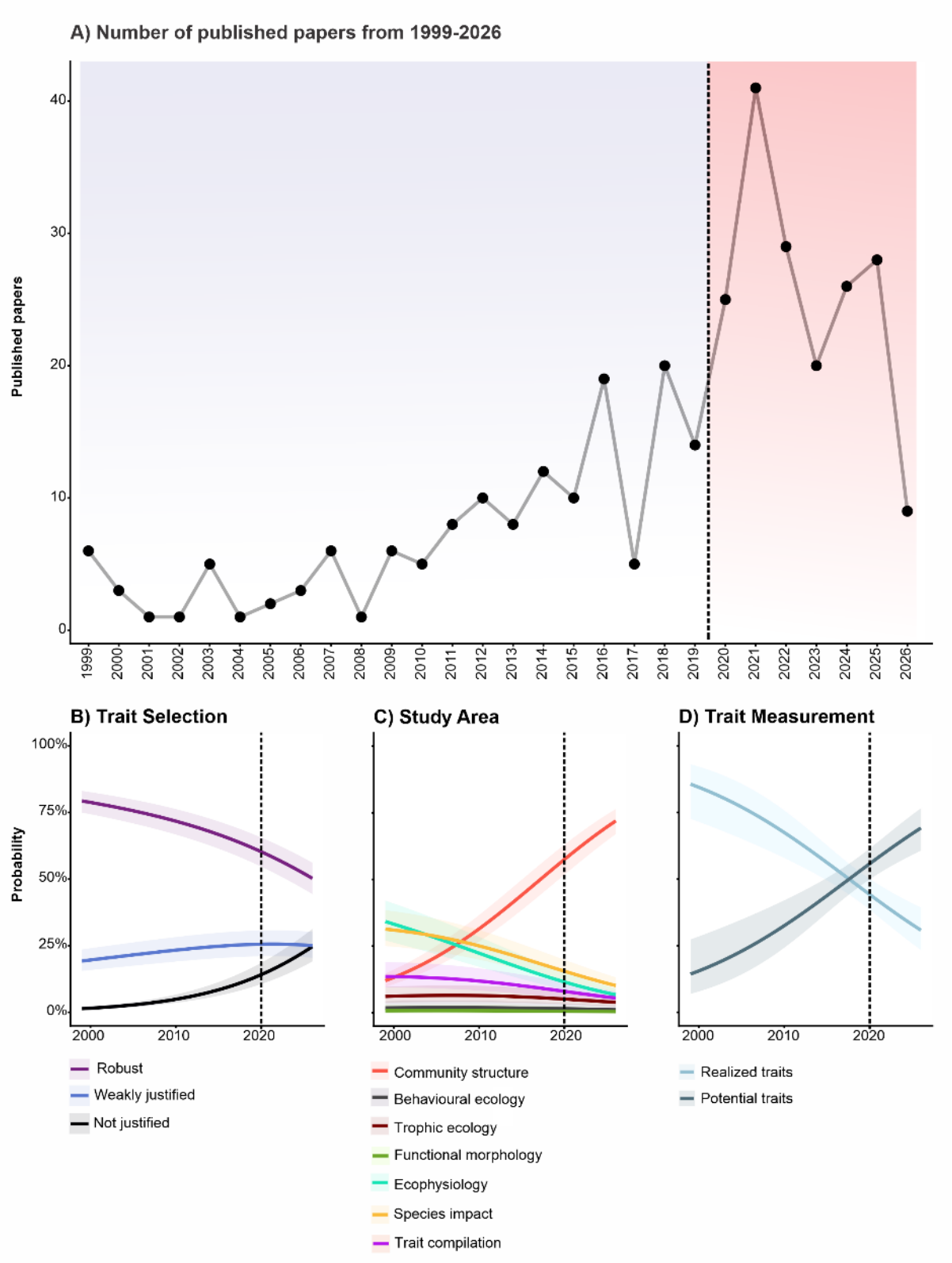

Figure 1.Temporal trends in the functional ecology of marine annelids from 1999 to 2026. (A) Annual number of publications retrieved from the literature survey. The blue-shaded area represents the pre-pandemic period (1999–2019), whereas the red-shaded area denotes the pandemic and post-pandemic period (2020–2026). (B) Predicted temporal trends from the multinomial regression model describing changes in trait-selection categories through time. (C)

Predicted temporal trends from the multinomial regression model describing shifts in the thematic areas of the ecological questions addressed by the studies. (D) Predicted probabilities from the binomial generalized linear model (GLM) showing temporal changes in trait measurement approaches, contrasting studies based on potential traits (derived from literature and databases) with those based on realized traits (directly measured on organisms). Lines represent model predictions and shaded areas indicate 95% confidence intervals.

The three most frequent methodological pathways captured by the Sankey diagram workflow were associated with studies conducted in the North Atlantic, Indian, and South Atlantic oceans (Fig 2). In the North Atlantic, most studies relied on direct observations of functional traits, including effect traits related to species' influence on sediment biogeochemistry and response traits linked to ecophysiology (Fig 2). As for community functional structure, trait database consultation was also frequent, especially in studies typically designed to answer questions related to responses to anthropogenic activities (pollution and/or contamination) or natural environmental gradients (Fig 2). Approaches based on the assessment of community functional structure commonly operationalized functional diversity using RLQ analysis and/or trait diversity indices, such as: Rao's Quadratic Entropy (Rao's Q) (Botta-Dukat, 2005), Functional Richness (FRic), Functional Divergence (FDiv), and Functional Evenness (FEve) (Villéger et al. 2008).

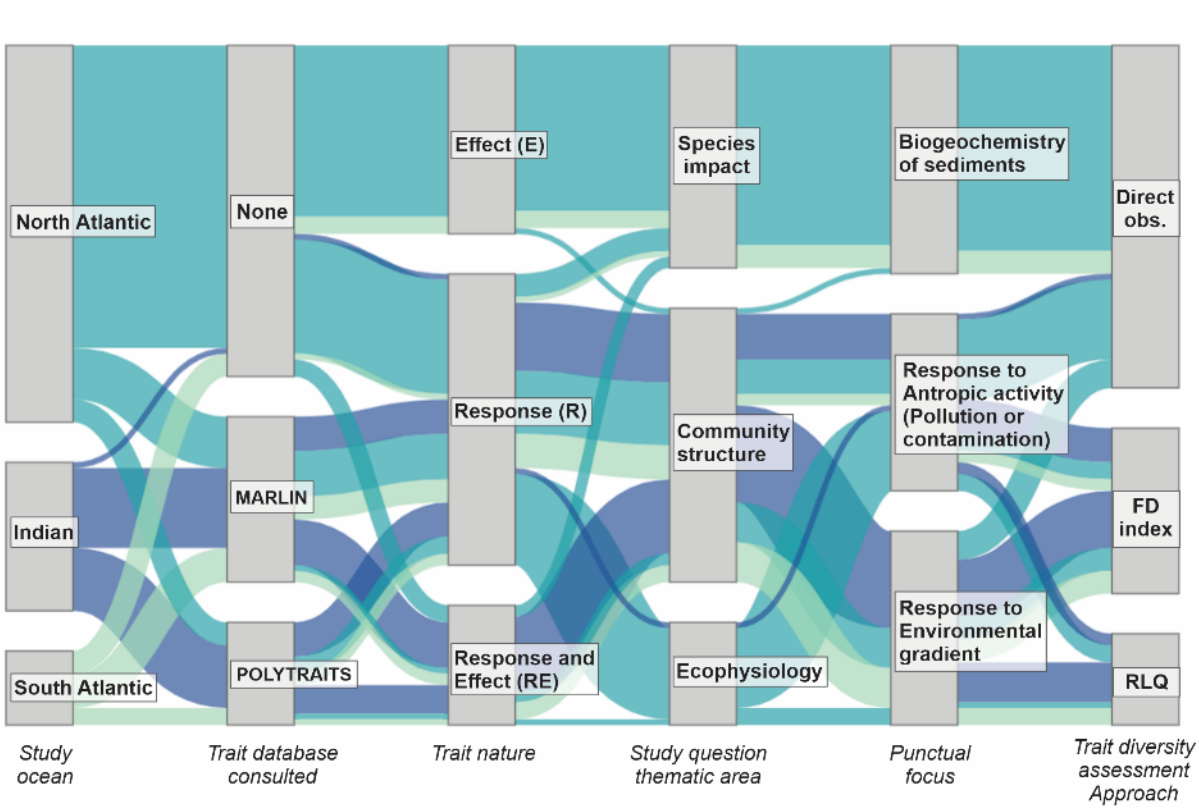

Figure 2. Sankey diagram workflow. The sankey diagram is representing the most frequent logical pathways of research within marine annelid functional ecology in relation to study ocean, trait database consulted, trait nature framework, study question thematic area, its respective punctual focus and the functional trait diversity operationalization approach.

In contrast, studies conducted in the Indian Ocean showed an inverse methodological pattern relative to the North Atlantic (Fig 2). These studies predominantly relied on literature and database trait consulting, focusing mainly on response traits or combining both response and effect traits within the same framework to describe the overall functional diversity of communities. Their primary aim was to investigate community functional structure in relation to anthropogenic activities and environmental gradients, typically through RLQ analysis or functional diversity index modeling. Finally, studies from the South Atlantic exhibited a more balanced distribution of methodological approaches, although fewer works addressed species' effects on sediment biogeochemistry (Fig 2). Similarly to the Indian Ocean, studies tended to rely on trait data compiled from databases derived from previous research, particularly those based on North Atlantic species, especially "MARLIN" and "POLYTRAITS", followed by the family-level classification of annelids by Jumars et al. (2015). A compilation of all sources of potential traits information extracted from the analyzed literature is provided in the supplementary material (Table S2).

Accumulation and rarefaction curves based on the four most frequently assessed functional traits revealed contrasting efforts between potential and realized traits (Fig 3). Works based on literature and/or database consulting exhibited a consistent, near-linear increase with sampling effort across all traits in both accumulation (Fig 3A–D) and rarefaction curves (Fig 3E–H), indicating that saturation has not yet been reached. Across the time intervals 2015–2020 and 2020–2025, accumulation curves displayed a recurrent pattern characterized by periods of near stagnation followed by sharp increases, resulting in an overall positive, stepwise ("ladder-like") trajectory (Fig 3A–D). In contrast, realized traits showed positive trends in both accumulation and rarefaction curves, but . Notably, the accumulation curves revealed a sharp increase between 2025 and 2026, differing markedly from the potential traits (Fig 3A–D). As for the other traits, the unique exception to this pattern of predominance of potential trait consulting with a positive growth trend was body energy (biomass, calories), which presented an inverse pattern of more realized trait measurements than potential trait consulting, but with both still presenting positive trends (Figs S3–5).

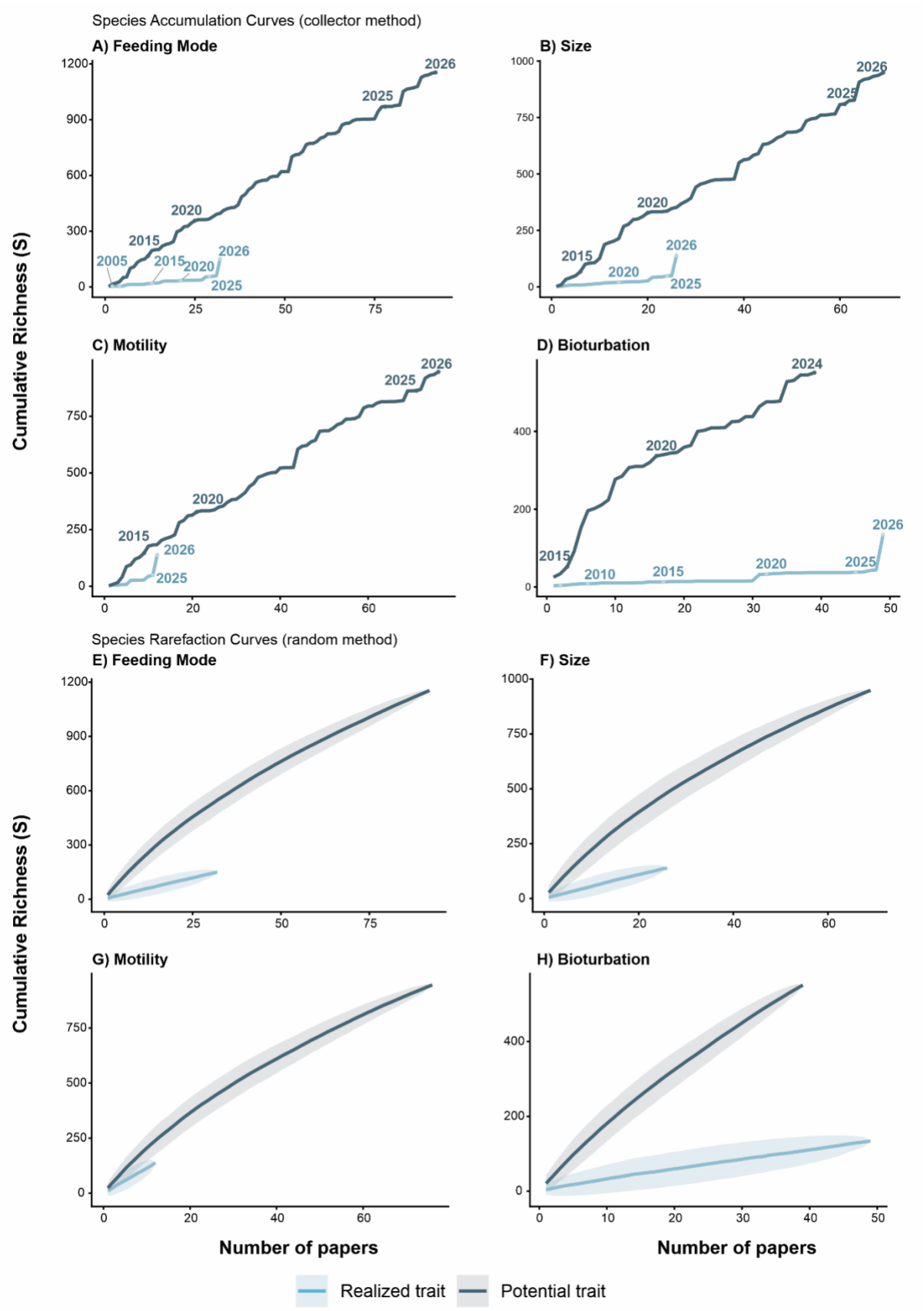

Figure 3. Evolution of annelid species knowledge for the four most frequently measured traits. Scientific effort was assessed by estimating the cumulative species richness recorded

through potential and realized trait measurement approaches across published studies, using accumulation curves (A–D) and rarefaction curves (E–H).

Dissecting the social structure of the research field

Although the total number of publications shows a clear upward trajectory (Figure 1A), particularly during the pandemic and post-pandemic periods (>2019), citation metrics display the opposite pattern (Fig 4A–B). Citation levels peak for studies published between 2003 and 2009, after which a sharp decline is observed. Following this drop, average total citations per year exhibit a steady downward trend (Fig 4A), while average citations per article initially stabilize before undergoing a second marked decrease (Fig 4B). These results indicate that, despite the expansion in publication output, citation performance has not kept pace, with more recent studies (especially those published between 2020 and 2026) showing, comparatively, lower average impact. A summary of most cited papers is provided in the supplementary material, which are related to community structure, species impact on sediment biogeochemistry, and ecophysiological responses (Table S3). Specifically, the top cited paper is Bremner et al. (2003), which offers a comparative view of several approaches to calculate community functional diversity in benthic systems.

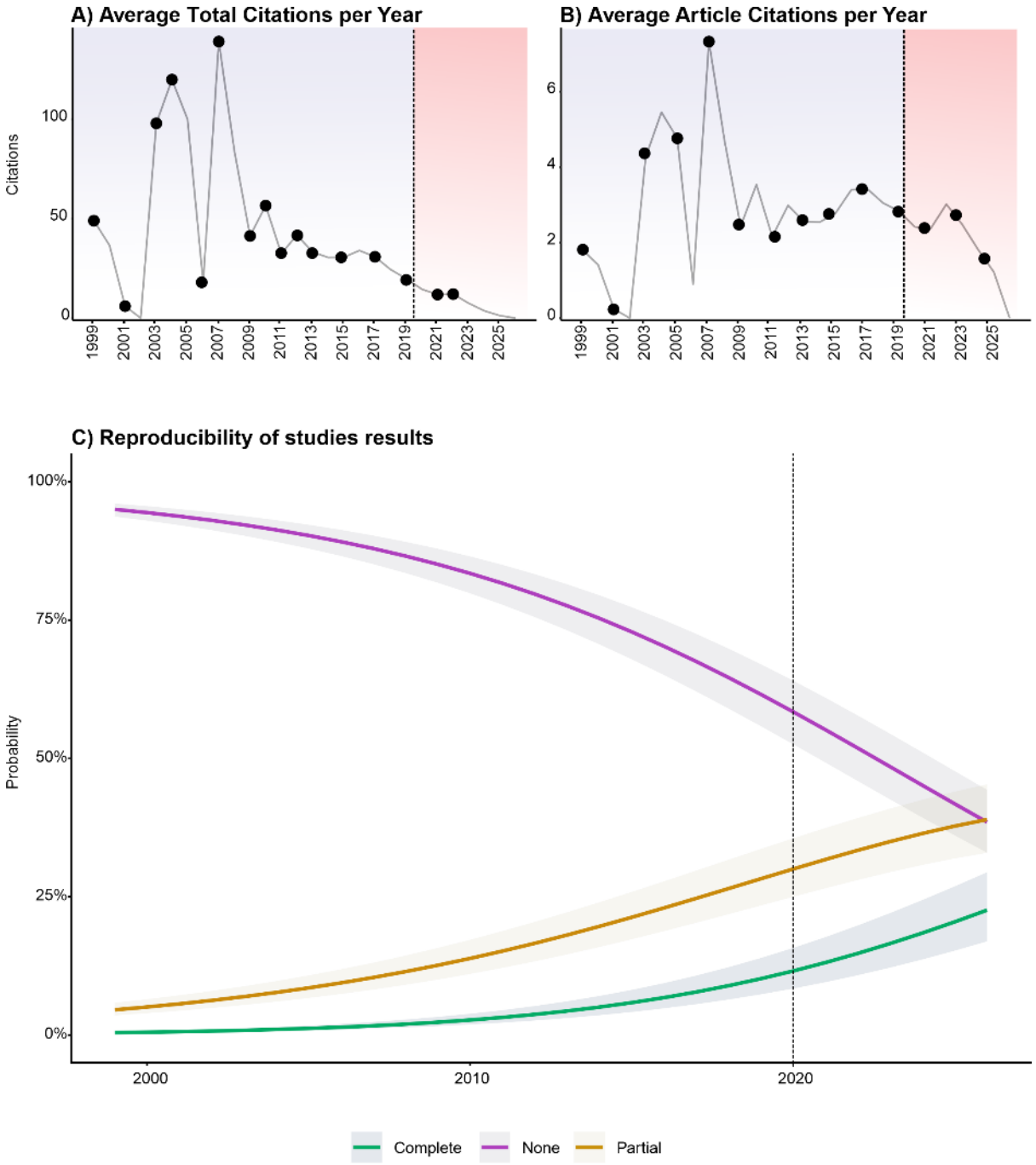

Figure 4. Publication impact and study reproducibility level over time. (A) Average total citations per year. (B) Average article citations per year. (C) Predicted probabilities from the multinomial regression model describing shifts in the reproducibility levels of studies over the years. Lines represent model predictions and shaded areas indicate 95% confidence intervals.

The analysis of studies' reproducibility levels indicates that the growing emphasis on open science in ecology has begun to reshape common practices within this field, as evidenced by contrasting temporal trends among reproducibility categories in the multinomial model (Fig 4C). This model provided a substantially better fit than the null expectation, with a difference exceeding 10 AICc units (Table S1). Overall, most studies did not make their datasets fully

available to reproduce their analyses. However, the prevalence of non-reproducible studies has declined during and after the pandemic period, accompanied by an increase in studies providing partial or complete data availability, suggesting a slow shift towards more transparent research practices (Fig 4C).

Author affiliations were predominantly concentrated in Europe, China, Brazil, United States, India, and Australia (Fig. 5A). Overall, countries bordering the North Atlantic Ocean accounted for a disproportionately large share of total publications in the field, with particularly strong contributions from France and Italy (Fig. 5A). In the South Atlantic, Brazil and more modestly Argentina emerged as the most productive contributors, while in the Indian Ocean, research output was primarily driven by India and Australia (Fig. 5A). In the North Pacific, China and the United States dominated scientific production, whereas in the South Pacific, Australia and Chile were the leading contributors. These patterns indicate that research efforts are geographically structured, with countries predominantly contributing within their own political and oceanic boundaries and showing limited multinational collaboration (Fig. S6). At the same time, scientific impact appears to be channelled through a consistent and relatively restricted group of core journals (Fig 5B). According to Bradford's law, the core sources of research impact were concentrated in a relatively small set of journals, they are ranked as follows: Marine Ecology Progress Series, Marine Pollution Bulletin, Marine Environmental Research, Frontiers in Marine Science, Journal of Sea Research, and Estuarine, Coastal and Shelf Science (Fig. 5B). Thus, while scientific production is strongly structured by geopolitical boundaries, the distribution of research impact and publication effort is concentrated within a relatively small set of core sources.

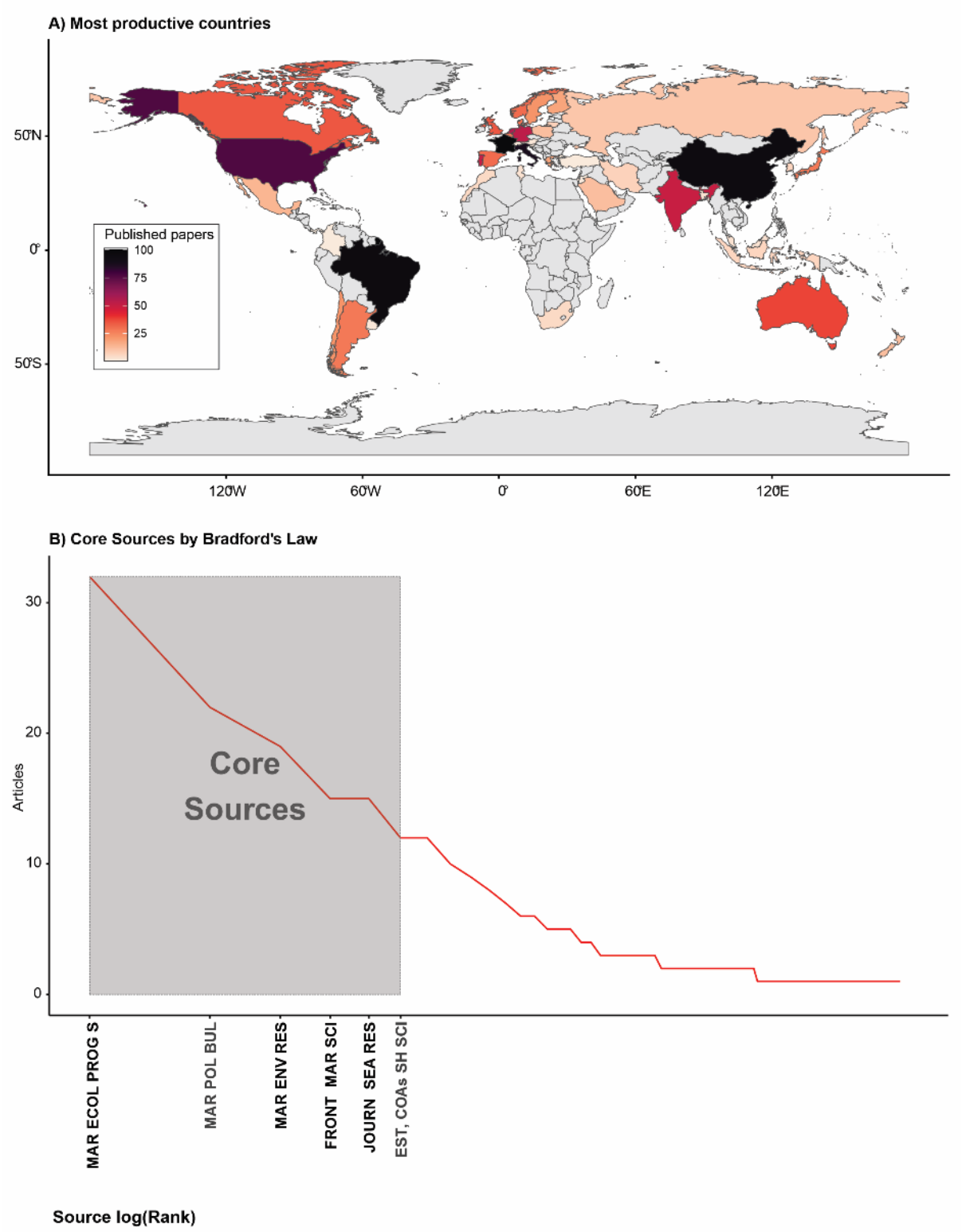

Figure 5. Publication effort per country and core sources. (A) Total number of published papers per country. (B) Core sources ranked by relevance within the research field calculated according to Bradford's approach.

Finally, collaboration patterns of researchers further reinforced this geopolitical structuring (Fig. 6), revealing well-defined regional networks, particularly within Asian (Indian Ocean) and European (North Atlantic Ocean and Mediterranean Sea) contexts, for both co-

authorship (Fig. 6A) and institutional collaborations (Fig. 6B). Extra-community collaborations were comparatively limited and predominantly centred within the European context, although two small communities of research partnership between Portuguese with Brazilian and Canadian institutions were also observed (Fig. 6B).

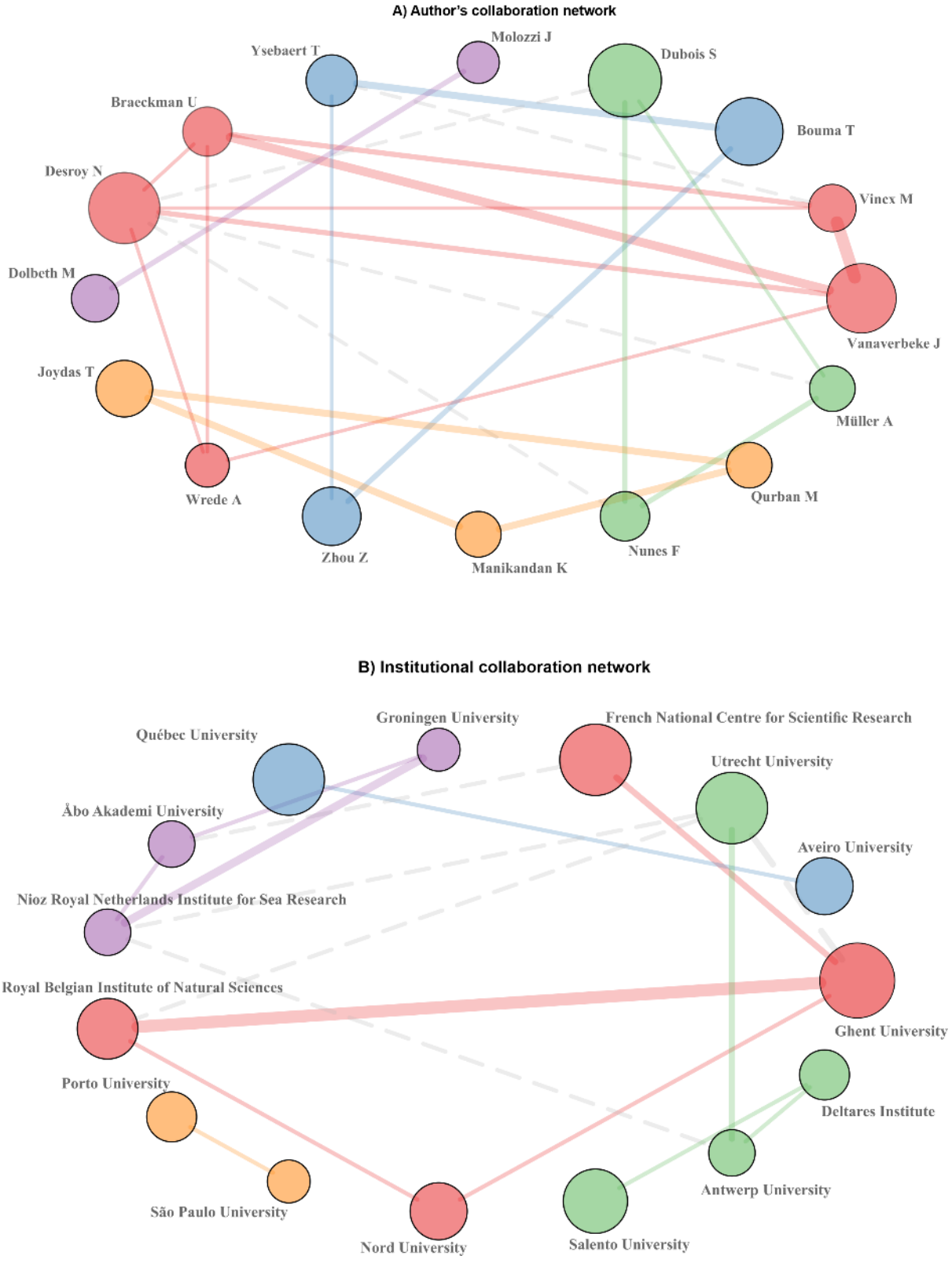

Figure 6. Network analysis of publication collaborations. (A) Authorship network, focusing on the 20 most productive research communities. (B) Institutional research network, focusing on the 20 most productive institutional collaboration networks.

Dissecting the cognitive structure of the research field

Analyzing the cognitive structure of the field has revealed three main clusters, hereafter referred to as Cluster I, Cluster II, and Cluster III (Fig. 7A). Cluster I encompasses the core aspects of the biological trait-based approach and community ecology, grouping studies that measure or incorporate functional traits of marine annelids to address ecological questions primarily related to community assembly processes under varying abiotic conditions (Medeiros et al. 2021; Beauchard et al. 2022; Mendes et al. 2025) and the assessment of the direct impacts of well-known polychaete ecosystem engineers on multiple dimensions of benthic biodiversity (de Smet et al. 2016). Representative examples of the latter case include studies on the community or ecosystem-level effect of Lanice conchilega (Pallas, 1766) burrows in the Baltic Sea (de Smet et al. 2016) and *Sabellaria alveolata* (Linnaeus, 1767) biogenic reefs in the English Channel (Jones et al. 2020).

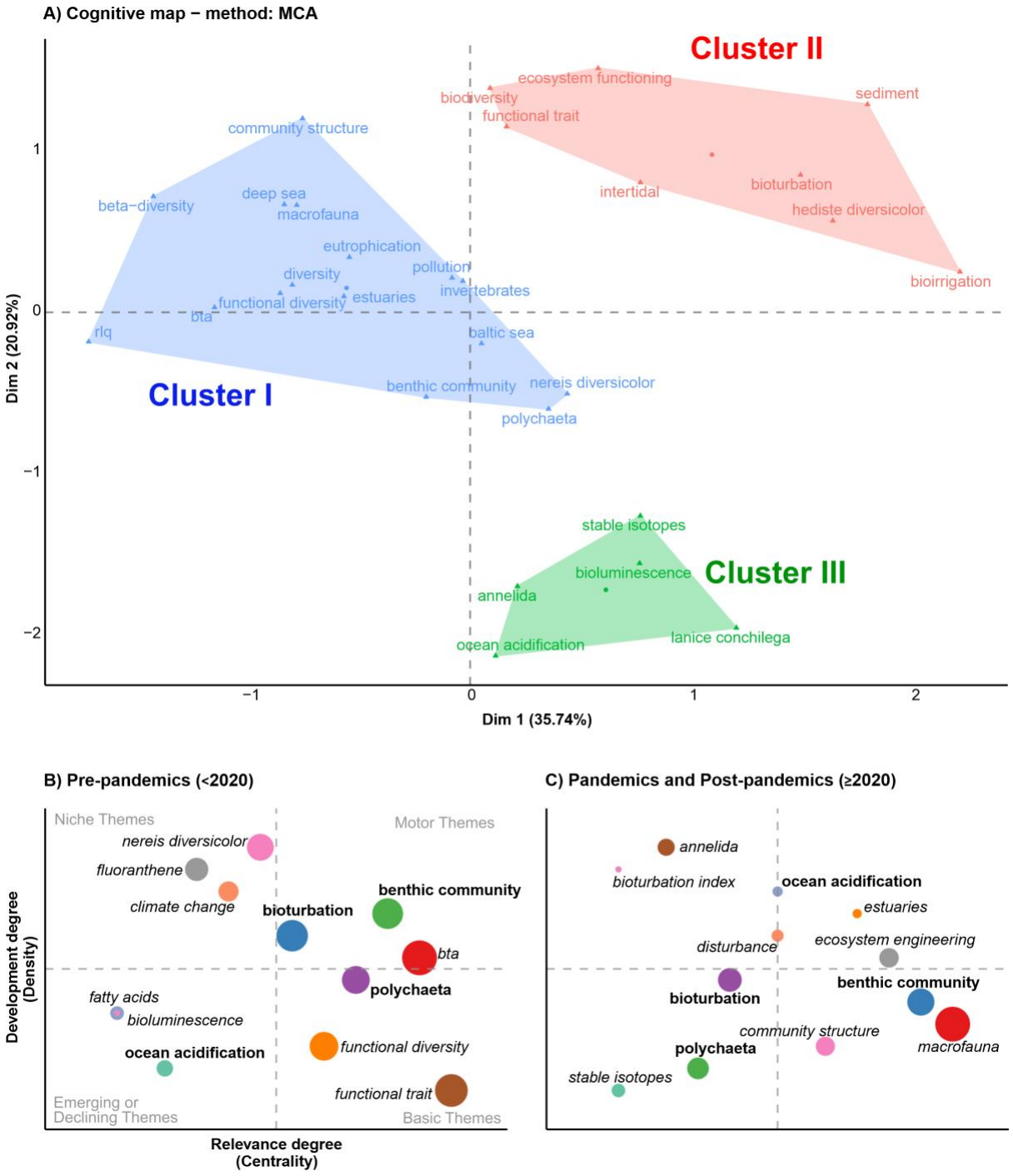

Figure 7. Representation of the cognitive structure of the research field and its thematic mapping analysis. (A) Multiple correspondence analysis (MCA) of keywords co-occurrence, characterizing the research field into 3 main clusters of research approaches. (B) Thematic map analysis of the research field before the pandemics. (C) Thematic map analysis of the research field during and after the COVID-19 pandemics. Themes in bold are those that remained in both time intervals, whereas the ones in italic are restricted to the time interval in which they appeared.

The Cluster II represents approaches focused on quantifying benthic fluxes mediated by bioturbation activities of model species, such as *Hediste diversicolor* (O.F. Müller, 1776)

(Murray et al. 2017), *Arenicola marina* (Linnaeus, 1758) (Volkenborn et al. 2017), and the invasive *Marenzelleria* species in the Baltic Sea (Urban-Malinga et al. 2013). Finally, Cluster III captures studies addressing the ecophysiological and life-history aspects of marine annelids, including species feeding preferences through isotopic niche characterization (e.g. McGovern et al. 2020; Cronau et al. 2023; van Rensburg et al. 2023; Pèrez-Posada et al. 2025). Regarding the ecophysiological studies, they predominantly model physiological responses of annelids to environmental changes, with a particular emphasis on ocean warming and acidification experiments (Linke-Gamenick et al. 1999; Del Pasqua et al. 2019; Munari et al. 2022). These studies are often conducted using model species, such as *Ophryotrocha labronica* La Greca & Bacci, 1962 (e.g., Massamba–N'Siala et al. 2022), and *H. diversicolor* (e.g., Sokołowski et al. 2025). On the other hand, life history is represented by studies based on laboratory or field observations of organismal biology (e.g., Taboada et al. 2020; Kin & Oba, 2020).

A marked shift in the cognitive structure of the field was detected in response to the COVID-19 pandemic, based on thematic map analyses (Fig. 7B–C). Only a limited number of themes persisted across periods, although exhibited substantial changes in their centrality and density. These themes were primarily represented by the keywords "Polychaeta", "ocean acidification", "bioturbation", and "benthic community", but none of them remained stable in the thematic space across the two periods. First, the theme "ocean acidification" shifted from an emerging or declining theme to a motor theme, suggesting increased development and centrality in the broader research landscape. On the other hand, "bioturbation" and "Polychaeta" both lost centrality and density. Finally, the motor theme "benthic community" lost its development degree, becoming a basic theme.

DISCUSSION

The study agenda focusing on the functional ecology of marine annelids has evolved into a sophisticated, albeit geographically and methodologically structured research domain. While the field has experienced significant quantitative growth in publication output, particularly peaking during the COVID-19 pandemic, this expansion is characterized by a strong reliance on a plethora of potential traits, mostly derived from European databases consulting over realized trait measurements at the individual level. Notably, potential trait selection often presented distinct terms referring to the same mechanisms, creating a non-negligible nomenclatural redundancy, despite the well-known efforts to advance this subject in terrestrial, marine and aquatic sciences (Violle et al. 2007; Lichman & Klausmeier, 2008; Beauchard et al. 2017; Moretti et al. 2017; Lam-gordillo et al. 2020; Martini et al. 2021; de Juan et al. 2022; Gonçalves-Souza et al. 2023; Martins et al. 2024).

This tendency toward a "database-driven research" practice, coupled with a decline in explicit theoretical justifications for trait selection and the associated nomenclatural ambiguities, suggest a field in transition: moving away from the robustly justified selection of realized traits from localized, labor-intensive, ecophysiological and/or life history assessments of annelid species biology, towards large-scale community functional structure modelling, based on potential traits, without proper justification. Moreover, despite the global distribution of research effort, the field remains structured by persistent geopolitical boundaries, favoring

restricted regional collaboration networks, with a clear concentration of scientific impact within a small core of traditional and specialized journals on marine ecology.

On the Raunkiæran shortfalls: initial considerations

The Raunkiæran shortfall can be dissected into a series of limitations associated with the lack of species traits information and its subsequent scaling consequences (Hortal et al. 2015; Gonçalves-Souza et al. 2023; de Bello et al. 2023). These limitations encompass issues related to trait definition and standardization (SF1), to the incorporation of intraspecific trait variability (ITV) (SF2), the establishment of mechanistic trait–fitness relationships (SF3), the mapping of trait evolution (SF4), the limited understanding of community assembly from a functional perspective (SF5), difficulties in disentangling response–effect trait frameworks within integrated phenotypes (SF6), the poor linkage of multitrophic interactions effects on ecosystem functioning (SF7), and the lack of robust methods for developing large scale eco-evolutionary analyses laying on comprehensive global repositories of functional trait information (SF8) (de Bello et al. 2023).

Within the context of the present review, these shortfalls (SFs1 to 8) are particularly pervasive. Although a relevant number of studies have attempted to investigate regional-scale patterns linking marine annelid traits to environmental gradients, a clear demand persists for greater "nomenclatural stability" and the implementation of standardized realized trait measurement protocols to follow up recent advances in aquatic trait-based ecology as a whole (SF1) (Queirós et al. 2013; Beauchard et al. 2017; Martini et al. 2021). In addition, most of the surveyed studies did not incorporate intraspecific trait variability (ITV) into their analytical frameworks (SF2). This decision implicitly assumes that mean differences in species trait values are sufficient to capture the main mechanisms underlying their research questions, which are mostly related to community assembly processes. However, such an assumption has been increasingly recognized as context-dependent, so an exclusive reliance on between-species trait variation (BTV) may blind the proper understanding of marine community assembly and ecosystem functioning, thus linking SF2 with SFs 3 to 8 (Albert et al. 2011; Bolnick et al. 2011; Violle et al. 2012; Siefert et al. 2015). In this sense, seeking trait nomenclatural stability based on its biological meaning and incorporating robust measurements of ITV in future works would provide a more nuanced understanding of how species occupy the functional space within communities, especially because the subjacent information from ITV might reveal in more detail species coexistence patterns at finer scales, ranging from trait overlap (individual specialization or fitness equalization) towards trait packing (stabilizing niche differences) (Araújo et al. 2011; Violle et al. 2012; HilleRisLamber et al. 2012).

Still on individual-level measurements, the works surveyed were predominantly associated with effect traits, especially focusing on bioturbation-related processes, reinforcing the notion that marine annelids exert a major influence on the biogeochemistry of sediments and functioning of benthic ecosystems (de Smet et al. 2016; Martins et al. 2026). On the other hand, at smaller accumulation rates, response traits have also been measured, especially in relation to ecophysiology and life history. They revealed that marine annelids can be sensitive to abrupt changes in environmental conditions, especially under predicted climate change scenarios (Linke-Gamenick et al. 1999; Del Pasqua et al. 2019; Grimes et al. 2021; Munari et

al. 2022). However, there is a persistent lack of proper understanding of the annelid phenotypic integration continuum, with few descriptive works pointing out the mechanistic relations between worm body plan and its ecological functioning.

Now, at the species level, the few approaches related to studies that have explored trait evolution (SF3) demonstrated that life habits associated with habitat occupation can exert non-negligible influences on morphological traits linked to growth and survival (Gonzalez et al. 2018; Cerca et al. 2020; Gonzalez et al. 2021). This pattern seems to be reflected at community-level scales, as several studies aiming at the understanding of benthic community assembly often observed patterns of morphological trait syndromes related to habitat occupation patterns and resource exploitation responding to environmental contrasts related to hydrological regimes and sediment texture gradients over space and time (Pagliosa 2005; Otegui et al. 2016; Mendes et al. 2025). However, no study has effectively attempted to link these aspects at broader scales, truly integrating the phylogenetic effect on the analysis of trait variation across environmental gradients, thus leaving this question as an open, fruitful research prospect.

Hence, despite the advances that the analyzed studies provided for the field of functional ecology of marine annelids, the pervasive methodological constraints still represent significant barriers to the broader application of an annelid-oriented trait-based ecology within response–effect frameworks related to the understanding of phenotypic integration, trait evolution, multitrophic interactions, community assembly and benthic ecosystem functioning (SFs 5 to 8). These shortfalls are closely aligned with the core questions addressed in this study, which are examined in greater detail in the following sections.

On the Raunkiæran shortfalls: Which types of annelid functional traits have been measured?

The incorporation of functional traits, especially within a response framework, has emerged as a need to deepen the understanding of assembly rules that are not easily captured by "taxonomic-based' approaches (HilleRisLambers et al. 2012; Kraft et al. 2015; de Bello et al. 2023). In this sense, different species might coexist in a given community through the interplay of distinct assembly processes related to speciation, dispersal, and ecological selection and drift (HilleRisLambers et al. 2012; Vellend 2016). Consequently, the analysis of functional trait diversity patterns within ecological communities has the potential to disentangle the relative influences of such processes across multiple spatio-temporal scales (Beauchard et al. 2022; Munkemüller et al. 2022; Rohr et al. 2025; Mendes et al. 2025).

There is a growing call in the ecological literature for deepening the development of trait-based approaches capable of comparing taxa from distinct phyla in order to assess assembly patterns (Luza et al. 2023). In this context, marine annelid traits have predominantly been incorporated within broad cross-phyla frameworks in benthic ecology, which seems to be a positive remark. However, the studies were conducted with a marked emphasis on BTV. This reliance on species mean trait dissimilarity has recently been systematized within marine community ecology through the proposal of "bestiaries" of biological traits, with subjacent species-level information often organised within regional datapapers that integrate functional traits, their biological meanings, standardized terminologies, and recommended practices for biological trait diversity analyses (Bremner et al. 2003; Bremner et al. 2006b; MacDonald et

al. 2010; Faulwetter et al. 2014; Beauchard et al. 2017; Cardeccia et al. 2018; Degen & Faulwetter 2019; Yamakita et al. 2020; Quintanar-Retama et al. 2022; Clare et al. 2022; Meijer et al. 2023; Claes et al. 2024; Chevalier et al. 2025; Weng et al. 2025). In parallel, more specialized syntheses focused specifically on Annelida have also been developed, encompassing response and effect traits related to body size, external morphology, feeding behaviour, motility, habitat occupation, bioturbation (Fauchald & Jumars 1979; Bartolomaeus & Purschke 2005; Pagliosa 2005; Queirós et al. 2013; Faulwetter et al. 2014; Jumars et al. 2015; Otegui et al. 2016; Martins & Barros 2022; Mendes et al. 2025), as well as life-history characteristics (e.g., Wilson 1991; Rouse & Fitzhugh 1994; Giangrande 1997; Rouse 2000; Kupriyanova et al. 2001; Jamieson et al 2006; Giese 2012; Faulwetter et al. 2014) (Table S2).

Collectively, these syntheses have established important conceptual and methodological foundations for the construction of species x trait matrices, also referred to as "Q matrices", following the RLQ framework proposed by Dray et al. (2014). The "Q matrices" are subsequently processed by several techniques to characterize community trait structure (Beauchard et al. 2017; de Bello et al. 2021a,b). Briefly, these techniques commonly integrate matrices with multiple trait types (fuzzy, binary, nominal categories, continuous or discrete direct measurements), then transform them into generalized distance matrices, such as Euclidean or Gower, to calculate distance-based functional diversity indices (de Bello et al. 2021a). Moreover, the trait matrices can also be subjected to multivariate dimensionality-reduction approaches, such as Principal Components Analysis (PCA), Fuzzy Correspondence Analysis (FCA), and Principal Coordinates Analysis (PCoA) or Cluster analysis of a trait distance matrix. Notably, FCA and PCoA are especially applied for the quantification and decomposition of functional beta-diversity partitions for multiple qualitative and/or semi-quantitative traits by using the principal components as synthetic traits (Villéger et al. 2010, 2014; Beauchard et al. 2017; Muller et al. 2021; Lelièvre et al. 2023; Beauchard et al. 2023). These procedures enable the estimation of functional diversity and the investigation of trait–environment relationships through bivariate or multivariate analytical frameworks (Dray et al. 2014; Beauchard et al. 2017, 2023).

Among the approaches concerned with the quantification of traits, the semi-quantitative fuzzy coding technique was predominant, especially in studies relying on potential trait information. Fuzzy-coded traits are dummy variables particularly useful when a given species exhibits multiple states of affinity to a given trait either simultaneously or context-dependently (Chevene et al. 1994; Oug et al. 2012). Feeding mode provides a representative demonstration of this issue in general for marine annelids (e.g., Fauchald & Jumars 1979; Pardo & Dauer 2003), for example, species within the family Spionidae may act both as deposit feeders and suspension feeders, since their morphology and behavioral plasticity allow shifts between these strategies according to environmental conditions and resource availability (Shimeta 1997; Fauchald & Jumars 1979; Jumars et al. 2015). In this sense, spionids cannot be accurately classified as exclusive representatives of a single microphagic feeding mode. Thus, fuzzy coding functional traits overcomes this limitation by assigning affinity scores that represent the degree to which a species is associated with each modality of a given trait, often varying from 0 (no affinity), 1 (low affinity), 2 (high affinity), and 3 (absolute affinity) (Chevene et al. 1994; Oug et al. 2012; Mendes et al. 2025). In the case of the spinoid example, the species must receive an equally high score for both suspension and deposit feeding, and zero for other

feeding mode modalities (see Beauchard et al. (2022) and Mendes et al. (2025) supplementary material).

The selection of traits and trait modalities remains inherently flexible but should be guided by their ecological relevance to the research questions that are being addressed, as well as by the coding resolution of trait information (Beauchard et al. 2017; Wilkes et al. 2020; Kohli & Jarzyna 2021). Notably, most of the surveyed studies have neglected the implications of taxonomic resolution disparities in trait coding schemes. Trait matrices are often populated using a mixture of species-, genus-, and family-level information, whereby trait data from higher taxonomic categories are employed to fill knowledge gaps for poorly characterized taxa. Although this practice increases data completeness, it may introduce uncertainty and obscure biologically meaningful variation among species. This is a pervasive problem for benthic functional ecology in general (de Juan et al. 2022), as the resolution at which traits are coded can fundamentally influence observed patterns of functional trait diversity of communities and, consequently, the interpretation of underlying ecological processes (Kohli & Jarzyna 2021). Thus, we argue that future work based on potential traits should develop alternatives for controlling the disparity bias in trait information inference, such as coding the Q matrix under the same resolution as the L matrix (e.g., Mendes et al. 2025).

On the Raunkiæran shortfalls: How and how much have annelid functional traits been measured?

Despite the substantial advances provided by frameworks that integrates marine benthic macrofauna trait information across several environmental gradients, as well as by recent guidelines for calculating multitrait functional diversity in benthic ecology (Bremner et al. 2003; Bremner et al. 2006a,b; Beauchard et al. 2017; Beauchard et al. 2023), most initiatives remain restricted to coarse resolution compilations of trait information (such as the family-level classification from Jumars et al. 2015) or to arbitrary classifications of species into "functional groups", often without proper statistical support. The rarefaction and accumulation curves of the assessed functional traits in the surveyed literature further highlight this issue, as potential and realized traits exhibited markedly distinct sampling efforts and, consequently, accumulation patterns. Although both curves showed positive trends through time, their accumulation rates differed substantially.

Notably, realized trait knowledge accumulated at considerably slower rates, reflecting the greater methodological and logistical effort required to obtain empirical trait measurements directly from organisms. In contrast, potential traits research effort displayed an almost linear increase in the number of species per study, reflecting the widespread practice of extrapolating information from congeneric or confamilial species within existing databases. The observed discrepancy in scientific knowledge accumulation rates by trait type thus reinforces a practice that has been characterized as one of the "dead-ends" of marine trait-based ecology as a whole (de Juan et al. 2020). This pattern was especially evident in the alluvia distributions of the Sankey diagram, which revealed that North Atlantic studies most frequently relied on realized traits and generated the empirical information necessary to establish regional trait databases. These databases were subsequently consulted by researchers investigating functional diversity in other oceanic regions (mostly Indian and South Atlantic), which frequently extrapolated trait

information from congeneric or confamilial species, particularly from labor-intensive derived measurements of traits that are closely linked to organismal performance.

Consequently, species-level trait measurements at finer resolutions remain comparatively underexplored, indicating that the Raunkiæran shortfalls have not been effectively reduced. Rather than fully overcoming these limitations, such initiatives based on potential trait information frequently generate only an apparent sense of progress, particularly for studies conducted outside the North Atlantic region. Hopefully, the awareness of potential vs realized trait knowledge scarcity appears to be increasing among researchers, as few recent studies have returned to provide realized measurements of both response and effect traits of annelids from several oceanic regions outside the North Atlantic. Specifically, some important works have been conducted in the South Atlantic (e.g., van Rensburg et al. 2023; Otegui et al. 2024; Martins et al. 2025), Indian (e.g., Sarker et al. 2024; Hartati et al. 2025), South Pacific (e.g., Lee et al. 2018; Doherty-Weason et al. 2025), and North Pacific oceans (e.g., Hayman et al. 2020; Sánchez-Ovando et al. 2025).

Despite these encouraging developments, the accumulation of realized trait measurements alone is still insufficient. A critical unresolved question is whether the traits currently being measured genuinely reflect organismal fitness, and addressing this issue requires moving beyond descriptive trait inventories towards the modeling of robust specific response functions (SRFs) and specific effect functions (SEFs) (de Bello et al. 2023). By definition, functional traits capture the relationship between form and function through their "proximal" or "distal" connections with fitness (Violle et al. 2007; de Bello et al. 2023). Proximal traits are those directly associated with fitness dimensions, whereas distal traits are linked to them indirectly (de Bello et al. 2023). Accordingly, such terminology related to SRFs and SEFs has frequently been conflated with the dichotomy between "soft" and "hard" traits, under the assumption that traits that are easier to measure ("soft traits") are necessarily more distal, whereas laborious or experimentally demanding traits measurements ("hard traits") are inherently more proximal (Violle et al. 2007; de Bello et al. 2023). However, this interpretation may be misleading, since some easily measurable traits can still integrate phenotypic functionality with considerable accuracy and ecological relevance (Violle et al. 2007; de Bello et al. 2023). In this sense, the extent to which a given trait accurately reflects actual organismal performance has rarely been tested in annelids, particularly by modeling SRFs and their ultimate effects on fitness, even in the North Atlantic. Comparatively, the establishment of SEFs has been more explored. This issue is not exclusive to the phylum Annelida, but rather represents a broader trend observed across multiple taxonomic groups (de Bello et al. 2023).

The few approaches focusing on the establishment of SRFs of marine annelids can be illustrated by studies examining morphological, ecophysiological, life-history plasticity, adaptive responses to environmental variation, and biotic interactions (Prevedelli et al. 2006; Grimes et al. 2021; Munari et al. 2022; Radhakrishnan et al. 2026). Indeed, these studies focus on "hard" traits, providing key insights into trait variation by directly quantifying shifts in resource allocation across distinct fitness dimensions. From an organism–organism perspective, Radhakrishnan et al. (2025) offer a compelling example using the protandrous hermaphrodite model species *Ophryotrocha puerilis* Claparède & Mecznikow, 1869. In this study, the authors investigated how variation in growth responds to mating competition by establishing three experimental conditions: control, monogamous pairs (absence of sexual

competition), and triplets (presence of sexual competition). Marked differences emerged among treatments, with triplets exhibiting pronounced male size hierarchies, in contrast to the monogamous system, where no consistent size ranking was observed. So, the study provides an SRF relating sexual competition to individual growth, clearly indicating that sexual selection on species reproductive strategy has a direct effect on individual growth rates, culminating in the establishment of intraspecific size hierarchies.

On the other hand, Martins et al. (2026) provide another illustrative case, this time focusing on annelid SEFs that were previously quantified (Martins et al. 2025). This framework demonstrates how annelids influence sediment biogeochemistry by integrating realized and laborious trait measurements into regional databases that can subsequently inform potential trait assignments at larger spatial scales. By doing so, the study reveals relevant patterns of species contributions to ecosystem functioning without requiring direct measurement of effect traits at every sampling unit for each organism. The combination of empirical trait quantification, high-quality trait database development, and model-based inference thus represents a promising pathway for incorporating functional traits into broader response–effect frameworks, particularly in multitrait studies where direct measurements are logistically constrained, and helps mitigate biases associated with estimating functional diversity based on coarse taxonomic resolution trait assignments.

Nevertheless, attention should be taken whenever conducting such response-effect approaches, especially regarding the conceptual mismatch between Grinnellian (e.g., niche as habitat) and Eltonian (e.g., niche as function) niche perspectives (Rosado et al. 2016). First, studies based on the assessment of annelid traits from large datasets to disentangle assembly mechanisms at regional scales (grinnelian view) have not validated their functional significance (SRFs) at local scales within the studied systems (eltonian view) (Rosado et al. 2016). So, the lack of relevant information on species biology, evolution, and population dynamics significantly hampers the detection of response traits that condition community assembly, as traits that predict species coexistence patterns across broad environmental gradients might not explain how they coexist at local scales (Rosado et al. 2010, 2016). Second, the inverse theoretical pathway of scaling organismal contributions (local scale) to understand ecosystem functioning (broad scale) is also deeply affected by two influential aspects widely neglected in the literature: the extent of intraspecific trait variation (especially along species ontogeny), and the lack of realized field measurements of effect traits proximally related to fitness (Chacon-Labella et al. 2023). Basically, approaches oriented by laboratory experiments to build up potential trait information are intrinsically assuming that phenotypes are static unities (lack of phenotypic responses) and that the simulated observations are enough to understand organismal performance (lack of contextual dependency), a methodological bias that ignores the response-effect overlap, as ecosystem functioning is the end result of a hierarchy of multiple acting processes emerging initially from organismal responses to the surrounding biotic and abiotic setting (Lavorel & Garnier 2002). Thus, future work on annelid functional ecology should explore these aspects in benthic systems in more detail.

Beyond the mismatch of niche concepts within trait-based ecology overall (Rosado et al. 2016), criticism on the reliance on potential traits within benthic ecology has often centered on the usage of extrapolated information compiled from geographically and taxonomically heterogeneous data sources as well (Lam-Gordillo et al. 2020; de Juan et al. 2022).

Accordingly, recent studies have adopted more rigorous approaches to address this issue by combining high-quality potential trait information derived from well-curated regional databases (Beauchard et al. 2022, 2023; Martins et al. 2026). In the case of marine annelids, although realized measurements for several traits related to reproduction, growth and survival are lacking for most species, trait datasets focusing on morphology and body-plan organization have revealed consistent and ecologically meaningful patterns of trait diversity responses along environmental gradients (Pagliosa 2005; Otegui et al. 2016; Mendes et al. 2025).

For several taxonomic groups, including Annelida, morphological traits have been widely used to assess responses to environmental variation, largely because they are relatively accessible through the consultation of previous specialized zoological literature and species descriptions, both based on realized individual-level measurements (Nishida et al. 2002; Sigwart et al. 2015; Otegui et al. 2016; Malpica et al. 2017). Such information is often considered as reliable potential traits due to the assumption that some morphological traits can be conserved at higher taxonomic levels, reflecting the way the species explore the surrounding environment, capture food and, thus, mediate their overall impact on ecosystems (Otegui et al. 2016; Crane & Merz 2017; Malpica et al. 2017; Cerca et al. 2020; Mendes et al. 2025). Yet, the presence of phylogenetic signal is implicitly assumed without a proper test, representing a prolific research avenue for future work.

Particularly in relation to organism–environment interactions, morphological traits of annelids might, in fact, exhibit strong and proximal links to fitness by influencing movement efficiency, body mechanical support, food processing, and defence, all of them directly connected to the life habits and "ecological position" of the worm (Pagliosa 2005; Otegui et al. 2016; Dorgan 2018; Gonzalez et al. 2018, 2021; Mendes et al. 2025). By directly influencing how individuals interact with and modify their surroundings, morphology has also been found to exert a key role in mediating annelid species responses to abiotic factors (Crane & Merz 2017; Grimes et al. 2021; Ferri et al. 2024). From an evolutionary perspective, worm morphology has been shown to either respond significantly in relation to distinct life habits (Gonzalez et al. 2018, 2021) or remain relatively conserved under selective pressures that favor efficient persistence within a given environmental context (Cerca et al. 2020), thereby reinforcing its functional relevance. In this sense, using morphological traits to infer ecological processes, coupled with efforts to generate new empirically derived trait data, provides a more robust approach to counterbalance the current prevalence of Raunkiæran shortfalls (SFs) related to relying on potential traits inferred from higher taxonomic levels.

An illustrative example of morphology as a "proximal trait" was provided by Crane & Merz (2017), who modeled two lugworm species' morphological responses to sediment characteristics, especially from an ultrastructural perspective. Their results demonstrated that individuals from the species inhabiting firmer sediments possessed thicker body-wall musculature and maintained more rigid body postures than the other one occurring in softer sediments. In addition, subtle differences were detected in the papillae covering the proboscis surface, potentially influencing worm–sediment interactions by enhancing excavation efficiency. Another example was published by Grimes et al. (2021), as the authors demonstrated that fireworms can display significant changes in branchial morphology in response to chronic hypoxia. So, these findings highlight that even traits commonly classified as "soft" may exhibit strong proximal relationships with organismal performance and fitness

under specific environmental conditions (Violle et al. 2007). Pagliosa (2005), Otegui et al. (2016), Otegui et al. (2024) and Mendes et al. (2025) also found strong evidence in favor of morphological traits' responsiveness to environmental gradients, with distinct annelid ecomorphological body plans showing contrasting responses to variation in abiotic conditions along multiple spatial and temporal scales.

Finally, not all traits reported in the literature have a clear functional meaning. Many are broadly classified as 'biological', 'ecological', or 'demographic' traits based on population-level observations, affinities to abiotic conditions, or taxonomic information, rather than reflecting individual-level SRFs or SEFs that ultimately capture organismal fitness (Martini et al. 2021). As such, they lack true response–effect functionality (Violle et al. 2007; Martini et al. 2021; de Bello et al. 2023). This includes traits and indices that have been previously criticized within marine functional ecology (Beauchard et al. 2017; Martini et al. 2021), such as the ecological indicator role, captured by AMBI index (along with its derivatives), and several traits describing biological preferences that are more closely associated with sampling location characteristics, then, leading to tautological reasonings when implemented within a functional perspective (Martini et al. 2021). Therefore, we emphasize that trait selection must be conducted with caution and guided by a clear hypothesis-driven framework linked to organismal biology, the studied system context, and spatio-temporal scale (Rosado et al. 2013).

On the Raunkiæran shortfalls: What types of scientific questions have been addressed, and are the selected traits mechanistically linked to them?

Most primary research questions have focused on describing the functional structure of polychaete assemblages and benthic communities, revealing a clear increase in interest over time. These studies have largely investigated how communities respond to natural environmental gradients, biological invasions, climate change, and a wide range of anthropogenic disturbances and stressors (Oug et al. 2012, 2018; Medeiros et al. 2021; Clemente et al. 2025). We suggest that this trend of positive growth may be driven by three main factors: (1) the increasing availability of data papers on benthic invertebrates traits across multiple regions (e.g., Degen & Faulwetter 2019; Meijer et al. 2023), alongside dedicated syntheses of annelid biological traits (e.g., Faulwetter et al. 2014; Jumars et al. 2015; Otegui et al. 2016); (2) the incipient accessibility of analytical frameworks and statistical routines publicly available on online repositories to be runned in open source softwares, facilitating the application of similar approaches by independent researchers (Mendes et al. 2015; Dray et al. 2014; Beauchard et al. 2017; de Bello et al. 2021a); and (3) a broader recognition of the importance of trait-based ecology for biodiversity conservation in the current scenario of climate change threats (Green et al. 2022; de Bello et al. 2023). Together, we argue that these developments have established a common ground for stimulating ecological research based on the assessment of communities' functional diversity, especially in benthic systems through the lens of annelids and several other invertebrate phyla (Beauchard et al. 2017; Beauchard et al. 2023; Bolam et al. 2023).

In the last 20 years, several systematic reviews were conducted in the context of benthic functional ecology (Bremner et al. 2003; Bremner et al. 2006b; Beauchard et al. 2017; de Juan et al. 2022; Martins et al. 2022; Beauchard et al. 2023) and also within attempts to provide an

unified perspective of trait-based ecology in aquatic sciences as a whole (Kiørboe et al. 2018; Martini et al. 2021). The authors converged on several arguments regarding trait functional meaning, trait measurement approaches, trait selection biases, nomenclatural ambiguities, and trait diversity analysis routines. These issues have been summarized by Keller et al. (2023), indicating ten rules to properly incorporate trait information within trait-based approaches.

However, despite such conceptual advances advocating for more informed trait selection, a widespread practice persists, in which multiple traits are combined to characterize the functional diversity of benthic communities or annelid assemblages under the assumption that increasing the number of traits inherently captures a greater extent of niche dimensions, encompassing broader facets of the phenotypic integration continuum (Beauchard et al. 2017; Fontana et al. 2021). In parallel, with the growing availability of functional trait datasets, we also observed an increased uncertainty regarding the choice of appropriate methods and conceptual frameworks to guide trait selection and soundly address ecological questions (Rosado et al. 2013, 2016; Keller et al. 2023). This issue is particularly critical given that organism–environment interactions — density- and non-density-dependent — are inherently scale- and context-dependent, which complicates the identification of biologically meaningful relationships linking trait syndromes to community assembly processes (response framework) or ecosystem functioning (effect framework) (Rosado et al. 2013, 2016; Keller et al 2023; de Bello et al 2023). As a result, this scenario often promotes the uncritical use of easily "accessible and justifiable" attributes called "fashionable traits", that always "get along" with every research question, irrespective of hypothesis, scale and biological context (Rosado et al. 2013).

A representative example of the "fashionable trait selection" problem was highlighted by Beauchard et al. (2017), particularly regarding the frequent conflation of species diet and feeding mode. Although feeding mode is among the most commonly incorporated traits in the extracted literature, several studies treat terms such as "feeding strategy," "diet," "food preference," "trophic position," "primary food source," "trophic group," "feeding guild," and "feeding type" as interchangeable terms (Table 2). However, diet and feeding mode capture distinct dimensions of species' nutritional ecology and should not be used analogously (Raubenheimer & Boggs 2009). Their indiscriminate synonymization undermines conceptual clarity and may lead to incorrect associations between research questions and trait selection.

In contrast to the observed emergence in the assessment of functional structure of benthic communities from the combination of multiple "fashionable traits", studies measuring traits related to species ecophysiology and ecosystem impacts have declined over time, whereas others focusing on annelid behavioral ecology, functional morphology, trophic ecology, and trait compilations remain scarce and stagnant. Despite this, investigations on species impacts have predominantly incorporated effect traits related to sediment biogeochemistry and bioengineering (Volkenborn et al. 2007; Dornhoffer et al. 2015; de Smet et al. 2016; Jones et al. 2018, 2020; Anglade et al. 2023; Ventura et al. 2024; Martins et al. 2026), while ecophysiological approaches have largely focused on species metabolic responses to multiple abiotic stressors, often framed within the context of climate change, revealing species tolerance limits (Lucey et al. 2020; Fernandes et al. 2023; Sánchez-Ovando 2025). In these cases, trait selection tended to be strongly supported by a theoretical and physiological basis, therefore presenting an expected mechanistic link with study questions. Moreover, studies addressing

species impacts, particularly those linking annelid assemblages or benthic community functional structure with ecosystem processes, consistently support the expectation that higher levels of taxonomic and functional diversity enhance ecosystem functioning and, consequently, the delivery of ecosystem services (Belley et al. 2016; Politi et al. 2025).

On the social structuring of the research field

The present review frames the functional ecology of marine annelids as an interdisciplinary field at the interface between zoological research on the phylum and marine ecology, being particularly characterized by evolving conceptual and methodological frameworks addressing community assembly and ecosystem functioning from a trait perspective. However, the field was observed to be centered within a pronounced context of geopolitical fragmentation. Our findings indicate that it has also matured into distinct and well-separated domains of scientific production under a gradual shift towards open science practices, but marked by a decoupling between publication volume and overall citation impact. These patterns align with broader trends in the social structuring of diverse scientific research agendas, especially those lying within biodiversity-related subdisciplines (Titley et al. 2017; Maitner et al. 2023).

While the upward trend observed since 2010, followed by the sharp increase in publication amount after 2019, reflects the expansion of the academic community, the concurrent decline in recent citation metrics suggests that the growing volume of research has not yet been translated into a proportional increase in scholar impact. This pattern becomes qualitatively evident when the total number of publications per year is contrasted with both average total citations per article and annual citation counts, revealing an apparent inverse relationship between productivity and citation performance over time. Part of this tendency may be likely explained by the natural delay required for newly published studies to accumulate citations. Even so, it also reflects a broader proliferation of comparatively low-impact recent publications, particularly those focusing on functional diversity modeling of benthic communities that are based on weakly justified potential trait selection and poor-resolution species trait assignments.

Because trait-coding resolution directly influences analytical outcomes (Kohli & Jarzyna 2021), such methodological limitations may ultimately lead to questionable ecological interpretations and an overall citation of previous studies that have coded the same traits with higher refinement for their focal study systems, ultimately establishing general multi-trait combinations that have been considered by the scientific community as a guide for subsequent works (e.g., Bremner et al. 2003; Bremner et al. 2006a,b; Oug et al. 2012). It explains the enduring influence of seminal contributions published before 2010 (e.g., Bremner et al. 2003; Bremner et al. 2006a,b) that further accentuate the apparent decline in the impact of more recent publications.

These temporal patterns in publication impact also highlight an important limitation of citation-based metrics themselves. Although citation counts often convey an appearance of "objectivity" regarding the relevance of a study and the magnitude of its contributions, they are strongly shaped by subjective and socioeconomical factors (Leimu & Koricheva 2005; Fox et al. 2016). Such influences extend beyond scientific quality alone and include authorship-related

characteristics, such as countries and institutions, as well as rhetorical aspects, such as writing persuasiveness and flattery (Leimu & Koricheva 2005). Editorial variables, including publication fees, review process duration, publishing delay, manuscript length, and the number of cited references, have likewise been shown to affect citation performance (Leimu & Koricheva 2005; Alves-Silva 2016; Fox et al. 2016; Tang et al. 2017). Within marine annelid functional ecology, our findings suggest that these biases may be particularly associated with geographic disparities in research visibility and impact. Indeed, the field appears to operate within distinct oceanic and political silos sustained by localized co-authorship networks, while the dissemination of scientific influence remains concentrated within a relatively small and highly centralized core of marine science journals. Consequently, future studies should also examine how structural and geographic inequalities shape the production, circulation, and recognition of functional trait knowledge, also for benthic invertebrates (de Juan et al. 2022).

Despite the abovementioned issues, a positive trend was observed in the increasing level of computational reproducibility of published studies, although many works still lacked the coding routines necessary to achieve a complete analytical replication. This represents an important advance that should be further encouraged, particularly because ecological analyses have become progressively more complex and sophisticated over time. So, reviewers and readers must be able to accurately follow the decision-making processes underlying the reported results (Powers et al. 2019). Achieving this level of transparency requires that authors ensure, at the time of manuscript submission, that an independent researcher could reproduce the findings presented in the paper using the provided code and data. Such reproducibility depends not only on the availability of raw code and/or datasets, but also on their clear and comprehensive documentation (Powers et al. 2019). A representative example of such good practice is the work conducted by Nogueira et al. (2023), when the authors analyzed the functional structure of annelid assemblages associated with corals and made the data publicly available. Within trait-based ecology, reproducibility becomes especially relevant when studies rely on subjective or literature-based trait coding schemes, making the proper referencing and justification of trait information essential (Keller et al. 2023).

Nevertheless, although the complete documentation of datasets has become increasingly common in the analyzed literature as a whole, a parallel tendency toward studies leaving the data only partially available also emerged. This limitation is mainly expressed in two ways. First, some studies provide only final trait scores, often accompanied by generalized references for all species or no supporting references at all, while omitting species incidence matrices and abiotic environmental data. Second, others make trait data available, with adequate references supporting the assigned scores, but provide species incidence and abiotic data only in summarized forms, such as mean values per sampling station, rather than the raw replicate-level data necessary for full reproducibility and reanalysis. In both situations, readers and reviewers may still be able to reconstruct trait dissimilarity matrices and perform subsequent dimensionality reduction analyses. However, these represent only preliminary stages of the analytical workflow and, thus, are insufficient for the complete reproducibility of the reported results (Powers et al. 2019). Consequently, such practices continue to limit research transparency and hinder the consolidation of a fully open-science framework within this research domain.

On the cognitive structuring of the research field

The field of marine annelid functional ecology has historically been structured around three major and interconnected conceptual foundations: the analysis of the biological trait-based structure of benthic communities (Cluster I), the role of species and/or "functional entities" in mediating sediment biogeochemical processes (Cluster II), and the life history, trophic, and ecophysiological responses of organisms to biotic interactions, environmental stressors, and disturbances (Cluster III). Together, these thematic domains constitute the intellectual backbone of the discipline, allowing the integration of trait information on organismal responses and effects across multiple ecological scales. Within the broader scope of the so-called "Polychaete science" or "Polychaetology", several studies have previously quantified and characterized the scientific effort directed toward deepening knowledge about the phylum Annelida (Magalhães et al. 2021; Nascimento et al. 2023). In particular, Brazil has consistently emerged as one of the main global centers of annelid research, largely due to the presence of numerous prolific researchers and consolidated research groups dedicated to ecology and systematics (Lana et al. 2017; Magalhães et al. 2021; Nascimento et al. 2023). Moreover, a previous scientometric assessment, focusing on the "Brazilian polychaete school", identified three major conceptual axes within annelid-related research: taxonomic studies, ecotoxicological investigations, and broader ecological approaches, including the assessment of functional diversity in estuarine systems (Nascimento et al. 2023). Our results strongly align with these earlier descriptive syntheses, while simultaneously expanding them through a trait-based perspective. Moreover, the thematic structure recovered here closely mirrors the conceptual organization previously described for general benthic trait-based ecology (Lam-Gordillo et al. 2020), reinforcing the notion that marine annelid functional ecology has developed in parallel with broader transformations occurring within benthic ecological research and "Polychaetology".

In this sense, the observed clusters not only reflect recurring research topics within marine annelid functional ecology but also reveal how methodological approaches and research priorities have historically interacted to shape its socio-cognitive architecture. Early and intermediate phases of the field were largely characterized by localized studies on model organisms and relatively compartmentalized analytical perspectives, with emphasis placed on describing species traits, linking organismal activity to sedimentary processes, and evaluating physiological tolerances under specific environmental conditions. Subsequently, as analytical tools and trait data became increasingly available over the years, the description of community functional diversity became a widespread milieu, manifesting a growing tendency that was consolidated after the COVID-19 pandemic.

The pandemic period appears to have consolidated the tendency toward broader thematic reorganization within the research domain. Beyond its immediate logistical and operational impacts on scientific activity, the pandemic accelerated an ongoing transition toward more integrative, synthetic, and large-scale analytical practices, particularly those relying on collaborative laboratory networks from which previously established research datasets have been shared (Chacón-Labella et al. 2020). In this context, gradient-based analyses of functional trait diversity rapidly gained momentum through greater thematic development and centrality in the marine annelid functional ecology domain. Such approaches, especially

1148 those based on potential traits coding from previously built databases, are comparatively
1149 independent of laboratory experimentation and field sampling, thus allowing research
1150 productivity to persist despite the severe restrictions imposed during lockdown periods.
1151 Consequently, a relative decline in density and thematic centrality was observed among
1152 studies focused on bioturbation modelling. Investigations grounded in traditional model
1153 organisms and highly developed methodological routines also suffered thematic changes, as
1154 they became proportionally more confined to narrower cognitive and methodologically niched
1155 themes. Moreover, although previous works were conducted towards building systematic
1156 reviews and bibliometric accounts on trait based benthic ecology (e.g., Bremner et al. 2006b;
1157 Bremner et al. 2008; Beauchard et al. 2017; Lam-Gordillo et al. 2020; Martini et al. 2021; de
1158 Juan et al. 2022; Martins et al. 2022), none of them incorporated the effect of pandemics on the
1159 structuring of marine functional ecology. Herein, we demonstrated that it has a non-negligible
1160 effect on the conceptual structure of marine annelids functional ecology research field; thus, it
1161 has probably exerted relevant influences in benthic ecology that should be prospected in future
1162 works.
1163
1164 **FUTURE DIRECTIONS**
1165
1166 The present synthesis demonstrates that progress toward overcoming the Raunkiæran
1167 shortfalls regarding marine annelids has been highly asymmetric across the three major
1168 cognitive domains that structure this research field, herein referred to as Clusters I, II, and III.
1169 Firstly, Cluster I prevailed in the analyzed literature, a cognitive domain that focuses on the
1170 description of functional diversity of benthic communities and/or annelid assemblages, which
1171 is predominantly based on modeling multiple-trait variation across environmental gradients
1172 between species. This approach has substantially advanced our understanding of patterns of
1173 community assembly in marine systems across natural environmental gradients and within the
1174 context of anthropogenic perturbations. However, this apparent progress is often underpinned
1175 by fashionable trait information from database consulting, with many studies relying on
1176 potential rather than realized life history and functional trait measurements, usually
1177 extrapolating trait data from congeneric or confamilial taxa. Therefore, the expansion of trait-
1178 based ecology of marine annelids has been driven more by the circulation and reuse of poor-
1179 resolution trait information than by the generation of new empirical knowledge, a combination
1180 that might cause serious biases in study conclusions (Kohli & Jarzina 2021). Taken together,
1181 the conclusions from conceptual and bibliometric perspectives are aligned, as these aspects
1182 reinforce the need to prioritize the establishment of properly designed protocols for realized
1183 trait measurements rather than relying predominantly on database-derived potential trait
1184 information, especially for species sampled outside the North Atlantic, where direct
1185 observations on species traits remain comparatively scarce.
1186 In contrast, Clusters II and III constitute the principal engines of realized trait
1187 observations within the field. Through ecophysiological experiments and the quantification of
1188 species effects on ecosystem processes, respectively, these domains generate the real
1189 measurements that support the construction of SRFs and SEFs, thereby allowing the
1190 establishment and testing of the hypothetical mechanistic links between “form and function”,
1191 especially in the context of species tolerance limits, biological interactions and effects on key

ecosystem processes. Yet, despite their central role in reducing the Raunkiæran shortfalls related to basic empirical information on trait acquisition and the subsequent mechanistic linkages with organismal performance and fitness dimensions within response-effect perspectives, these domains remain comparatively small and are characterized by a slow accumulation rate of knowledge, often concentrated on a limited subset of model species. This imbalance reveals a fundamental bottleneck for the future of annelid functional ecology, as the predictive power of trait-based approaches ultimately depends on the continuous production of empirical trait data capable of incorporating SRFs and SEFs across broader ecological and evolutionary contexts. Therefore, future research should prioritize expanding Clusters II and III, providing high-quality trait information for newer species.

Besides the cognitive domains, geopolitical biases, research trends, and major study areas identified herein, trait-based studies of marine annelids remain constrained by several key challenges previously highlighted by Wilkes et al. (2020). These include disentangling statistical correlations among traits, accounting for phylogenetic constraints on species trait syndromes, and quantifying how spatial processes shape both trait structure and trait–environment relationships. Trait correlations arise when combinations of traits confer integrated ecological advantages, resulting in recurrent trait syndromes associated with specific environmental conditions and exerting non-negligible effects on functional diversity modeling (Beauchard et al. 2017; Wilkes et al. 2020). Addressing these correlations requires a multidimensional understanding of annelid phenotypes, because functionally dissimilar species may achieve similar performance under the same environmental conditions through alternative phenotypic designs (Dias et al. 2020). Such "alternative designs" are ultimately affected by community assembly, where multitrait covariance structures and trait interactions are shaped simultaneously by environmental filtering and other selective processes, a prospect that has been rarely tested in ecological literature overall (Dias et al. 2020). These issues can be investigated through approaches such as trait probability density functions, multivariate trait diversity indexes, modeling frameworks, and statistical tests for bivariate relationships between traits and environmental factors (Dray et al. 2014; Carmona et al. 2019; Beccari et al. 2024; Rohr et al. 2025). Likewise, incorporating phylogenetic information and reconstructing trait evolution can help disentangle whether observed trait syndromes within communities reflect organismal plasticity or shared ancestry, a dichotomy deeply affected by evolutionary trade-offs or spin-offs that constrain the range of viable trait combinations to couple with the surrounding environment (Cornwell & Nakagawa 2017; Wilkes et al. 2020).

An additional poorly explored potential of integrating high-resolution functional trait measurements with evolutionary information is the enhanced capacity to detect, quantify, and predict the ecosystem goods and services provided by species (Villéger et al. 2017). Ecosystem goods comprise tangible products derived from natural systems for human use, whereas ecosystem services encompass the ecological processes and conditions through which ecosystems and their constituent species sustain human well-being (Brown et al. 2007). Consequently, understanding the long-term sustainability of ecosystem services under global environmental change requires robust knowledge of both how organisms contribute to ecosystem functioning and how their functional roles may be altered by changing environmental conditions, processes that are fundamentally mediated by species traits.

Despite increasing recognition of the value of trait-based approaches, our understanding of the direct and indirect pathways through which invertebrates influence ecosystem services remains limited (Prather et al. 2013). This knowledge gap is particularly relevant for marine annelids, which, through activities such as feeding, bioturbation, bioirrigation, biogenic structures construction, and the formation of complex gallery networks, can regulate microbial communities, enhance nutrient cycling, modify habitat structure, provide nursery spots for other species, and, in synthesis, promote overall biodiversity maintenance in benthic ecosystems (Kollars et al. 2016; Liversage et al. 2018; Martins et al. 2026; Reynolds et al. 2026). However, the contribution of annelid functional diversity to ecosystem services remains poorly quantified, with recent advances detected regarding their bioturbation potential, habitat creation, bioremediation of intensive fish farming waste and related fisheries provisioning services, whose supply, demand, and societal value exhibit strong regional variation (Marques et al. 2018; Cole et al. 2018; Nederlof et al. 2020; Pombo et al. 2020; Martins et al. 2026).

Beyond the priorities identified by de Juan et al. (2022), Gonçalves-Souza et al. (2023) and de Bello et al. (2026) for reducing the Raunkiæran shortfalls and properly addressing better practices for biodiversity conservation from a trait perspective under the current scenario of climate change, our study reveals annelid-specific knowledge gaps that remained poorly addressed. We therefore outline key research priorities below, highlighting 9 critical directions for advancing the understanding of marine annelids' functional ecology (Box 1).

Box 1: Summary of the future directions for advancing marine annelids' functional ecology based on the current scientific knowledge

1. Develop robust and reproducible protocols to properly measure annelid functional traits: from ecophysiology and ecomorphology to their underlying impacts on marine ecosystems.
2. Capture patterns of intraspecific variation of species traits in the context of community assembly and organismal ecosystemic impacts across broad spatio-temporal gradients.
3. Establish robust SRFs and SEFs to quantify trait correlations, trade-offs, and spin-offs across the annelid phenotypic integration continuum, identifying alternative designs of trait combinations that achieve similar ecological performance.
4. Track annelid functional trait evolution and the subsequent influence of phylogenetic conservatism of their niches on the observed patterns of trait diversity across distinct environmental gradients.
5. Advance the understanding of annelid biotic interactions and integrate their ecological and evolutionary consequences into broader community and ecosystem-level frameworks.
6. Compilate and refine such trait information into comprehensive databases.
7. Properly quantify the ecosystem services provided by marine annelids.
8. Incorporate explicitly functional trait information on marine biodiversity conservation planning

9. Dissect the patterns, causes, and consequences of the geographic distribution of annelid traits worldwide.

Addressing these challenges, therefore, should constitute a central research priority. Integrating annelid functional ecology within an explicit evolutionary framework would not only improve our understanding of how trait syndromes have originated, varied intraspecifically, and diversified through time, but also provide critical insights into the evolutionary processes underpinning patterns of functional diversity across benthic ecosystems. Such advances would ultimately move the field toward a truly evolutionary-oriented trait-based ecology, linking ecological function, phylogeny, biodiversity patterns, and ecosystem services across fine to broad spatial and temporal scales, thus providing proper information to guide conservation policies to protect marine ecosystems worldwide.

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REFERENCES

Albert CH, Grassein F, Schurr FM, Vieilledent G, Violle C (2011) When and how should intraspecific variability be considered in trait-based plant ecology? Perspect Plant Ecol Evol Syst 13(3):217–225. https://doi.org/10.1016/j.ppees.2011.04.003

Alkhammash R (2023) Bibliometric, network, and thematic mapping analyses of metaphor and discourse in COVID-19 publications from 2020 to 2022. Front Psychol 13:1062943. https://doi.org/10.3389/fpsyg.2022.1062943

Alves-Silva E, Porto AC, Firmino C, Silva HV, Becker I, Resende L, Borges L, Pfeffer L, Silvano M, Galdiano MS, Silvestrini R (2016) Are the impact factor and other variables related to publishing time in ecology journals? Scientometrics 108(3):1445–1453. https://doi.org/10.1007/s11192-016-2040-0

Anglade I, Kristensen BS, Dahl TH, Hagemann A, Malzahn AM, Reitan KI (2023) Upcycling of carbon, nitrogen, and phosphorus from aquaculture sludge using the polychaete Hediste

diversicolor (OF Müller, 1776) (Annelida: Nereididae). Front Sustain Food Syst 7:1278586. https://doi.org/10.3389/fsufs.2023.1278586

Aria M, Cuccurullo C (2017) bibliometrix: An R-tool for comprehensive science mapping analysis. J Informetr 11(4):959–975. ttps://doi.org/10.1016/j.joi.2017.08.007

Araújo MS, Bolnick DI, Layman CA (2011) The ecological causes of individual specialisation. Ecol Lett 14(9):948–958. https://doi.org/10.1111/j.1461-0248.2011.01662.x

Bartolomaeus T, Purschke G (2005) Morphology, molecules, evolution and phylogeny in Polychaeta and related taxa. Springer Science & Business Media, Berlin

Batagelj V, Cerinsek M (2013) On bibliographic networks. Scientometrics 96(3):845–864. https://doi.org/10.1007/s11192-012-0940-1

Beauchard O, Veríssimo H, Queirós AM, Herman PM (2017) The use of multiple biological traits in marine community ecology and its potential in ecological indicator development. Ecol Indic 76:81–96. https://doi.org/10.1016/j.ecolind.2017.01.011

Beauchard O, Mestdagh S, Koop L, Ysebaert T, Herman PM (2022) Benthic synecology in a soft sediment shelf. Mar Ecol Prog Ser 682:31-50. https://doi.org/10.3354/meps

Beauchard O, Thompson MS, Ellingsen KE, Piet G, Laffargue P, Soetaert K (2023) Assessing sea floor functional biodiversity and vulnerability. Mar Ecol Prog Ser 708:21–43. https://doi.org/10.3354/meps14270

Beccari E, Capdevila P, Salguero-Gómez R, Carmona CP (2024) Worldwide diversity in mammalian life histories: environmental realms and evolutionary adaptations. Ecol Lett 27:e14445. https://doi.org/10.1111/ele.14445

Belley R, Snelgrove PVR (2016) Relative contributions of biodiversity and environment to benthic ecosystem functioning. Front Mar Sci 3:242. https://doi.org/10.3389/fmars.2016.00242

Bolam SG, Cooper K, Downie AL (2023) Mapping marine benthic biological traits to facilitate future sustainable development. Ecol Appl 33:e2905. https://doi.org/10.1002/eap.2905

Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM, Novak M, Rudolf VHW, Schreiber SJ, Urban MC, Vasseur DA (2011) Why intraspecific trait variation matters in community ecology. Trends Ecol Evol 26:183–192. https://doi.org/10.1016/j.tree.2011.01.009

Bradford SC (1934) Sources of information on specific subjects. Engineering 137:85–88

Bremner J, Rogers SI, Frid CLJ (2003) Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. Mar Ecol Prog Ser 254:11–25. https://doi.org/10.3354/meps254011

Bremner J, Rogers SI, Frid CLJ (2006a) Matching biological traits to environmental conditions in marine benthic ecosystems. J Mar Syst 60:302–331. https://doi.org/10.1016/j.jmarsys.2006.02.004

Bremner J, Rogers SI, Frid CLJ (2006b) Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). Ecol Indic 6:609–622. https://doi.org/10.1016/j.ecolind.2005.08.026

Bremner J (2008) Species' traits and ecological functioning in marine conservation and management. J Exp Mar Biol Ecol 366:37–47. https://doi.org/10.1016/j.jembe.2008.07.007

Brown TC, Bergstrom JC, Loomis JB (2007) Defining, valuing, and providing ecosystem goods and services. Nat Resour J 47:329–376

Callon M, Courtial JP, Laville F (1991) Co-word analysis as a tool for describing the network of interactions between basic and technological research: the case of polymer chemistry. Scientometrics 22:155–205. https://doi.org/10.1007/BF02019280

Cardoso P, Erwin TL, Borges PAV, New TR (2011) The seven impediments in invertebrate conservation and how to overcome them. Biol Conserv 144:2647–2655. https://doi.org/10.1016/j.biocon.2011.07.024

Carmona CP, de Bello F, Mason NWH, Lepš J (2019) Trait probability density (TPD): measuring functional diversity across scales based on TPD with R. Ecology 100:e02876. https://doi.org/10.1002/ecy.2876

Carmona CP, Beccari E (2025) The path toward a unified trait space: synthesizing plant functional diversity. New Phytol 248:2236–2242. https://doi.org/10.1111/nph.70584

Cerca J, Meyer C, Stateczny D, Siemon D, Wegbrod J, Purschke G, Dimitrov D, Struck TH (2020) Deceleration of morphological evolution in a cryptic species complex and its link to paleontological stasis. Evolution 74:116–131. https://doi.org/10.1111/evo.13884

Clemente CC, Paresque K, Santos CS, Santos PJ (2025) Small-scale spatial pattern of the trophic structure of polychaetes from coral reefs: implications of future sea level rise. Estuar Coast Shelf Sci 316:109162. https://doi.org/10.1002/ece3.7026

Chacón-Labella J, Boakye M, Enquist BJ, Farfan-Rios W, Gya R, Halbritter AH, Middleton SL, von Oppen J, Pastor-Ploskonka S, Strydom T, Vandvik V et al (2021) From a crisis to an

opportunity: eight insights for doing science in the COVID-19 era and beyond. Ecol Evol 11:3588–3596. https://doi.org/10.1002/ece3.7026

Chacón-Labella J, Hinojo-Hinojo C, Bohner T, Castorena M, Violle C, Vandvik V, Enquist BJ (2023) How to improve scaling from traits to ecosystem processes. Trends Ecol Evol 38:228–237. https://doi.org/10.1016/j.tree.2022.10.007

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

Cooper N, BES Data and Code Hackathon Group (2026) Data- and code-archiving in the British Ecological Society journals: present status and recommendations for future improvements. Methods Ecol Evol 00:1–13. https://doi.org/10.1111/2041-210X.70338

Dean HK (2008) The use of polychaetes (Annelida) as indicator species of marine pollution: a review. Revista de biologia tropical 56(4): 11–38.

de Bello F, Carmona CP, Dias ATC, Götzenberger L, Moretti M, Berg MP (2021a) Handbook of trait-based ecology. Cambridge University Press, Cambridge

de Bello F, Botta-Dukát Z, Lepš J, Fibich P (2021b) Towards a more balanced combination of multiple traits when computing functional differences between species. Methods Ecol Evol 12:443–448. https://doi.org/10.1111/2041-210X.13537

de Juan S, Bremner J, Hewitt J, Törnroos A, Mangano MC, Thrush S, Hinz H (2022) Biological traits approaches in benthic marine ecology: dead ends and new paths. Ecol Evol 12:e9001. https://doi.org/10.1002/ece3.9001

Dias ATC, Rosado BH, de Bello F, Pistón N, de Mattos EA (2020) Alternative plant designs: consequences for community assembly and ecosystem functioning. Ann Bot 125:391–398. https://doi.org/10.1093/aob/mcz180

Díaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Prentice IC et al (2016) The global spectrum of plant form and function. Nature 529:167–171. https://doi.org/10.1038/nature16489

Diniz-Filho JAF, Loyola RD, Raia P, Mooers AO, Bini LM (2013) Darwinian shortfalls in biodiversity conservation. Trends Ecol Evol 28:689–695. https://doi.org/10.1016/j.tree.2013.09.003

Doherty-Weason D, Oyarzun F, Vera L, Bascur M, Guzmán F, Silva F, Urzúa Á, Brante A (2020) Bioenergetics of parental investment in two polychaete species with contrasting

reproductive strategies: the planktotrophic Boccardia chilensis and the poecilogonic Boccardia wellingtonensis (Spionidae). Mar Ecol 41:e12574. https://doi.org/10.1111/maec.12574

Dornhoffer TM, Waldbusser GG, Meile C (2015) Modeling lugworm irrigation behavior effects on sediment nitrogen cycling. Mar Ecol Prog Ser 534:121–134. https://doi.org/10.3354/meps11381

Dray S, Choler P, Dolédec S, Peres-Neto PR, Thuiller W, Pavoine S, ter Braak CJF (2014) Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. Ecology 95:14–21. https://doi.org/10.1890/13-0196.1

Fauchald K, Jumars PA (1979) The diet of worms: a study of polychaete feeding guilds. Oceanogr Mar Biol Ann Rev 17: 193–284.

Faulwetter MS, Markantonatou MV, Pavloudi MC, Papageorgiou N, Keklikoglou MK, Chatzinikolaou E, Arvanitidis C et al (2014) Polytraits: a database on biological traits of marine polychaetes. Biodivers Data J 2:e1024. https://doi.org/10.3897/BDJ.2.e1024

Fernandes JF, Calado R, Jerónimo D, Madeira D (2023) Thermal tolerance limits and physiological traits as indicators of Hediste diversicolor acclimation capacity to global and local change drivers. J Therm Biol 114:103577. https://doi.org/10.1016/j.jtherbio.2023.103577

Ferri A, Costa PM, Simonini R (2024) Secretory cells in Halla parthenopeia (Oenonidae): potential implications for the feeding and defence strategies of a carnivorous burrowing polychaete. J Morphol 285:e21781. https://doi.org/10.1002/jmor.21781

Fox CW, Paine CT, Sauterey B (2016) Citations increase with manuscript length, author number, and references cited in ecology journals. Ecol Evol 6:7717–7726. https://doi.org/10.1002/ece3.2505

Giangrande A (1997) Polychaete reproductive patterns, life cycles and life histories: an overview. Oceanogr Mar Biol Annu Rev 35:323–386

Giangrande A, Licciano M, Musco L (2005) Polychaetes as environmental indicators revisited. Mar Pol Bul 50(11): 1153–1162. DOI: 10.1016/j.marpolbul.2005.08.003.

Giese A (ed) (2012) Reproduction of marine invertebrates. Vol 3: Annelids and echiurans. Elsevier, Amsterdam

Gonzalez BC, Worsaae K, Fontaneto D, Martínez A (2018) Anophthalmia and elongation of body appendages in cave scale worms (Annelida: Aphroditiformia). Zool Scr 47:106–121. https://doi.org/10.1111/zsc.12258

Gonzalez BC, Martínez A, Worsaae K, Osborn KJ (2021) Morphological convergence and adaptation in cave and pelagic scale worms (Polynoidae, Annelida). Sci Rep 11:10718. https://doi.org/10.1038/s41598-021-89459-y

Green SJ, Brookson CB, Hardy NA, Crowder LB (2022) Trait-based approaches to global change ecology: moving from description to prediction. Proc R Soc B 289:1971. https://doi.org/10.1098/rspb.2022.0071

Grimes CJ, Paiva PC, Petersen LH, Schulze A (2020) Rapid plastic responses to chronic hypoxia in the bearded fireworm, Hermodice carunculata (Annelida: Amphinomidae). Mar Biol 167:140. https://doi.org/10.1007/s00227-020-03756-0

HilleRisLambers J, Adler PB, Harpole WS, Levine JM, Mayfield MM (2012) Rethinking community assembly through the lens of coexistence theory. Annu Rev Ecol Evol Syst 43:227–248. https://doi.org/10.1146/annurev-ecolsys-110411-160411

Hayman NT, Hentschel BT, Richardson K, Anderson TW (2020) Combined effects of predation, flow speed, and sub-lethal exposure to insecticide on the feeding behavior of a spionid polychaete. J Exp Mar Biol Ecol 524:151319. https://doi.org/10.1016/j.jembe.2020.151319

Hartati R, Widianingsih W, Riniatsih I, Kholilah N, Salim G, Mahendrajaya RT, Mujiyanto M (2025) Morphometric and length-weight relationship of six families of Polychaeta during the Bau Nyale season in Lombok Island, Indonesia. Egypt J Aquat Biol Fish 29:2005–2021

Jamieson BGM, Rouse GW, Pleijel F (2006) Reproductive biology and phylogeny of Annelida. Science Publishers, Enfield.

Jones AG, Dubois SF, Desroy N, Fournier J (2018) Interplay between abiotic factors and species assemblages mediated by the ecosystem engineer Sabellaria alveolata (Annelida: Polychaeta). Estuar Coast Shelf Sci 200:1–18. https://doi.org/10.1016/j.ecss.2017.10.001

Jones AG, Denis L, Fournier J, Desroy N, Duong G, Dubois SF (2020) Linking multiple facets of biodiversity and ecosystem functions in a coastal reef habitat. Mar Environ Res 162:105092. https://doi.org/10.1016/j.marenvres.2020.105092

Jumars PA, Dorgan KM, Lindsay SM (2015) Diet of worms emended: an update of polychaete feeding guilds. Annu Rev Mar Sci 7:497–520. https://doi.org/10.1146/annurev-marine-010814-020007

Kattge J, Bönisch G, Díaz S, Lavorel S, Prentice IC, Leadley P, Tautenhahn S, Werner GDA, Aakala T, Abedi M, Acosta ATR et al (2020) TRY plant trait database—enhanced coverage and open access. Glob Change Biol 26:119–188. https://doi.org/10.1111/gcb.14904

Keller A, Ankenbrand MJ, Bruelheide H, Dekeyzer S, Enquist BJ, Erfanian MB, Penone C et al (2023) Ten (mostly) simple rules to future-proof trait data in ecological and evolutionary sciences. Methods Ecol Evol 14:444–458. https://doi.org/10.1111/2041-210X.14033

Kohli BA, Jarzyna MA (2021) Pitfalls of ignoring trait resolution when drawing conclusions about ecological processes. Glob Ecol Biogeogr 30:1139–1152. https://doi.org/10.1111/geb.13275

Kin I, Oba Y (2020) Bioluminescent properties of Mesochaetopterus japonicus (Polychaeta: Chaetopteridae) with comparison to Chaetopterus. Plankton Benthos Res 15:228–231. https://doi.org/10.3800/pbr.15.228

Kollars N, Byers JE, Sotka EE (2016) Invasive décor: an association between a native decorator worm and a non-native seaweed can be mutualistic. Mar Ecol Prog Ser 545:135–145. https://doi.org/10.3354/meps11602

Kupriyanova EK, Nishi E, ten Hove HA, Rzhavsky AV (2001) Life-history patterns in serpulimorph polychaetes: ecological and evolutionary perspectives. Oceanogr Mar Biol Annu Rev 39:1–10

Ladle R, Hortal J (2013) Mapping species distributions: living with uncertainty. Front Biogeogr 5:8–9. https://doi.org/10.21425/F5FBG12942

Lee AL, Dafforn KA, Hutchings PA, Johnston EL (2018) Reproductive strategy and gamete development of an invasive fanworm, Sabella spallanzanii (Polychaeta: Sabellidae), a field study in Gulf St Vincent, South Australia. PLoS One 13:e0200027. https://doi.org/10.1371/journal.pone.0200027

Leimu R, Koricheva J (2005) What determines the citation frequency of ecological papers? Trends Ecol Evol 20:28–32. https://doi.org/10.1016/j.tree.2004.10.010

Lelièvre Y, Specq L, Lamy T, Boyé A, Downey RV, Saucède T (2023) Taxonomic and functional diversity of subtidal benthic communities associated with hard substrates at Crozet archipelago (sub-Antarctic, Southern Ocean). Front Mar Sci 10:1291038. https://doi.org/10.3389/fmars.2023.1291038

Liversage K (2018) First evidence of biogenic habitat from tubeworms providing a near-absolute habitat requirement for high-intertidal Ulva macroalgae. PLoS One 12:e0176952. https://doi.org/10.1371/journal.pone.0176952

Lucey NM, Collins M, Collin R (2020) Oxygen-mediated plasticity confers hypoxia tolerance in a corallivorous polychaete. Ecol Evol 10:1145–1157. https://doi.org/10.1002/ece3.5929

Macdonald TA, Burd BJ, Macdonald VI, Van Roodselaar A (2010) Taxonomic and feeding guild classification for the marine benthic macroinvertebrates of the Strait of Georgia, British Columbia. Fisheries and Oceans Canada, Ottawa.

McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. Trends Ecol Evol 21:178–185. https://doi.org/10.1016/j.tree.2006.02.002

Malpica A, Covarrubias S, Villegas-Patraca R, Herrera-Alsina L (2017) Ecomorphological structure of avian communities changes upon arrival of wintering species. Basic Appl Ecol 24:60–67. https://doi.org/10.1016/j.baae.2017.08.008

Marques B, Lillebø AI, Ricardo F, Nunes C, Coimbra MA, Calado R (2018) Adding value to ragworms (Hediste diversicolor) through the bioremediation of a super-intensive marine fish farm. Aquac Environ Interact 10:79–89. https://doi.org/10.3354/aei00255

Martini S, Larras F, Boyé A, Faure E, Aberle N, Archambault P, Bacouillard L, Beisner BE, Bittner L, Castella E, Danger M et al (2021) Functional trait-based approaches as a common framework for aquatic ecologists. Limnol Oceanogr 66:965–994. https://doi.org/10.1002/lno.11655

Martins AD, Barros F (2022) Ecological functions of polychaetes along estuarine gradients. Front Mar Sci 9:780318. https://doi.org/10.3389/fmars.2022.780318

Martins A, Di Domenico M, Costa Y, Barros F (2024) Overcoming challenges to access ecological function: a marine soft-bottom perspective. R Soc Open Sci 11

Martins A, Barros F, Krull M (2025) Assessing ecological functions through polychaete traits in estuarine sediments. Mar Environ Res 210:107334. https://doi.org/10.1098/rsos.241176

Martins A, Krull M, Barros F (2026) Scaling up polychaete contributions to estuarine ecosystem functions. Discov Ecol 2:6. https://doi.org/10.1007/s44396-026-00023-2

Massamba-N'Siala G, Carignan MH, Calosi P, Noisette F (2022) Metabolic rate thermal plasticity in the marine annelid Ophryotrocha labronica across two successive generations. J Mar Biol Assoc UK 102:69–75. https://doi.org/10.1017/S0025315422000303

Miatta M, Bates AE, Snelgrove PVR (2021) Incorporating biological traits into conservation strategies. Annu Rev Mar Sci 13:421–443. https://doi.org/10.1146/annurev-marine-032320-094121

Moritz C, Meynard CN, Devictor V, Guizien K, Labrune C, Guarini JM, Mouquet N (2013) Disentangling the role of connectivity, environmental filtering, and spatial structure on metacommunity dynamics. Oikos 122:1401–1410. DOI: 10.1111/j.1600-0706.2013.00377.x.

Munari M, Chiarore A, Signorini SG, Cannavacciuolo A, Nannini M, Magni S, Binelli A, Gambi MC, Della Torre C (2022) Surviving in a changing ocean: tolerance to acidification might affect the susceptibility of polychaetes to chemical contamination. Mar Pollut Bull 181:113857. https://doi.org/10.1016/j.marpolbul.2022.113857

Münkemüller T, Gallien L, Pollock LJ, Barros C, Carboni M, Chalmandrier L, Mazel F, Mokany K, Roquet C, Smyčka J, Talluto L et al (2020) Dos and don'ts when inferring assembly rules from diversity patterns. Glob Ecol Biogeogr 29:1212–1229. https://doi.org/10.1111/geb.13098

Muller A, Poitrimol C, Nunes FL, Boyé A, Curd A, Desroy N, Firth LB, Bush L, Davies AJ, Lima FP, Marzloff MP et al (2021) Musical chairs on temperate reefs: species turnover and replacement within functional groups explain regional diversity variation in assemblages associated with honeycomb worms. Front Mar Sci 8:654141. https://doi.org/10.3389/fmars.2021.654141

Nascimento RL, et al. (2022) The Fundão dam failure: Iron ore tailing impact on marine benthic macrofauna. Science of the Total Environment 838: 156205. DOI: 10.1016/j.scitotenv.2022.156205.

Nederlof MA, Fang J, Dahlgren TG, Rastrick SPS, Smaal AC, Strand Ø, Sveier H, Verdegem MCJ, Jansen HM (2020) Application of polychaetes in (de)coupled integrated aquaculture: an approach for fish waste bioremediation. Aquac Environ Interact 12:385–399. https://doi.org/10.3354/aei00371

Nishida S, Ohtsuka S, Parker AR (2002) Functional morphology and food habits of deep-sea copepods of the genus Cephalophanes (Calanoida: Phaennidae): perception of bioluminescence as a strategy for food detection. Mar Ecol Prog Ser 227:157–171. https://doi.org/10.3354/meps227157

Oug E, Fleddum A, Rygg B, Olsgard F (2012) Biological traits analyses in the study of pollution gradients and ecological functioning of marine soft bottom species assemblages in a fjord ecosystem. J Exp Mar Biol Ecol 432:94–105. https://doi.org/10.1016/j.jembe.2012.07.019

Oug E, Sundet JH, Cochrane SKJ (2018) Structural and functional changes of soft-bottom ecosystems in northern fjords invaded by the red king crab (Paralithodes camtschaticus). J Mar Syst 180:255–264. https://doi.org/10.1016/j.jmarsys.2017.07.005

Otegui MB, Brauko KM, Pagliosa PR (2016) Matching ecological functioning with polychaete morphology: Consistency patterns along sedimentary habitats. J Sea Res 114:13-21. https://doi.org/10.1016/j.seares.2016.05.001

Otegui MB, Brauko KM, Oortman MS, Pagliosa PR (2024) Body traits variation of a reef building polychaete across a latitudinal gradient. Mar Environ Res 194:106334. https://doi.org/10.1016/j.marenvres.2023.106334

Pardo EV, Dauer DM (2003) Particle size selection in individuals from epifaunal versus infaunal populations of the nereidid polychaete Neanthes succinea (Polychaeta: Nereididae). Hydrobiologia 496(1):355-360 https://doi.org/10.1023/A:1026181823273

Pérez-Posada I, Cabanillas-Terán N, Carrera-Parra LF, Lizcano DJ, Sánchez A (2025) Trophic ecology of Caribbean polychaetes: responses to environmental changes driven by massive Sargassum arrivals. Food Webs: e00411 https://doi.org/10.1016/j.fooweb.2025.e00411

Pombo A, Baptista T, Granada L, Ferreira SM, Gonçalves SC, Anjos C, Sá E, Chainho P, Cancela da Fonseca L, Fidalgo e Costa P, Costa JL (2020) Insight into aquaculture's potential of marine annelid worms and ecological concerns: a review. Rev Aquac 12:107–121. https://doi.org/10.1111/raq.12307

Politi T, Olenin S, Deja K, Oleszczuk B, Zilius M, Bonaglia S, Weslawski JM, Bartoli M (2025) Benthic metabolism and macrofauna bioturbation along a glacier-driven gradient in Kongsfjorden. Estuar Coast Shelf Sci 320:109304. https://doi.org/10.1016/j.ecss.2025.109304

Powers SM, Hampton SE (2019) Open science, reproducibility, and transparency in ecology. Ecol Appl 29:e01822. https://doi.org/10.1002/eap.1822

Prather CM, Pelini SL, Laws A, Rivest E, Woltz M, Bloch CP, Del Toro I, Ho CK, Kominoski J, Newbold TS, Parsons S (2013) Invertebrates, ecosystem services and climate change. Biol Rev 88:327–348. https://doi.org/10.1111/brv.12002

Prevedelli D, N'siala GM, Simonini R (2006) Gonochorism vs. hermaphroditism: relationship between life history and fitness in three species of Ophryotrocha (Polychaeta: Dorvilleidae) with different forms of sexuality. J Anim Ecol 75:203–212. https://doi.org/10.1111/j.1365-2656.2006.01040.x

Radhakrishnan P, Saboul N, Monclús R, Taboada S, Lorenzi MC (2026) Game over: conflict resolution through strategic growth in an invertebrate. Funct Ecol 40:36–50. https://doi.org/10.1111/1365-2435.70199

Raubenheimer D, Boggs C (2009) Nutritional ecology, functional ecology and Functional Ecology. Funct Ecol 23:1–3. https://doi.org/10.1111/j.1365-2435.2009.01530.x

R Core Team (2026) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Reu B, Proulx R, Bohn K, Dyke JG, Kleidon A, Pavlick R, Schmidtlein S (2011) The role of climate and plant functional trade-offs in shaping global biome and biodiversity patterns. Glob Ecol Biogeogr 20:570–581. https://doi.org/10.1111/j.1466-8238.2010.00621.x

Rohr M, Thuiller W, Chalmandrier L, Münkemüller T (2025) The role of observation scales, trait correlations, and competitive regimes in community assembly patterns. Ecol Evol 15:e71272. https://doi.org/10.1002/ece3.71272

Rouse G, Fitzhugh K (1994) Broadcasting fables: is external fertilization really primitive? Sex, size, and larvae in sabellid polychaetes. Zool Scr 23:271–312. https://doi.org/10.1111/j.1463-6409.1994.tb00390.x

Rouse GW (2000) Bias? What bias? The evolution of downstream larval-feeding in animals. Zool Scr 29:213–236. https://doi.org/10.1046/j.1463-6409.2000.00040.x

Rouse GW, Pleijel F, Tilic E (2022) Annelida. Oxford University Press, Oxford

Rosado BH, Dias ATC, de Mattos EA (2013) Going back to basics: importance of ecophysiology when choosing functional traits for studying communities and ecosystems. Nat Conserv 11:15–22. https://doi.org/10.4322/natcon.2013.002

Rosado BH, Figueiredo MS, de Mattos EA, Grelle CEV (2016) Eltonian shortfall due to the Grinnellian view: functional ecology between the mismatch of niche concepts. Ecography 39:1034–1041. https://doi.org/10.1111/ecog.01678

Sánchez-Ovando JP, Díaz F, Norzagaray-López O, Lafarga-De la Cruz F, Angeles-Gonzalez LE, Benítez-Villalobos F, Re-Araujo D (2025) Metabolic responses of Christmas tree worms (Serpulidae: Spirobranchus) to thermal acclimation. J Exp Zool A Ecol Integr Physiol 343:911–920. https://doi.org/10.1002/jez.70008

Sarker MJ, Sarker PK, Islam MA, Rima NN, Joydas TV, Sultana N, Islam MM, Hossain MY, Hossain MB (2024) Biometry, growth, and recruitment pattern of a commercially important nereid polychaete, Namalycastis fauveli, from the east coast of Bangladesh. J Mar Sci Eng 12:312. https://doi.org/10.3390/jmse12020312

Shimeta J (1996) Particle-size selection by Pseudopolydora paucibranchiata (Polychaeta: Spionidae) in suspension feeding and in deposit feeding: influences of ontogeny and flow speed. Mar Biol 126(3):479-488. https://doi.org/10.1007/BF00354630

Sigwart JD, Green PA, Crofts SB (2015) Functional morphology in chitons (Mollusca, Polyplacophora): influences of environment and ocean acidification. Mar Biol 162:2257–2264.https://doi.org/10.1007/s00227-015-2761-2

Siefert A, Violle C, Chalmandrier L, Albert CH, Taudiere A, Fajardo A, Aarssen LW, Baraloto C, Carlucci MB, Cianciaruso MV, Dantas VL, Bello F, Duarte LDS, Fonseca CR, Freschet GT, Gaucherand S, Gross N, Hikosaka K, Jackson B, et al (2015) A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. Ecol Lett 18:1406–1419. https://doi.org/10.1111/ele.12508

Sokołowski A, Świeżak J, Hallmann A, Ziółkowska M, Altin D, Øverjordet IB, Smolarz K (2025) Impact of CO_2-induced seawater acidification at increased hydrostatic pressure on cellular-level responses of the infaunal nereid Hediste diversicolor. Mar Environ Res 107669. https://doi.org/10.1016/j.marenvres.2025.107669

Taboada S, Serra Silva A, Díez-Vives C, Neal L, Cristobo J, Ríos P, Hestetun JT, Clark B, Rossi ME, Junoy J, Navarro J (2021) Sleeping with the enemy: unravelling the symbiotic relationships between the scale worm Neopolynoe chondrocladiae (Annelida: Polynoidae) and its carnivorous sponge hosts. Zool J Linn Soc 193:295–318. https://doi.org/10.1093/zoolinnean/zlaa146

Tang, M., Bever, J. D., & Yu, F. H. (2017). Open access increases citations of papers in ecology. Ecosphere, 8(7), e01887.

Titley MA, Snaddon JL, Turner EC (2017) Scientific research on animal biodiversity is systematically biased towards vertebrates and temperate regions. PLoS One 12:e0189577. https://doi.org/10.1371/journal.pone.0189577

Traag VA, Waltman L, Van Eck NJ (2019) From Louvain to Leiden: guaranteeing well-connected communities. Sci Rep 9:5233. https://doi.org/10.1038/s41598-019-41695-z

Van Rensburg H, Richoux NB, Simon CA (2023) The trophic position and isotopic niche of a cryptogenic tube-building polychaete in a protected clear-water estuarine bay. Estuar Coast Shelf Sci 295:108549. https://doi.org/10.1016/j.ecss.2023.108549

Vellend M (2016) The theory of ecological communities. Princeton University Press, Princeton

Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th edn. Springer, New York

Ventura D, Dubois S, Cardella E, Colloca F, Tiralongo F, Rakaj A, Bonifazi A, Lasinio GJ, Mancini E, Bertocci I, Casoli E (2024) Defining the role of Sabellaria alveolata reefs as nursery areas for juvenile fish: first evidence from drone-based imagery and underwater visual census data. Mar Ecol Prog Ser 735:103–123. https://doi.org/10.3354/meps14643

Villéger S, Miranda JR, Hernández DF, Mouillot D (2010) Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. Ecol Appl 20:1512–1522. https://doi.org/10.1890/09-1310.1

Villéger, S., Grenouillet, G., Brosse, S., 2013. Decomposing functional β-diversity reveals that low functional β-diversity is driven by low functional turnover in European fish assemblages. Glob. Ecol. Biogeogr. 22(6), 671-681.

Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional! Oikos 116:882–892. https://doi.org/10.1111/j.2007.0030-1299.15559.x

Violle C, Enquist BJ, McGill BJ, Jiang L, Albert CH, Hulshof C, Jung V, Messier J (2012) The return of the variance: intraspecific variability in community ecology. Trends Ecol Evol 27:244–252. https://doi.org/10.1016/j.tree.2011.11.014

Volkenborn N, Hedtkamp SIC, Van Beusekom JEE, Reise K (2007) Effects of bioturbation and bioirrigation by lugworms (Arenicola marina) on physical and chemical sediment properties and implications for intertidal habitat succession. Estuar Coast Shelf Sci 74:331–343. https://doi.org/10.1016/j.ecss.2007.05.001

Wilkes MA, Edwards FK, Jones JI, Murphy JF, England J, Friberg N, Hering D, Poff NL, Usseglio-Polatera P, Verberk WCEP, Webb JA (2020) Trait-based ecology at large scales: assessing functional trait correlations, phylogenetic constraints and spatial variability using open data. Glob Change Biol 26:7255–7267. https://doi.org/10.1111/gcb.15358