SYNTHESIS & INTEGRATION

Coastal and Marine Ecology

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

The interplay between terrestrial organic matter and benthic macrofauna: Framework, synthesis, and perspectives

J. C. F. Pardo[1,2] 🆔 | A. E. Poste[2,3] | H. Frigstad[1,2] | C. O. Quintana[4,5] |
H. C. Trannum[1,2]

[1]Centre for Coastal Research (CCR), Department of Natural Sciences, University of Agder (UiA), Kristiansand, Norway

[2]Norwegian Institute for Water Research, Oslo, Norway

[3]Department of Arctic and Marine Biology, UiT–The Arctic University of Norway, Tromsø, Norway

[4]Department of Biology, University of Southern Denmark, Odense M, Denmark

[5]SDU Climate Cluster, University of Southern Denmark, Odense M, Denmark

Correspondence
J. C. F. Pardo
Email: pardojcf3@gmail.com

Handling Editor: Hunter S. Lenihan

Abstract

Ecosystems are shaped by physical, chemical, and biological drivers, which affect the quality and quantity of basal energy sources, with impacts that cascade to higher trophic levels. In coastal, shelf, and marine habitats, terrestrial-derived organic matter (ter-OM) can be a key driver of ecosystem structure and function. Climate change is expected to alter land–ocean connectivity in many regions, with a broad range of potential consequences for impacted ecosystems, particularly in the coastal zone. The benthic compartment is an important link between the large organic carbon pools stored on land and the marine environment. At the same time, the macrofauna plays a key role in the processing, biological uptake, and fate of ter-OM in the aquatic environment, with implications for coastal ecosystem functioning, benthic–pelagic coupling, carbon burial, and biogeochemical cycles. However, information about relationships between land–ocean connectivity (including ter-OM loads) and coastal benthic community responses remains spread across disciplines, and a broad perspective on the potential impacts of a changing climate is still missing. Here, we explore the interplay between benthic macrofaunal communities and ter-OM through a paired narrative and research weaving analysis, which combines systematic mapping and bibliometric analysis. The review describes the past development and status of the research field as well as the lack of information in some geographical regions and habitats worldwide. We highlight the role of macrofauna in carbon cycling and the growing evidence that ter-OM plays a key role in the structure and function of benthic communities, not strictly limited to estuarine habitats. Climate change poses challenges for the prediction of future ter-OM fluxes and potential macrofauna responses to this additional stressor, thus requiring new methodological approaches (e.g., multimarker approaches for OM characterization) and long-term monitoring programs across different habitats and spatiotemporal scales.

INTRODUCTION

The exchange of material and nutrients across ecosystem boundaries can play a key role in shaping habitats as well as ecosystem structure and function (Loreau et al., 2003). This is particularly true for the organisms living at the land–ocean interface (Gounand et al., 2018; Polis et al., 1997; Stoler & Relyea, 2020). Organic matter (OM), with its diverse structure and nature, is central to ecosystem processes and an essential driver of marine pelagic and benthic community structure (Baldock et al., 2004; Fernández-Rodríguez et al., 2019; Lautenschlager et al., 2014). In coastal, shelf, and marine environments, terrestrial-derived organic matter (ter-OM) is an important factor in shaping the relationship and interactions between fauna and the environment as an essential energy source for many taxa as well as a potential stressor to others (Asmala et al., 2013; Bianchi, 2011; Capelle et al., 2020; Cragg et al., 2020). For many years, the origin and fate of ter-OM, and its interaction with other environmental stressors typically associated with river runoff (as a major source of ter-OM to the coastal zone), have been a topic of interest for researchers, policy makers, and civil society (De Wit et al., 2016; Deuser, 1988; Hedges et al., 1997). Thus, the understanding of the role of ter-OM in structuring ecosystems and connectivity between land and sea is a central ecological question (Asmala et al., 2013; Deininger & Frigstad, 2019; Jokinen et al., 2020; Witt et al., 2012).

Natural (i.e., nonanthropogenic) ter-OM is composed of a mix of vascular plants along with (black) carbon from soil and eroded carbonate rocks (Bianchi, 2011 and literature within). Recent and ancient OM stored in land soil, along with vascular plants and other sources, corresponds to the largest storage of carbon, one of the main constituents of ter-OM (Bianchi, 2011). A considerable amount of this material reaches the aquatic benthic compartment, turning it into an important sink for sedimentation and accumulation of land-derived carbon and nutrients (Burdige, 2007; Hedges et al., 1997), where as much as approximately one third of the OM buried in marine sediments is indeed land-derived (Burdige, 2005).

Benthic macrofauna has been included as a reliable indicator in short- and long-term environmental studies and monitoring programs (Jędruch et al., 2019; Trannum et al., 2018). The group is a key component in ecosystem functioning and services by supporting productivity of coastal habitats, nutrient cycling, carbon mineralization, and trophic chains (Griffiths et al., 2017; Janas et al., 2019; Volkenborn et al., 2007). Benthic communities rely on resources coming from within (autochthonous) and/or outside (allochthonous) their natural habitats. There is growing evidence for the use of less-nutritious ter-OM as food source by macrofaunal groups, varying between habitats and seasons (Attrill et al., 2009; Bianchi et al., 2021; Harris et al., 2018). Thus, the increasing trend of ter-OM inputs in some regions may lead to substantial bottom-up ecosystem changes (Drylie et al., 2020; Fernández-Rodríguez et al., 2019).

Benthic macrofauna is considered a crucial component of climate mitigation and adaptation due to its influence on soil biogeochemistry and carbon mineralization pathways (Bianchi et al., 2021; Solan et al., 2020). To support the understanding of the interplay between estuarine, coastal and shelf macrofauna, and ter-OM dynamics, we have, first, provided a narrative review of the current knowledge on the origin, composition, fate, and impacts of ter-OM on macrofauna functioning and structuring, by exploring the pathways of ter-OM from its source until reaching the benthos, and the outcomes of this interrelationship at species and community levels. Although discharge from farms and municipal wastewater remains the major source of OM from land in some regions worldwide (Mudge & Duce, 2005; Wassmann & Olli, 2005), our review focuses on natural sources of ter-OM. Secondly, we provide a research weaving analysis through a bibliographic review and systematic mapping (Nakagawa et al., 2019). This methodology allows us to synthesize the current knowledge, identify emerging research themes, and highlight critical knowledge gaps (*Current status of the research topic: ter-OM and macrofauna communities*). Lastly, we provide perspectives and potential future directions on the topic, mainly focusing on contemporary challenges under the prism of climate change (*Emerging themes on the research topic*).

THE ORIGIN AND FATE OF ter-OM

Sources of ter-OM to aquatic habitats

Composition of ter-OM

Natural OM is delivered in the form of dissolved or particulate OM (DOM and POM, respectively) (He et al.,

2016 and literature within). DOM is a major marine carbon reservoir (~662 Gt) (Hansell et al., 2009; He et al., 2016). The molecular structure of marine DOM depends on its source and previous transformation processes, and plays a key role in determining both the bioavailability (quality) as well as the light-attenuating properties of DOM. The light absorbing, or chromophoric, fraction of DOM is referred to as colored DOM (CDOM), and especially present in the surface and coastal ocean influencing both water color and light quality (Deininger & Frigstad, 2019; Nelson & Siegel, 2013).

OM from different terrestrial sources (e.g., plant end-members, primary and secondary producers) and in different degradation stages interact in the coastal zones (Massicotte et al., 2017; McGovern, Pavlov, et al., 2020). Terrestrial and marine OMs have distinct chemical patterns due to the different primary producers (e.g., multicellular plants vs. marine phytoplankton) and biogeochemical processes (Baldock et al., 2004; Burd et al., 2016 and literature within). Although difficult to generalize, ter-OM tends to have macromolecules with more complex structural polymers such as lignin, cellulose, peptidoglycans, and algaenans than marine resources, usually leading to a higher carbon-to-nitrogen ratio (Burd et al., 2016; Burdige, 2007; Dickens et al., 2006), although some marine components (e.g., macroalgae, seagrasses, salt marshes) may show similar values complicating the attribution to various OM sources (see *Emerging themes of the research topic*). Proteins (amino acids) and lipids represent a major fraction of marine OM components, followed by carbohydrates, which are more abundant in vascular plants (~70% of the source) (Burdige, 2007).

The major component of ter-OM is soil-derived material containing POM (Baldock et al., 2004; Bianchi, 2011), but its mixed origin makes it difficult to fit in a simple classification. Along with organic carbon, ter-OM includes nitrogen, phosphorous, and other nutrients and macromolecules (Meybeck, 1982; Wakeham & Canuel, 2006). The varied quality and quantity of compounds mirror the different sources of ter-OM. A considerable fraction of ter-OM derived from land use is composed of fossil refractory matter from erosion of carbonaceous rocks (Galy et al., 2007; Gordon & Goñi, 2004) and black carbon mainly originating from landscape fires and volcano eruptions, also observed in the form of pyrogenic OM (Coppola et al., 2018; Jones et al., 2020; Jones & Gislason, 2008; Li et al., 2021). Vascular plants are a major component of ter-OM not just for being the largest biomass on Earth, but their biochemical composition makes a relevant and eventually an exclusive resource (Bianchi, 2011; Cragg et al., 2020). Originating from diverse sources ranging from plant litter decay to soil erosion, these materials are seasonal or year-around organic

sources across brackish and marine environments (Drenzek et al., 2009; Feng et al., 2013; Massicotte et al., 2017).

Variation in ter-OM inputs

Geographical regions and habitats have marked variations in ter-OM stocks and dispersion mechanisms. The origin of ter-OM may vary, but natural landing areas are the aquatic compartments (Figure 1), where the three main processes of biodegradation, flocculation, and photodegradation are believed to drive the transformation of ter-OM (Bianchi et al., 2018; Massicotte et al., 2017) (Figure 1). In general, there is a decrease in the reactivity of the organic material (i.e., tendency to participate in chemical reactions, such as oxidation) along the aquatic continuum, indicating that the ter-OM reaching coastal areas is more refractory and potentially less bioavailable. Shallow estuarine regions have a longer retention time and organic material passes through a series of biogeochemical processes until reaching outer areas (Canuel et al., 2012; Middelburg & Herman, 2007). In the temperate northern hemisphere, boreal forests are known for the high contribution to the global terrestrial carbon pool (Bradshaw et al., 2009; Tagesson et al., 2020), with seasonal and continual decay of terrestrial material (mainly senescence leaves). Similarly, Arctic regions are marked by seasonal ter-OM fluxes during spring freshet and late-season melt, where ter-OM from rivers, glaciers, permafrost, and soil erosion flows into fjords and coastal areas (Bring & Destouni, 2011; Clark et al., 2022; McGovern, Pavlov, et al., 2020).

Rivers are responsible for a continuous input of ter-OM, and around 0.35 Pg of carbon are yearly transported by rivers to marine environments worldwide (Hedges et al., 1997). Global estimations predict that more than one tenth of the total carbon exported by major rivers is composed of black carbon, mainly from wildfires and fossil-fuel-derived compounds in its different forms (Jones et al., 2020), with 3%–10% reaching marine sediments (Coppola et al., 2018). However, the estimation of exports could be heavily influenced by intermittent rivers with temporal pulses containing variable ter-OM loads (Datry et al., 2014; del Campo et al., 2021). Regardless of the transportation pathway, the association of ter-OM with minerals supports the dispersion of OM to water compartments (Gordon & Goñi, 2004; Hedges & Keil, 1995; Simoneit, 2006). Muddy finer grained sediments, when compared with coarse grains, usually have a stronger affinity with ter-OM (Hedges & Keil, 1995), thus making it challenging to disassociate OM and sediments, and predict potential impacts to the faunal communities (Lohrer et al., 2006).
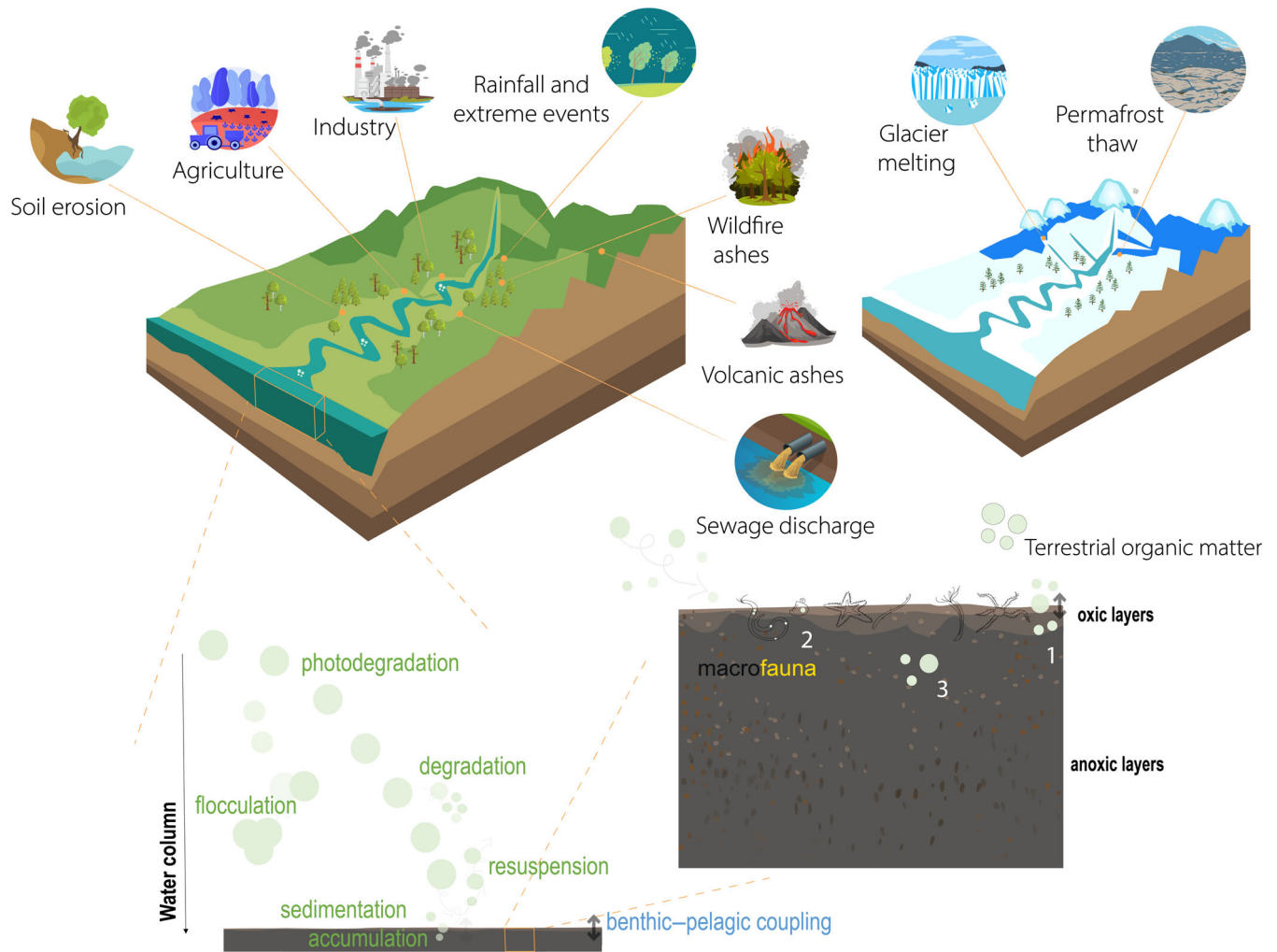
FIGURE 1 Conceptual representation of the land–ocean environmental interface and potential sources of terrestrial organic matter (ter-OM). The material from land has both natural and anthropogenic, or mixed origins. Following the aquatic continuum, a substantial amount of ter-OM reaches the coastal and shelf benthic compartments. When sedimented, the material can follow three paths: (1) remineralized into dissolved inorganic carbon and nutrients, and remixed with the water, (2) stored in the benthic biomass, or (3) buried in the deeper sediments. Thus, ter-OM influences macrobenthic communities in several forms by being a source of nutrients, refuge, physical stressor smoothing epibenthic groups, and also as an important component of benthic–pelagic dynamics, acting as an energy transfer among trophic levels.

Recent climate predictions and ter-OM export estimations have brought a different dimension to the discussion of terrestrial contributions in coastal OM cycles (Cragg et al., 2020; Kandasamy & Nagender Nath, 2016; Qiao et al., 2019; Smeaton et al., 2021). A recent estimation in UK coastal waters showed that benthic subtidal sediments are by far the most important carbon storage area with around 23.9 million tonnes of carbon stored (~0.1–0.5 million tonnes of carbon per annum) (Parker et al., 2021). Fjord systems, for instance, are expected to bury 10 Mt of organic carbon per year (=11% of the global annual budget in marine systems) (Smith et al., 2015), with temperate fjords alone responsible for nearly 12% of global budgets in the last 100,000 years (Nuwer & Keil, 2005). Atmospheric transportation also

drives ter-OM deposition in coastal and remote areas, for example, Galletti et al. (2020) have highlighted the importance of delivery of ter-OM associated with Saharan dust to the coast of remote Mediterranean Sea areas via sea spray, where the ter-OM transported by atmospheric inputs is locally higher than deliverables from riverine inputs.

Natural sources of ter-OM can be masked in some regions by anthropogenic-derived inputs. Land-based aquaculture, agriculture, industry, and other activities physically modify the landscape with potential long-lasting impacts on sediment dynamics, bringing up or adding substantial amounts of OM to the environment (Asmala et al., 2013; Bao et al., 2013; Kim et al., 2011; Louchouarn et al., 1999). Deforestation, erosion, and

changes in land use can lead to substantial increases in mobilization and downstream transport of sediment OM, often with high molecular weight and aromaticity, with implications for the bioavailability of ter-OM reaching aquatic compartments (Boyer & Groffman, 1996; Coppola et al., 2018; Farella et al., 2001). When evaluating boreal estuaries with different ter-OM sources (forest/peatland, agricultural, or mixed/urban), Asmala et al. (2013) showed via incubation experiments that ter-OM quality was driving the organic degradation, with higher mineralization rates and bacterial growth efficiency in coastal areas receiving OM inputs from agricultural landscapes.

Processes in the sediment compartment

Once deposited in the benthic compartment, there are three main "fates" for ter-OM: (1) remineralization into dissolved inorganic carbon and nutrients, and remixed with the water (and therefore returned to the hydrosphere, or even the atmosphere), (2) uptake and short- or medium-term storage in the benthic biomass, or (3) long-term burial in the deeper sediments (Klages et al., 2004) (Figure 1). The different sources of ter-OM and transformation processes to particulate and dissolved fractions make it complex to trace the inputs, mainly when it enters the sediment matrix and food webs (Geraldi et al., 2019). In tidal estuaries, the constant particle mixing of ter-OM and enhanced solid–liquid exchange chemically changes the particles due to ter-OM resuspension into upper and more oxygenated water layers (Komada & Reimers, 2001; Middelburg & Herman, 2007).

The quantity and quality of ter-OM reaching the sediment surface depend on the habitat's geomorphology, physical–chemical characteristics, biological processes on the way down, and the proximity from the land source to the aquatic compartment (source-to-sink) (Bianchi, 2011; Blair & Aller, 2012; Hedges et al., 1997; Hoeinghaus et al., 2011). Nearly half of the total annual budget of ter-OM is indeed degraded before reaching the coastal sediment compartments (Louchouarn et al., 1999), but still a considerable amount is estimated to reach the sediment surface and be consumed or sedimented (Hedges & Keil, 1995; Painter et al., 2018; Sarmiento & Gruber, 2013). The ter-OM burial estimation provided by Burdige (2005) highlighted the inefficient remineralization of ter-OM compared with marine-derived OM. Also, a less explored and associated process in aquatic systems is the priming effect (Aller & Cochran, 2019; Bianchi, 2011), where the interaction between the allochthonous and resident organic material changes the remineralization rates. Experimental assessments exploring the priming effect are scarce (e.g., Turnewitsch et al., 2007; van Nugteren et al., 2009), and required to provide a better understanding of the process, but multiscale priming involving ter-OM seems to vary depending on the geomorphology and physical–chemical characteristics (Bianchi, 2011).

Terrestrial-derived material can also exert influence far from the coast: the massive delivery of ter-OM into the Arctic Ocean Basins from Arctic rivers (~10% of global riverine discharge) is reflected in the prevalence of ter-OM far offshore (Forest et al., 2007; Hwang et al., 2015), with recent models estimating ter-OM POC sources hundreds of kilometers from the shore (e.g., Yukon River delta in Alaska, USA, Clark et al., 2022). Similar observations have been made in large river basins, such as the Amazon shelf, where a seasonal increase in riverine loads drives benthic community changes (Aller & Stupakoff, 1996) with tracers indicating ter-OM up to 700 km from the shelf break (Sun et al., 2017).

Ter-OM as a source of nutrients and food web link

An ongoing discussion topic is the potential role of ter-OM as a source of energy to coastal and marine food webs. This resource has traditionally been regarded as a low-quality food source for the marine trophic food chains (Cummings et al., 2009; Schell, 1983). Ter-OM has high carbon and nitrogen (C:N) ratio relative to, for example, phytoplankton due to the major presence of macromolecules with low nitrogen (e.g., cellulose, lignin) compared with protein sources. Thus, organisms may require more energy and time to process and assimilate this material, and a longer window to reach the required nutrient levels (Christofoletti et al., 2013; Cragg et al., 2015). Although ter-OM is low in the high-quality polyunsaturated fatty acids characteristic of phytoplankton, it can still have a high content of certain essentials (e.g., ω-3 and ω-6 FA families). The material can be separated into nutritional components that are directly (e.g., proteins, sugars) or indirectly (e.g., cellulose, lignin) available to macrofauna (Galloway et al., 2012). Most of the plant-derived compounds, which are a major part of ter-OM, have tissues composed of lignocellulose, a compound that is difficult to break into smaller molecules (i.e., depolymerization) (Cragg et al., 2020). When compared with the long phylogenetic history of major organismal groups, the recent evolution of land plants may explain the sparse appearance of the ability in degrading lignocellulose in the tree of life (Cragg et al., 2015). While several animal groups have cellulose-degrading enzymes, only a few carry modifying molecules able to break lignin. On the other hand, microbial and fungal activities

can play a key role in lignin degradation, depolymerizing the organic material, either as free-living organisms, or living symbiotically with benthic invertebrate taxa (Cragg et al., 2015; Distel et al., 2002). There is a high reliance on bioavailable ter-OM from bacteria depolymerization, and some macrobenthic communities are maintained by the recycled microbial by-products and biomass itself (Harris et al., 2018; McTigue & Dunton, 2014). The macrobenthic wood borers, such as teredinid bivalves, have well-known symbiotic associations with proteobacteria across several genera (Distel et al., 2002). The presence of endogenous cellulase, however, is present in other invertebrate groups (Tanimura et al., 2013 and literature within) but still poorly explored in marine species, with the Limnoriidae isopod crustacean *Limnoria quadripunctata* being the first group identified with the ability to degrade lignin-derived material unassisted by symbionts (King et al., 2010).

Several estuarine and coastal deposit and suspension feeders utilize ter-OM, in its varied forms, as a continuous or seasonally important food resource (see Table 1). Ter-OM has indeed lower nutritional value when compared with marine-derived organic sources, but the high continuous input of the source in tropical habitats, and pulses during spring and autumn floods in temperate and Arctic regions, turns it into a relevant energy resource, with varied significance (minor to important contribution), to macrobenthic communities' diet (Table 1). As an example, ter-OM was estimated via isotopic mixing models to be responsible for up to 74% of the diet of suspension (bivalve *Arthritica helmsi* and polychaete *Ficopomatus enigmaticus*) and deposit (bivalve *Soletellina alba*) feeders (Lautenschlager et al., 2014), and also the only resource available to some coastal amphipod *Gammarus insensibilis* populations (Mancinelli & Rossi, 2002).

Ter-OM as a major energy source can be dependent on large-scale events, and higher riverine discharge and ter-OM load may overcome the usual diet contribution of generalist consumers (e.g., oyster *Crassostrea gigas*, Riera & Richard, 1997; blue crab *Callinectes sapidus*, Olin et al., 2013). High ter-OM pulses can also potentially reshape the community composition (e.g., positive correlation between macrobenthic abundance and runoff events, Hagberg & Tunberg, 2000) or even trigger life cycle events (e.g., reproduction of lagoon snails due to an increase of ter-OM in rainy seasons, Badano et al., 2016). Notably, high sedimentation accompanies high ter-OM loads and may cause long-lasting burial with potential clogging of filter feeders (Topçu et al., 2019). At the same time, seasonal short-scale events significantly contribute to some species' diets, such as the role of pine pollen for benthic invertebrates

in the Baltic Sea coastal food webs during early summer (Liénart et al., 2022).

Although generalist species can utilize ter-OM resources, the higher intake of less nutrient-rich resources may bring acute to long-term impacts to some groups, particularly to nonselective and filter feeder organisms. For example, the input of lignin alone reduced the food quality and affected the growth of the brittle star *Amphiura filiformis*, lowering the lipid content and arm regeneration rate in an experimental setup (Gunnarsson et al., 1999). Nevertheless, experimental manipulative studies exploring the effects of ter-OM at the species level are still scarce. At the same time, some taxa rapidly adapt to organic availability changing their feeding strategy, such as *A. filiformis*, switching from deposit to suspension-feeding (Renz et al., 2018), and the Asian clam *Corbicula fluminea*, with clear shifts in their food quality intake (marine- or terrestrial-derived) along the estuarine gradient (Dias et al., 2016). Other species even hibernate and enter in aestivation state during unfavorable environmental conditions, a behavior observed across benthic taxa and habitats that potentially is linked to low food availability (Coma et al., 2000). Some taxa simply move to more suitable environments, such as capitellid and nereidid polychaete families (Fernández-Rodríguez et al., 2019 and literature within), a limited behavior for sessile and others living in restricted or fragmented habitats, such as mangroves and tidal salt marshes. Otherwise, several filter feeder species have the ability to sort particles before ingestion supported by morphological and behavior adaptations (Ward & Shumway, 2004 and literature within). Although also scarce in the literature, some species from food-rich areas (e.g., estuarine habitats) are adapted to select ter-OM sources at very fine levels with a better digestion efficiency to specific resources (e.g., fatty acids, chlorophyll-rich sources) (Boon & Duineveld, 2012; Godbold et al., 2009).

At the community level, the reliance on ter-OM is observed across functional macrofauna groups and habitats (Table 1), which also may change along the aquatic continuum and distance from the river outlet (Antonio et al., 2012). McGovern, Poste, et al. (2020) found a higher reliance on ter-OM for subsurface deposit feeders (which feed directly on sediments) than for more selective feeders (such as scavengers/carnivores) in an Arctic fjord, a finding mirroring that of Harris et al. (2018) in the Beaufort Sea, Alaska. However, most studies have focused on general riverine inputs, thus not distinguishing which specific source of ter-OM that had been utilized. Estuarine habitats, such as mangroves, receive a larger input of nondegraded ter-OM directly to the benthic compartment when compared with other

TABLE 1 Summary of the systematic analysis and additional articles exploring the interplay between macrofauna communities and terrestrial organic material (ter-OM).

Reference	Country	Subject	Habitat	Type of ter-OM source	TOM-related variables	Effect/contribution
Netto and Lana (1999)	Brazil	Macrofauna community structure	Bay, estuary	*Spartina alterniflora* and detritus (plant material)	OM (LOI) and grain size	Higher density and diversity in salt marshes
Bell et al. (2016)	Alaska, USA	Food source assimilation	Coast	NS	δ^{13}C, δ^{15}N, C:N ratio, TOC, and TN	Important food resource
Bongiorni et al. (2016)	Italy	Food source assimilation	Coast	NS	SOM, δ^{13}C, δ^{15}N, and POM	Important food source
Bonifácio et al. (2014)	France	Macrofauna community structure	Coast	NS	TOC, TN, chloropigments, amino acids, THAA, EHAA, and grain size	Change in species composition
Forrest et al. (2007)	New Zealand	Macrofauna community structure	Coast	NS	δ^{13}C and δ^{15}N, C/N, and lipids	Higher density of opportunistic species (capitellidae *Heteromastus filiformis*)
Hermand et al. (2008)	France	Macrofauna community structure	Coast	NS	TOC, TC, pheopigments, and grain size	Higher density and biomass and lower diversity at river outlet (e.g., polychaeta)
Dunton et al. (2006)	Alaska, USA	Food source assimilation	Coast	NS	δ^{13}C and δ^{15}N	Important food resource
Lee (1999)	Hong Kong	Macrofauna community structure	Coast	*Kandelia candel*	OM (LOI), total detritus unit, and tannin	Decreased species richness, diversity, evenness, and abundance with TOM enrichment (*)
Sampaio et al. (2010)	Portugal	Food source assimilation	Coast	NS	δ^{13}C and δ^{15}N	Important food resource
Sarà et al. (2007)	Iceland	Food source assimilation	Coast	NS	δ^{13}C and δ^{15}N, POM, SOM	Food resource
Szczepanek et al. (2021)	Poland	Food source assimilation	Coast	NS	TOC, TN, chl *a* and pheo concentration, POM, δ^{13}C, and δ^{15}N	Important food resource
Darnaude et al. (2004)	France	Food source assimilation	Delta	NS	δ^{13}C and δ^{15}N	Important food resource (deposit-feeding polychaetes)
Shilla and Routh (2017)	Tanzania	Food source assimilation	Delta	NS	δ^{13}C and δ^{15}N, FA	Important food resource (filter feeders and deposit-feeding consumers)

(Continues)

T A B L E 1   (Continued)

Reference	Country	Subject	Habitat	Type of ter-OM source	TOM-related variables	Effect/ contribution
Bongiorni et al. (2018)	Italy	Macrofauna community structure and functional traits	Delta lagoons	NS	$\delta^{13}C$ and $\delta^{15}N$, chloroplastic pigments, SOM, suspended POM, and grain size	Important food resource, higher biomass to suspension and surface-deposit feeders at river outlet
Nasi, Auriemma, et al. (2020)	Italy	Macrofauna community structure and functional traits	Delta lagoons	NS	TOC, TN, biopolymeric carbon, pigments, and grain size	Higher functional diversity and redundancy at river outlet
Abrantes et al. (2013)	Kenya	Food source assimilation	Estuary	NS	$\delta^{13}C$ and $\delta^{15}N$	Important food resource
Cummings et al. (2003)	New Zealand	Food source assimilation	Estuary	NS	$\delta^{13}C$ and $\delta^{15}N$, OM (LOI), POC, TN, TP, chl *a*, and grain size	Minor food resource
Currin et al. (1995)	USA	Food source assimilation	Estuary	*Spartina alterniflora*	$\delta^{13}C$ and $\delta^{15}N$	Food resource (e.g., fiddler crabs *Minuca pugnax* and *Leptuca pugilator*)
Hughes et al. (2000)	USA	Food source assimilation	Estuary	^{15}N-enriched nitrate	$\delta^{13}C$ and $\delta^{15}N$, and N	Important food resource/ assimilation by crustaceans (e.g., sand shrimp *Crangon septemspinosa*)
Lillebø et al. (1999)	Portugal	Soil/nutrients structure	Estuary	*Spartina maritima*	OM (LOI), TN, and TP	Macrofauna enhance TOM degradation
Lillebø et al. (2007)	Portugal	Soil/nutrients structure	Estuary	*Scirpus maritimus*	OM (LOI), TN, and TP	Macrofauna enhance TOM nutrients decomposition and mineralization (*)
Netto and Gallucci (2003)	Brazil	Macrofauna community structure	Estuary	Detritus (plant material)	Detritus (plant material) biomass, TOM, and grain size	Positive correlation between detritus biomass and species no./ abundance (important refuge [?])
Norkko et al. (2002)	New Zealand	Macrofauna community structure	Estuary	Terrigenous clay	OM (LOI) and grain size	High content induces hypoxia and anoxia (?)
Richoux and Froneman (2007)	South Africa	Food source assimilation	Estuary	NS	$\delta^{13}C$ and $\delta^{15}N$ and POM	Important food resource, bivalve *Solen cylindraceus*
Feng et al. (2018)	China	Food source assimilation	Estuary (mangrove, mudflat, bay)	*Spartina alterniflora*, *Kandelia obovata*	$\delta^{13}C$ and $\delta^{15}N$, SOM, and POM	Important food resource

(Continues)

TABLE 1 (Continued)

Reference	Country	Subject	Habitat	Type of ter-OM source	TOM-related variables	Effect/ contribution
Antonio et al. (2012)	Japan	Food source assimilation	Estuary, coast, shelf	NS	$\delta^{13}C$ and $\delta^{15}N$	Important food resource (e.g., bivalve *Corbicula japonica*)
Gladstone-Gallagher et al. (2020)	New Zealand	Macrofauna community structure and functioning	Estuary and intertidal sandflat	Nitrogen	TOC and grain size	Higher abundance of surface gastropods and deposit-feeding bivalves, and large no. burrows (*)
Cari et al. (2020)	Chile	Food source assimilation	Fjord	NS	Suspended OM, SPOM, POM, $\delta^{13}C$, and $\delta^{15}N$	Higher trophic redundancy or overlapping trophic niches
Hagberg and Tunberg (2000)	Sweden	Macrofauna community structure	Fjord	NS	...	Increased abundance due to runoffs and TOM deposition (?)
Kędra et al. (2012)	Norway	Food source assimilation	Fjord	NS	POM, $\delta^{13}C$, and $\delta^{15}N$	Important food resource
Kokarev et al. (2021)	Norway	Macrofauna community structure	Fjord	NS	$\delta^{13}C$, $\delta^{15}N$, TOC, TN, and grain size	No effect on community structure (?)
McGovern, Poste, et al. (2020)	Norway	Macrofauna community structure and functional traits	Fjord	NS	TOC, TN, $\delta^{13}C$, and $\delta^{15}N$, and grain size	Lower taxonomic and functional diversity, higher community biomass at river outlet
McLeod and Wing (2009)	New Zealand	Food source assimilation	Fjord	NS	$\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$, FA, TOC, and TN	Important food resource (e.g., sea urchin *Echinocardium cordatum* and polychate *Pectinaria australis*)
Quiroga et al. (2016)	Chile	Macrofauna community structure	Fjord	NS	$\delta^{13}C$ and $\delta^{15}N$, TOM, TOC, C/N ratio, chl *a* and Phaeo, and grain size	Higher diversity at inner fjord
Sokołowski et al. (2014)	Svalbard, Norway	Food source assimilation	Fjord	NS	$\delta^{13}C$ and $\delta^{15}N$	Food resource
Zapata-Hernández et al. (2014)	Chile	Food source assimilation	Fjord	NS	POM, TOM, $\delta^{13}C$, and $\delta^{15}N$	Lower contribution to benthic communities
Zapata-Hernández et al. (2016)	Chile	Macrofauna community structure	Fjord	NS	$\delta^{13}C$ and $\delta^{15}N$, SOM, and POM	Important food resource (wood-boring *Xylophagid*)
Fanelli et al. (2009)	Italy	Food source assimilation	Gulf	NS	$\delta^{13}C$ and $\delta^{15}N$	Food resource (e.g., amphipods, cumaceans, and decapods)

(Continues)

T A B L E 1 (Continued)

Reference	Country	Subject	Habitat	Type of ter-OM source	TOM-related variables	Effect/ contribution
Harmelin-Vivien et al. (2009)	France	Food source assimilation	Gulf	NS	Cisotope, chl *b*, carbohydrate, lipid, and protein contents	Decreased diversity and increased abundance of specific functional groups (e.g., deposit-feeding polychaetes *Laonice cirrata*, *Mediomastus* sp., *Cossura* sp., *Sternaspis scutata*, and *Polycirrus* sp.)
Misic et al. (2016)	Italy	Food source assimilation	Gulf	NS	$\delta^{13}C$ and $\delta^{15}N$, TOC, TN, and carbohydrate	Important food resource (deposit feeders)
Salen-Picard et al. (2002)	France	Macrofauna community structure	Gulf	NS	...	Higher density and biomass (e.g., polychaeta *Mediomastus* sp. and *Aricidea claudiae*)
Dunton et al. (2012)	Alaska, USA	Food source assimilation	Lagoon	NS	$\delta^{13}C$ and $\delta^{15}N$, POM	Important food resource
Frouin (2000)	French Polynesia	Macrofauna community structure	Lagoon	NS	Grain size, pheop pigment, and organic load	Important food resource
Harris et al. (2018)	Alaska, USA	Food source assimilation	Lagoon	NS	$\delta^{13}C$, $\delta^{15}N$, and molar C:N ratios	Important food resource
Jędruch et al. (2019)	Poland	Metal assimilation (Hg)	Lagoon	NS	OM (LOI) and grain size	Increased Hg accumulation on filter feeders
Kanaya et al. (2011)	Japan	Macrofauna community structure	Lagoon	NS	Oxidation-reduction potential, acid-volatile sulfide, TOC, TN, and $\delta^{13}C$	Lower density of opportunistic species (?)
Marcelina et al. (2018)	Poland	Food source assimilation	Lagoon	NS	$\delta^{13}C$ and $\delta^{15}N$	Food resource
Nasi, Ferrante, et al. (2020)	Italy	Macrofauna bioturbation	Lagoon	NS	TOC, TN, $\delta^{13}C$ and $\delta^{15}N$, radionuclides ^{137}Cs and ^{7}Be, and grain size	Modify the spatial pattern of community traits
Andrade et al. (2014)	Brazil	Macrofauna community structure	Mangrove	*Rhizophora mangle*	...	Important refuge
Bouillon et al. (2002)	India	Food source assimilation	Mangrove	NS	$\delta^{13}C$ and $\delta^{15}N$, and SOM	Minor food resource
Chen et al. (2018)	China	Food source assimilation	Mangrove	*Spartina alterniflora*	$\delta^{13}C$ and $\delta^{15}N$	Important food resource
De Oliveira et al. (2012)	Brazil	Macrofauna community structure	Mangrove	*Rhizophora mangle*, *Laguncularia racemosa*	...	Food resource and refuge

(Continues)

TABLE 1 (Continued)

Reference	Country	Subject	Habitat	Type of ter-OM source	TOM-related variables	Effect/contribution
Demopoulos et al. (2007)	USA, Hawai	Food source assimilation	Mangrove	*Rhizophora mangle*	$\delta^{13}C$ and $\delta^{15}N$	Food resource (e.g., polychaetes)
Gladstone-Gallagher et al. (2014)	New Zealand	Macrofauna community structure	Mangrove	*Avicennia marina*	TOM, chl *a*, and phaeophytin (phaeo)	Decrease abundance of few taxa (e.g., polychaeta *Prionospio aucklandica*), but no effect on composition and density (*)
Churchwell et al. (2016)	Alaska, USA	Macrofauna community structure and food source assimilation	River delta	NS	$\delta^{13}C$ and $\delta^{15}N$, and POM	Important food resource
Bergamino and Richoux (2015)	South Africa	Food source assimilation	Salt marsh	Salt marsh *Chenolea diffusa* and *Sarcocornia perennis*, Marsh grass *Spartina maritima*	$\delta^{13}C$ and $\delta^{15}N$, and FA	Important food resource
Neira et al. (2007)	USA	Macrofauna community structure	Salt marsh	*Spartina*	Grain size and TOM	Reduced species richness, increase dominance and shift in feeding modes (surface microalgal feeders to subsurface detritus/Spartina feeders, oligochaeta, and polychaeta)
Rezek et al. (2017)	USA	Food source assimilation	Salt marsh	*Spartina alterniflora*	$\delta^{13}C$ and $\delta^{15}N$	Important food resource
Tang and Kristensen (2010)	Denmark	Macrofauna community structure	Salt marsh	*Spartina anglica*	OM (LOI)	Low infaunal abundance and diversity; higher abundance of epibenthic grazers and high abundance of *Corophium volutator* at the mudXat–marsh boundary
Mancinelli and Rossi (2002)	Italy	Macrofauna community structure	Shelf	NS	TOC, OM (LOI), and grain size	Support-adapted species (e.g., *Gammarus insensibilis*)
McTigue and Dunton (2014)	Alaska, USA	Food source assimilation	Shelf	NS	SPOM, $\delta^{13}C$, $\delta^{15}N$, and C:N ratios	Important food source, link with microbial alteration

(Continues)

T A B L E   1   (Continued)

Reference	Country	Subject	Habitat	Type of ter-OM source	TOM-related variables	Effect/contribution
Stasko et al. (2018)	Canada	Food source assimilation, Benthic–pelagic coupling	Shelf	NS	$\delta^{13}C$, $\delta^{15}N$, grain size, chl *a* and phaeopigment concentrations, LOI, and C:N	Minor and important food source, close link between TOM source and benthic–pelagic trophic coupling strength
Galeron et al. (2009)	Congo	Macrofauna community structure	Shelf (canyon)	NS	TOC, TN, and sulfur	Seasonal density and vertical profile variance
Liao et al. (2018)	China	Macrofauna community structure	Tidal mudflat	*Spartina alterniflora*, *Kandelia candel*	...	Reduced abundance and species no. in *Kandelia candel*, community ID shifts between *Spartina alterniflora* and tidal flat habitats
Netto and Lana (1997)	Brazil	Macrofauna community structure	Tidal mudflat	*Spartina alterniflora*	Grain size and TOM	Correlation between higher density of detritivorous or omnivorous species and higher detritus biomass

Note: The content of the articles was organized by country in which the studies were conducted, subject (main content of the article), habitat, type of ter-OM source, ter-OM-related variable, and effect/contribution originated from the ter-OM inputs. Studies with nonspecified type of ter-OM quality (e.g., total riverine input) were specified with NS. Relevance of food resource was split into three levels of magnitude: minor (low relevance to macrofauna diet), ordinary (i.e., food resource), and important food resource (seasonal or permanent relevant resource to macrofauna diet and/or trophic chain). When only specific group/species are affected by ter-OM, functional groups or species are specified in the effect/contribution column. Effects with vague, uncertain, or hypothesized descriptions were indicated with (?). Manipulative experiments were indicated with (*) after the effect/contribution description. Table is sorted by habitat type, and the complete list of references is provided in Appendix S1.

Abbreviations: EHAA, enzymatically hydrolysable amino acids; FA, fatty acids; LOI, loss in ignition; POC, particulate organic carbon; SOM, sediment organic matter; TC, total carbon; THAA, total hydrolysable amino acids; TN, total nitrogen; TOC, total organic carbon; TOM, total organic matter; TP, total phosphorus.

coastal and marine environments. In areas with a constant input of fresh and nondegraded ter-OM, macrofauna diet plays a central ecological role in habitat dynamics. As an example, the presence of endogenous cellulase was observed in several leaf eater crabs (e.g., *Parasesarma erythodactyla*, Bui & Lee, 2015; *Parasesarma bidens*, Kawaida et al., 2019) and, by consuming and enhancing the degradation of mangrove litter, they hold an important link in the food web, making nutrients available to both lower and higher trophic levels (Cannicci et al., 2008; Werry & Lee, 2005).

While much research has, quite naturally, focused on macrofaunal utilization of ter-OM in its particulate form, terrestrial DOM can also impact energy sources to macrofaunal communities indirectly by stimulating basal productivity and enhancing vertical carbon export, through plankton and microbial communities. This influence is tightly dependent on light availability in shallow waters and stimulated by riverine inputs of nutrients. Thus, by obtaining energy from ter-OM, macrofauna turns into a crucial link between terrestrial primary production and marine secondary production, through the processes of benthic–pelagic coupling (Antonio et al., 2010; Attrill et al., 2009). Some filter-feeding organisms (e.g., ascidians) are also capable of direct uptake of dissolved and colloidal OM (Riisgård & Larsen, 2010).

Recent studies using multimarker approaches (i.e., approaches combining analysis of multiple geochemical markers) have challenged the paradigm that ter-OM has low importance in marine and coastal food webs (e.g., stable isotopes, lignin phenol). In an Arctic fjord, the large annelid *Scoloplos armiger* was the most abundant species close to the river mouth, and its low $\delta^{13}C$ value

indicated a considerable terrestrial resource utilization (McGovern, Poste, et al., 2020), thus illustrating how terrestrial inputs may fuel benthic communities. In the Arctic Beaufort Sea, a community trophic characterization highlighted the role of ter-OM as an important subsidy to food webs (Harris et al., 2018) even into higher trophic levels, where microbes efficiently process ter-OM enhancing the availability of high-quality food sources to macrofauna (Bell et al., 2016).

THE RELATIONSHIP BETWEEN ter-OM AND MACROFAUNA DYNAMICS

Diversity and functional traits

Ter-OM brings either positive, neutral, or negative effects to the community (e.g., structuring and diversity, abundance, recruitment) with both POM and DOM leading

complex multilevel implications to the benthic community (see Figure 2 for a schematical representation of the interrelationship between the effects of ter-OM and macrofauna). Although caution is required while making generalizations about community-level impacts on benthic communities due to the lack of experiments using ter-OM, previous studies suggest that decreased species richness, diversity, evenness, and abundance may be expected under high terrestrial loads (Harmelin-Vivien et al., 2009; Lee, 1999). Similarly to the nonlinear macrofauna responses along the enrichment gradient (Pearson & Rosenberg, 1978), higher richness in the outer estuarine areas (i.e., closer to the marine environment) is expected to have natural ter-OM inputs as an important driver (Giménez et al., 2005; Laurino et al., 2021; McGovern, Poste, et al., 2020).

As components of dynamic environments, benthic estuarine and coastal species are evolutionarily adapted to fluctuating environmental conditions. When ter-OM enrichment is higher than the communities support, it
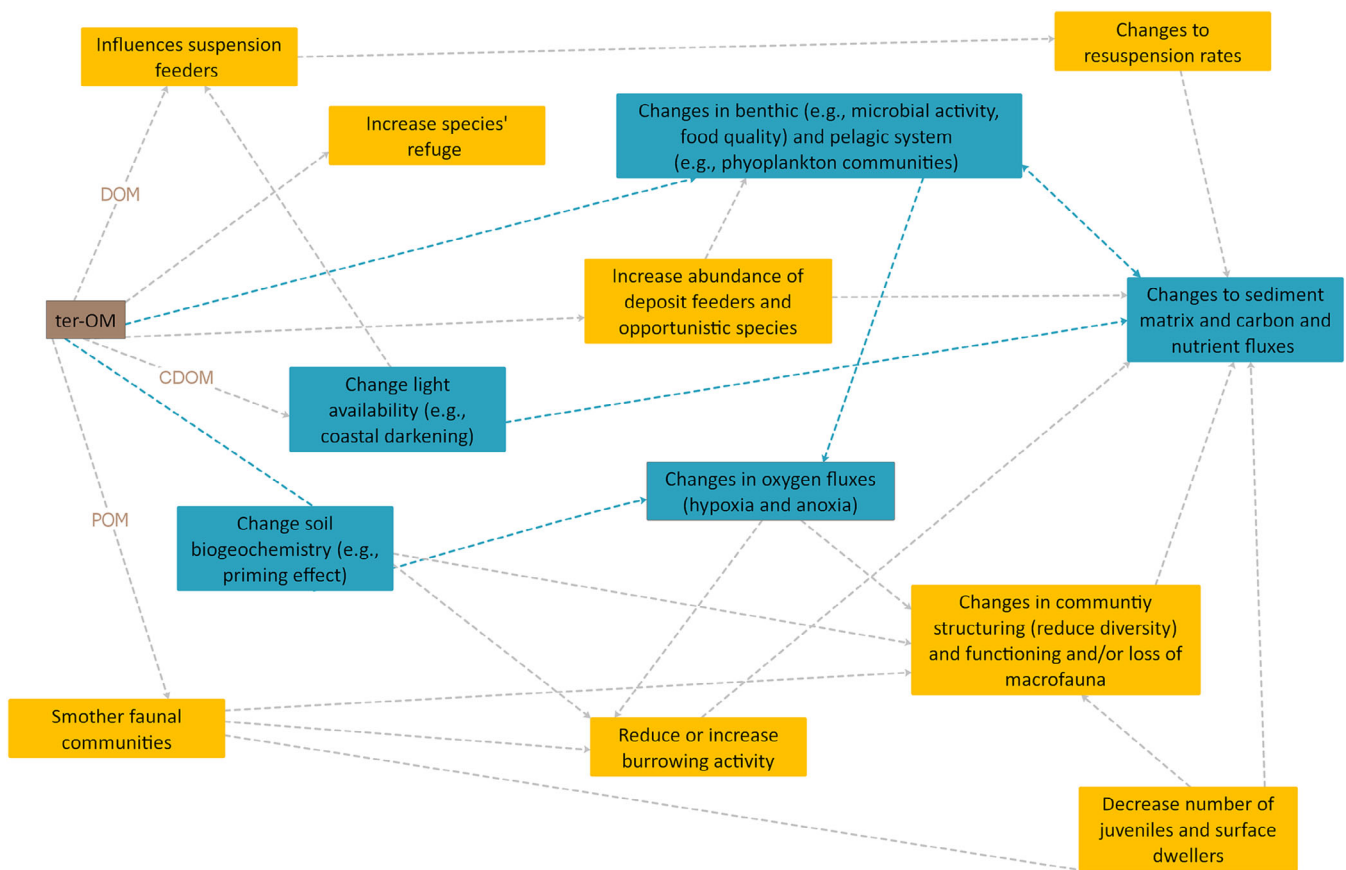

FIGURE 2 General schematical interrelationship between the effects of terrestrial organic matter (ter-OM) and macrofauna. Particulate and dissolved organic matter (POM and DOM, respectively) from land, including the dissolved colored form (CDOM), directly affects macrofauna (individuals and community) bringing a cascade of impacts at different levels. In the representation, blue color boxes indicate changes in the biogeochemistry and yellow indicates the effects on the benthic communities structuring and functioning and species fitness. Arrows connecting boxes have uni- or multidirectional impacts.

can suppress species behavior and metabolic activity via O_2 depletion, with negative outcomes for both biodiversity and community functions (Drylie et al., 2020). Usually under high ter-OM loadings, opportunistic species tend to dominate the functional groups (Drylie et al., 2020; Fernández-Rodríguez et al., 2019) and higher biomass of suspension, filter- and surface-deposit feeders may be also expected (e.g., Bongiorni et al., 2018; Feng et al., 2018). As an example, Gladstone-Gallagher et al. (2020) showed that similar ter-OM enrichment in a mangrove system affects groups from the same community in different manners: surface gastropods increased and deposit-feeding bivalves decreased in abundance. Community changes, however, vary in intensity and time lags starting several months to even years (e.g., 1–2 years) after the ter-OM input events (e.g., Salen-Picard et al., 2003), depending on the event magnitude and source, as well as the dominant taxa in the impacted communities. Also, ter-OM inputs are often coupled to sediment inputs from land, which can drive community shifts to high abundance of more adapted taxa to high sedimentation rates.

Links between macrofauna communities, biogeochemical processes, and carbon cycle

Benthic macrofauna is a central player in moderating sediment burial processes and biogeochemical processes within the sediment matrix (Welsh, 2003). Benthic fauna, in association with physical processes, is known to accelerate remineralization by increasing the reoxidation rates and mixing fresh and refractory OM repeatedly into the same reaction zones (Sarmiento & Gruber, 2013; Volkenborn et al., 2012), thereby enhancing ter-OM remineralization. This process may also be facilitated by other faunal groups. For example, macrofauna combined with meiofauna promoted nutrient turnover and supported an increase of up to 90% in the mineralization rate in a *Scirpus maritimus* salt marsh (Lillebø et al., 2007). While microbial communities are the major drivers of organic remineralization, it is the macrofaunal activity that promotes the sediment mixing through bioturbation, thereby bringing up sediments (including ter-OM) from anoxic to oxic layers and pumping oxygenated water into deeper layers (i.e., biorrigation), which can enhance microbial degradation and heterotrophic metabolism (Wakeham & Canuel, 2006).

Changes in macrofauna community composition limit sediment irrigation and oxygen availability by reducing their remineralization capacity to near-total inefficiency under high anoxic conditions (Levin et al., 2009). The macrofauna also supports the microbial

community structure and habitat nutrient cycling by controlling the distribution of key elements (e.g., nitrogen, iron, sulfur) (Kristensen et al., 2012; Sarker et al., 2021; Solan et al., 2019; van de Velde et al., 2020). Although the influence of faunal bioturbation/biorrigation has been better explored in recent decades, the effects of organisms on particle mixing, long-term degradation of ter-OM, and associated processes are still not fully predicted and require a good understanding of the community to provide habitat functional inferences (Kristensen et al., 2014; Sarmiento & Gruber, 2013).

Macrofauna–sediment interactions control and preserve carbon in different ways, and this theme has been extensively reviewed (Bianchi et al., 2021; Kristensen et al., 2008; Snelgrove et al., 2018; Wakeham & Canuel, 2006), but the interplay between habitat dynamics and macrobenthos is sometimes overlooked and neglected in carbon budget assessments (Andreetta et al., 2014; Bianchi et al., 2021; Kristensen et al., 2022; Lillebø et al., 2007). Macrofauna biomass itself is a source and storage of carbon of terrestrial origin, and the ter-OM consumption and sediment mixing behavior make carbon bioavailable to the environment in its different forms (Doering et al., 1986; McLeod & Wing, 2009). There is an increasing interest in the role of particular species able to digest lignocellulose (King et al., 2010) and in macrofauna bioturbation (Bianchi et al., 2021), due to their intrinsic relationship with nutrient regeneration and more specifically carbon cycling.

CURRENT STATUS OF THE RESEARCH TOPIC: ter-OM AND MACROFAUNA COMMUNITIES

To complement our knowledge synthesis on the interplay between ter-OM and macrofauna communities, we have performed a research weaving systematic review (Nakagawa et al., 2019), using bibliometric and mapping across research networks (see Appendix S1 for our methodological strategy). Studies have been conducted worldwide, however with the majority of knowledge production in European and North American countries (Figure 3). As highlighted by Pearson and Rosenberg (1978) decades ago, most of the studies and collaboration among researchers are still conducted in the northern hemisphere, although some countries from the southern hemisphere are represented in the top 10 countries in number of publications (Figure 4A). Publications included date back to the mid-1990s (Figure 4B) and are primarily published in specialized journals focusing on coastal and marine ecology (Appendix S1: Table S2). These articles explore a wide range of OM-related themes
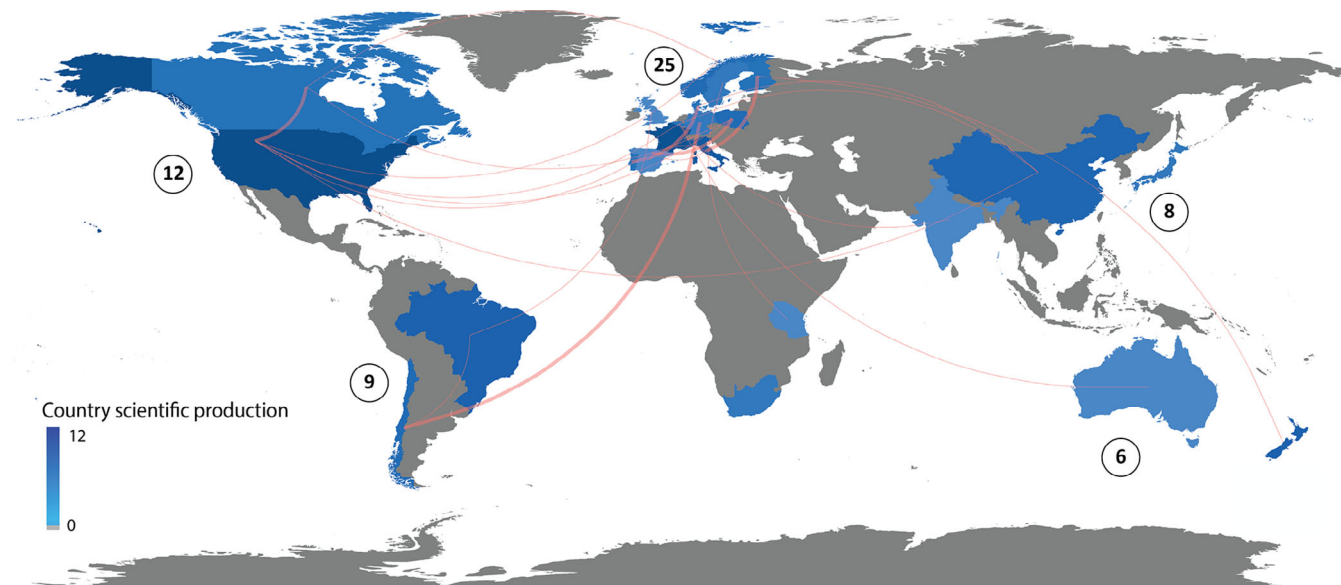
FIGURE 3 Global overview of articles exploring the interplay between terrestrial organic material and macrofauna communities. Geographical distribution of publications and number of publications per continent (study sites). The color gradient represents the number of publications based on the corresponding authors' affiliations and lines the collaborations across countries obtained from authors' affiliations.

(e.g., OM-cycling, food web uptake) with a clear shift to carbon-related topics in recent years (Appendix S1: Figure S2, Table S3).

Articles, with few exceptions, cover two main themes: macrofauna community structure and food source assimilation (Table 1). The former explores how functional and diversity traits respond to ter-OM, and how communities (re)arrange to the potential stressors, with some exploring the functional traits of the communities. The latter explores how communities utilize ter-OM as a potential energy source. The use of functional analysis and trait-based approaches has been more recently incorporated into the ter-OM and benthic macrofauna studies (2016–present) (Table 2). Despite the small number of studies available limiting the potential to make broad inferences, studies exploring sediment- and feeding-related effect traits are relatively well-represented and show that suspension and sediment surface feeders tend to be more abundant and/or cope relatively well compared with other taxa where ter-OM inputs are high. Long, thin, and threadlike shape of macrofauna was indicated as a response trait to habitats receiving larger inputs of ter-OM inputs (inner fjord stations); however, other drivers (e.g., grain size) may also exert a significant influence in the group (McGovern, Poste, et al., 2020). Trait-based approaches complement species composition measurements to predict and determine ter-OM as a stressor. Feeding-mode traits support the understanding of OM pathways and how it is incorporated and passed across trophic levels (McTigue & Dunton, 2014).

Additional articles exploring changing sediment biogeochemistry, bioturbation potential, and metal assimilation as a consequence of benthic macrofauna and ter-OM interactions were also observed, although less in number.

Most of the studies were conducted in estuarine habitats (51 out of 65), followed by coastal (10) and shelf (4) environments, as well as one study that covered all the gradients (Antonio et al., 2012). Fjords, followed by lagoons and mangroves, are the most explored estuarine habitat. The majority of the studies are field-based evaluating the effect of total riverine input on the communities. However, just a few have explored the net effects of specific plant material (e.g., *Spartina alterniflora*, *Scirpus maritimus*) or organic compounds (e.g., nitrogen) on macrofauna, even less under manipulative laboratory or field experiments (Table 1).

Emerging themes on the research topic

Bridging the traditionally separate fields of terrestrial and marine research is a challenging task (Munguia & Ojanguren, 2015), and investment in interdisciplinary studies targeting key knowledge gaps related to terrestrial–marine coupling is still required. Climate change and other anthropogenic-derived stressors impact ecosystems and connectivity between land and sea, making the need for a better understanding of these complex multifaceted changes. Despite the potential bias from the languages used in the literature search (i.e., excluding
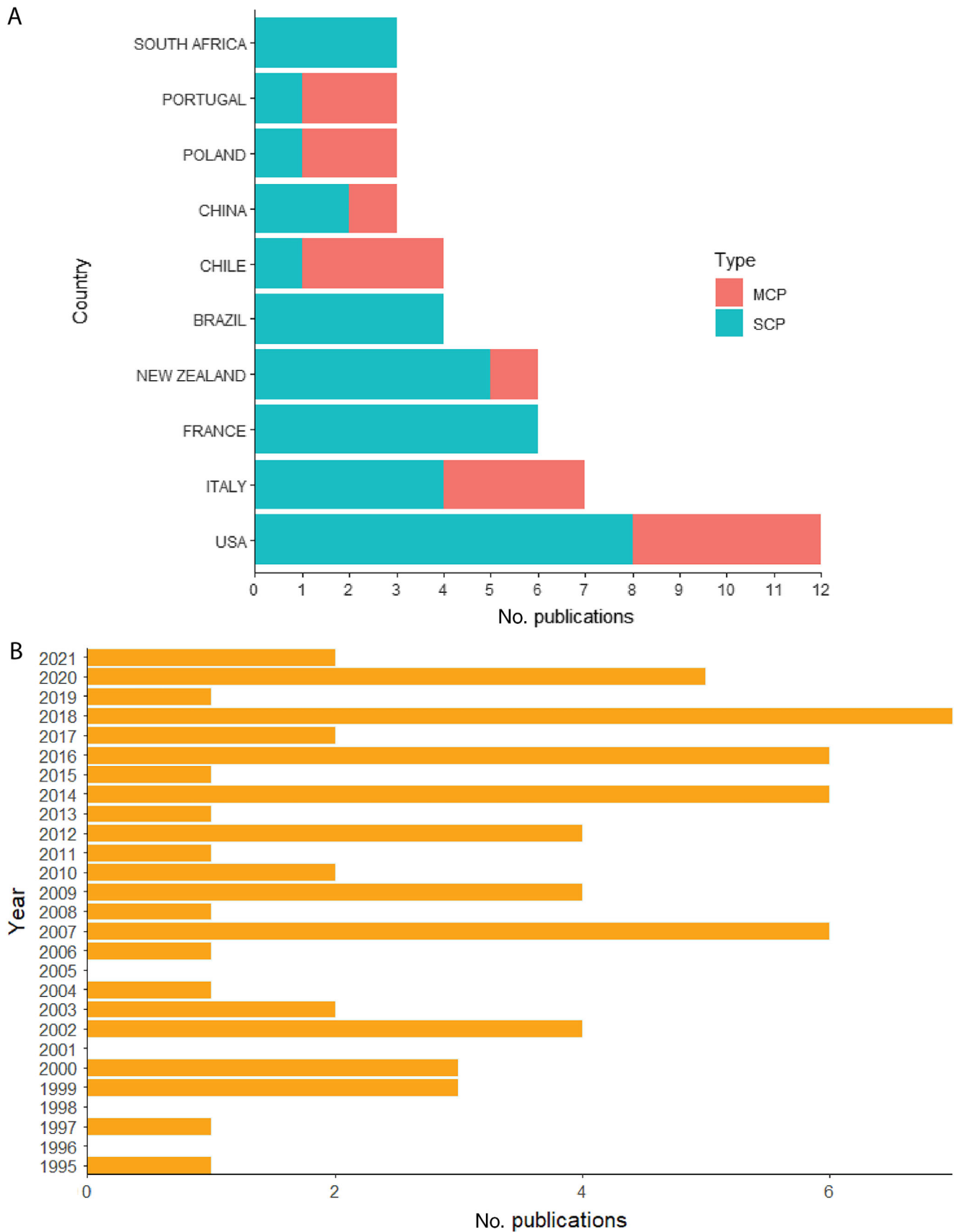
FIGURE 4 (A) Top 10 countries in the number of publications exploring the interplay between terrestrial organic material and macrofauna communities based on the country of the authors' affiliations. MCP, multiple country publication; SCP, single country publication. (B) Number of publications on the topic per year.

TABLE 2 Effect and response functional traits used in studies exploring the interplay between terrestrial organic material (ter-OM) and macrofauna communities on estuarine, coastal, and shelf habitats. Specific functional trait levels used for each study can be traceable in each reference.

| Study | Functional traits | | ter-OM-related traits | |
	Response	Effect	Response	Effect
McGovern, Poste, et al. (2020)	Diversity, larval type, adult habitat, degree of attachment, adult mobility, and body form	Normal size, life duration, sediment depth, sediment reworking, fecal deposition, and feeding habit	Body form: long, thin, and threadlike shape[a]	Sediment dwelling depth: deep dwellers (5–15 cm); Sediment reworking: upward conveyor, biodiffusors; fecal deposition: subsurface (0–5 cm); feeding habit: subsurface deposit feeders[a]
Nasi, Auriemma, et al. (2020)	Sediment position, adult mobility, and adult movement method	Maximum size, adult longevity, reproductive frequency, adult feeding habit, and bioturbation	...	...
Cari et al. (2020)	...	Feeding habitat	...	...
Nasi, Ferrante, et al. (2020)	...	Feeding strategy, mobility, sediment reworking, and burrow ventilation	...	Sediment reworking: semi-motile and conveyors
Jędruch et al. (2019)	...	Feeding strategy	...	Suspension feeders
Bongiorni et al. (2018)	...	Feeding strategy	...	Suspension and surface-deposit feeders
Shilla and Routh (2017)	...	Feeding strategy	...	...
Stasko et al. (2018)	...	Feeding habit and feeding strategy	...	...

[a]Functional traits observed in the riverine stations.

other non-English language publications than Portuguese and Spanish), our bibliographic analysis highlighted fewer studies and lower levels of multicountry collaboration in the Global South, which is consistent with previously reported trends in ecological science (Massicotte et al., 2017; Nuñez et al., 2021; Pearson & Rosenberg, 1978). The lack of knowledge in certain regions or collaboration across disciplines and countries can lead to a bias toward generalizations based on studies with limited global coverage, particularly when dealing with climate-change-related topics where impacts on north temperate systems often dominate the scientific discourse (Nuñez et al., 2021).

Climate change alters the fluxes of ter-OM (and other terrestrial material) into aquatic systems, with an increase due to heavy precipitation and erosion (Panagos et al., 2017) mainly in Europe, Asia, and southeastern South America (IPCC, 2021). For example, several studies have pointed to an ongoing increase in runoff of freshwater and terrigenous material from land to the Arctic Ocean (Bring & Destouni, 2011; Saito et al., 2021), where

the land–ocean connectivity is particularly strong (McClelland et al., 2012). The region has been warming at unprecedented rates and contains large natural organic carbon stocks, such as permafrost regions, which store the largest pool of organic carbon in the world along with a high nitrogen reservoir (Abbott, 2022; Turetsky et al., 2019). Since macrofauna is recognized as a strong indicator of environmental conditions, and as a potential tool to manage protected areas under climate change scenarios (Laurino et al., 2021), investments in poorly explored areas are crucial to support multiple-scale mitigation measures.

Ter-OM is a good indicator of environmental quality due to its influence on carbon budget and nutrient composition; however, it is usually degraded, consumed, or stored quickly, making it challenging to trace when entering aquatic systems. Even when considering OM derived only from vascular plant material, the polysaccharides, lignin, and other compounds differ in their degradation rates and bioavailability to organisms (Wakeham & Canuel, 2006). Tracing ter-OM utilization

by benthic macrofauna can also be complex, where geochemical signatures of ter-OM (e.g., $\delta^{13}C$, fatty acid composition) are often seasonally and spatially heterogeneous and can overlap with marine OM sources. Specific biomarkers have been used to trace ter-OM along the land–ocean gradient, performing better when integrated into multimarker approaches (Forrest et al., 2007; Rodil et al., 2020). As previously mentioned, stable isotopes or carbon and nitrogen have been broadly utilized, but their use as single tracers should be carefully applied, for example, in Arctic systems, where the high inorganic nitrogen may lead to an underestimation of ter-OM if not properly removed (Kumar et al., 2016). Thus, apart from habitat-specific approaches, the use of multi and complementary ter-OM tracers is needed for more reliable estimations, such as using radiocarbon (Feng et al., 2013; Guo et al., 2004) and lignin phenols (Rezende et al., 2010; Sobrinho et al., 2021), and a strong need to focus on the integrative use of land-derived tracers, especially in environmental monitoring programs.

Ter-OM influences all living coastal sediment taxa, including the more marine-restricted species (Birchenough et al., 2015). Looking to the past, paleoclimatic events with ter-OM overloading have shaped benthic community composition and functioning (Barash, 2012; Bianchi et al., 2021). Apart from the rapid temperature increase, the Paleocene-Eocene Thermal Maximum (~56 Mya) period experienced a larger input of sediments with high carbon content and $\delta^{13}C$-depleted carbon entering the coastal and marine systems; these changes resulted in high benthic fauna extinction rates due to changes in food sources and high productivity and low-oxygen conditions (McInerney & Wing, 2011). Thus, predicted environmental changes (e.g., an increase in flood events) may bring complex impacts to the macrofauna, highlighting the need for long-term, seasonal ecological studies and experimental manipulative approaches to clarify the role of ter-OM as a driver for the structure and function of macrofauna communities. Presently, tube-building infauna group support sediment stability and thereby represent an ecosystem engineering role for the surrounding and associated taxa (Bailey-Brock, 1984; Van Hoey et al., 2008). However, builder species tend to be more sensitive to organic enrichment than free-living species, such as the tube-builder polychaete *Diopatra neapolitana*, (Carregosa et al., 2014; Harkantra & Rodrigues, 2004). A potential negative effect on tube builders' density may modify the whole community structure including the environmental dynamics. Additionally, the increasing input of CDOM into aquatic systems resulting in the darkening of coastal and shelf waters (Aksnes et al., 2009; Deininger & Frigstad, 2019) have more obvious implications for light-dependent organisms living in the pelagic compartment, but changes in the food supply for the benthic compartment and cascading trophic level changes may also be expected (e.g., Frigstad et al., 2023).

Biogeochemical models have focused efforts on disentangling processes between benthic and pelagic compartments (Griffiths et al., 2017). Recent efforts support the observation and improvement of models to address the lack of baseline information and predictions on aquatic processes (Kandasamy & Nagender Nath, 2016; Rühl et al., 2020). Global models are limited (e.g., faunal biomass, Jones et al., 2014; Yool et al., 2017) and estimations of the direct impacts on faunal activity are inexistent (Bianchi et al., 2021). Recent advances in modeling approaches have included e.g. improved representation of the role of benthic substrate in driving biogeochemical cycling (e.g., European Regional Seas Ecosystem Model [ERSEM], Aldridge et al., 2017) and the inclusion of benthic bioturbation and bioirrigation (e. g., BAltic sea Long-Term large Scale Eutrophication Model [BALTSEM], Ehrnsten et al., 2022; Bottom RedOx Model [BROM v.1.1], Yakushev et al., 2017). However, all of the studies listed above point to the need for improved modeling tools for capturing the complexity of the interactions between benthic biota and biogeochemical cycling.

CONCLUSION AND PERSPECTIVES

Our review highlights the current knowledge of the interplay between coastal, shelf and marine macrofauna communities and ter-OM. A large amount of ter-OM is brought to the coast from land, however there are still many knowledge gaps related to the transformation and fate of this material, especially in the context of a changing climate (Bianchi, 2011). Although marine systems are shaped by a complex set of abiotic and biotic drivers, understanding the impacts of ter-OM as an individual stressor can provide important insight into potential combined and cumulative impacts (Crain et al., 2008). In general, the direct or indirect effect of ter-OM depends on the benthic community structure and functional groups and the characteristics and amount of the OM itself.

Most studies explore the ultimate impacts of ter-OM stressors on macrofauna communities (e.g., species richness, biomass), but physiological and behavior impairments may bring ecological consequences yet are still not well explored. Changes in the source, quality and quantity of ter-OM inputs may lead to unimodal and more complex multimodal cascade responses. As the evidence of ter-OM contribution to coastal and marine food webs grows, novel relationships with ter-OM sources and

macrofauna are observed. Both the interplay between terrestrial versus marine and anthropogenic versus natural organic sources, have different chemical compositions and residence time, and thus generalizing their impacts on benthic communities may lead to inaccurate conclusions.

The role played by macrofauna in carbon cycling and sequestration is not fully understood due to the lack of experimental information, but its importance in controlling these processes is unquestionable (Snelgrove et al., 2018; Solan et al., 2020). It seems also clear from recent studies and our compiled information that classifying ter-OM as a nonrelevant energy resource to estuarine, coastal, and shelf regions is no longer valid. As highlighted by Attrill et al. (2009), this consensus may origin from not considering estuarine studies and the closer evolutionary affinity of estuarine species with freshwater groups. The use of biogeochemical tracers for understanding OM sources and cycling, including food web utilization, has also contributed to a changing perspective on the topic.

When it comes to global ter-OM fluxes and characterization, the lack of in situ observations mainly in (sub) tropical areas and small riverine systems and the general lack of benthic–pelagic biogeochemical and integrative approaches contribute as missing pieces to this environmental puzzle. Monitoring macrofauna under a changing climate scenario is challenging with the traditionally used community indices, which are the tools mainly supporting environmental assessments worldwide. Community traits, for example, inform on evolutionary adaptations to stressors and species shifts to buffer areas. Such approach could be coupled with newly developed community indices safeguarding decision makers to protect the benthic ecosystem goods and services in coastal, shelf, and marine environments.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
Data (Pardo, 2023) are available from Zenodo: https://doi.org/10.5281/zenodo.7702058.

ORCID
J. C. F. Pardo https://orcid.org/0000-0003-2323-6342

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SUPPORTING INFORMATION

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