Influence of habitat in structuring spatiotemporal taxonomic and functional dynamics of benthic macrofauna under natural and anthropogenic constraints

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Influence of habitat in structuring spatiotemporal taxonomic and functional dynamics of benthic macrofauna under natural and anthropogenic constraints

Influence de l'habitat sur les dynamiques spatiotemporelles des structures taxonomique et fonctionnelle des communautés de macrofaune benthique sous contraintes naturelles et anthropiques

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Introduction

1. Coastal ecosystems

1.1. Structure, functions, services and threats

Coastal ecosystems, at the interface between land and sea, include intertidal and subtidal areas to depth of ~ 200 meters and immediately adjacent lands (Burke et al. 2001). Their location allows them to encompass a diverse array of habitats such as coral reefs, seagrass meadows, mangroves or estuaries (Burke et al. 2001). Moreover, they harbor a greater diversity of species, are largely open, with less isolated communities, reduced levels of endemism and more singletons than terrestrial ecosystems (Burke et al. 2001; Hawkins 2004; Raffaelli et al. 2005).

Structure and functions of an ecosystem are closely linked as the functional elements of an ecosystem represent what their structural elements do. Structural elements include the description of populations, species composition of communities and habitat heterogeneity of the ecosystem while functional elements are used as a measure of ecosystem health, productivity, recycling and yield of energy and matter (Thrush et al. 2021a). For example, species diversity (often considered as a potential driver of ecosystem functioning) is a major determinant of ecosystem productivity, stability, invasibility and nutrient dynamics (Tilman et al. 2014; Gamfeldt et al. 2015).

The structure and functioning of coastal ecosystems as well as their proximity to land, the contribution of fresh water rich in nutritive elements and the propensity for coastal upwelling, make them one of the most productive in the world. For example, the continental shelf accounts for approximately 10-30% of global primary productivity, 30-50% of global inorganic and 80% of global organic carbon burial in marine sediments, 50% of global denitrification and 90% of global sedimentary production (Agardy et al. 2005; Bauer et al. 2013). Indeed, coastal systems tightly couple water column and seafloor carbon and nutrient cycling (Figure 1). In shallow coastal zones, the availability of sunlight through the water column to the bottom enables benthic organisms such as phytoplankton, microphytobenthos or macrophytes to photosynthesize. Sinking organic matter is intercepted by the seabed and its benthic faunal communities and is recycled in dissolved nutrients available for primary production. Furthermore, large plants and macrophytes can sequester carbon in coastal sediments and organisms of the seafloor can modify habitat for microbes altering carbon flux, storage and recycling of nutrients over multiple timescales (Snelgrove et al. 2014).

Ecosystem goods and services represent the benefits human populations derive, directly or indirectly, from ecosystem functions (Costanza et al. 1997). More than half of the estimated global value of these services come from marine systems and especially coastal systems (Costanza et al. 1997). Furthermore, the high heterogeneity of habitats and species they harbor underpin most of the goods and services that are derived from them such as tourism, coastal protection, erosion control, nutrient cycling, carbon sequestration or food and raw-material products (Figure 1). Collectively, these services produce cumulative benefits more significant than services provided by any single ecosystem (Burke et al. 2001; Barbier et al. 2011). Their high productivity, resources and attractiveness have made them a focal point for the settlement of human populations with about 40% of the world's population living within 100 km of the coast (UNEP 2017).

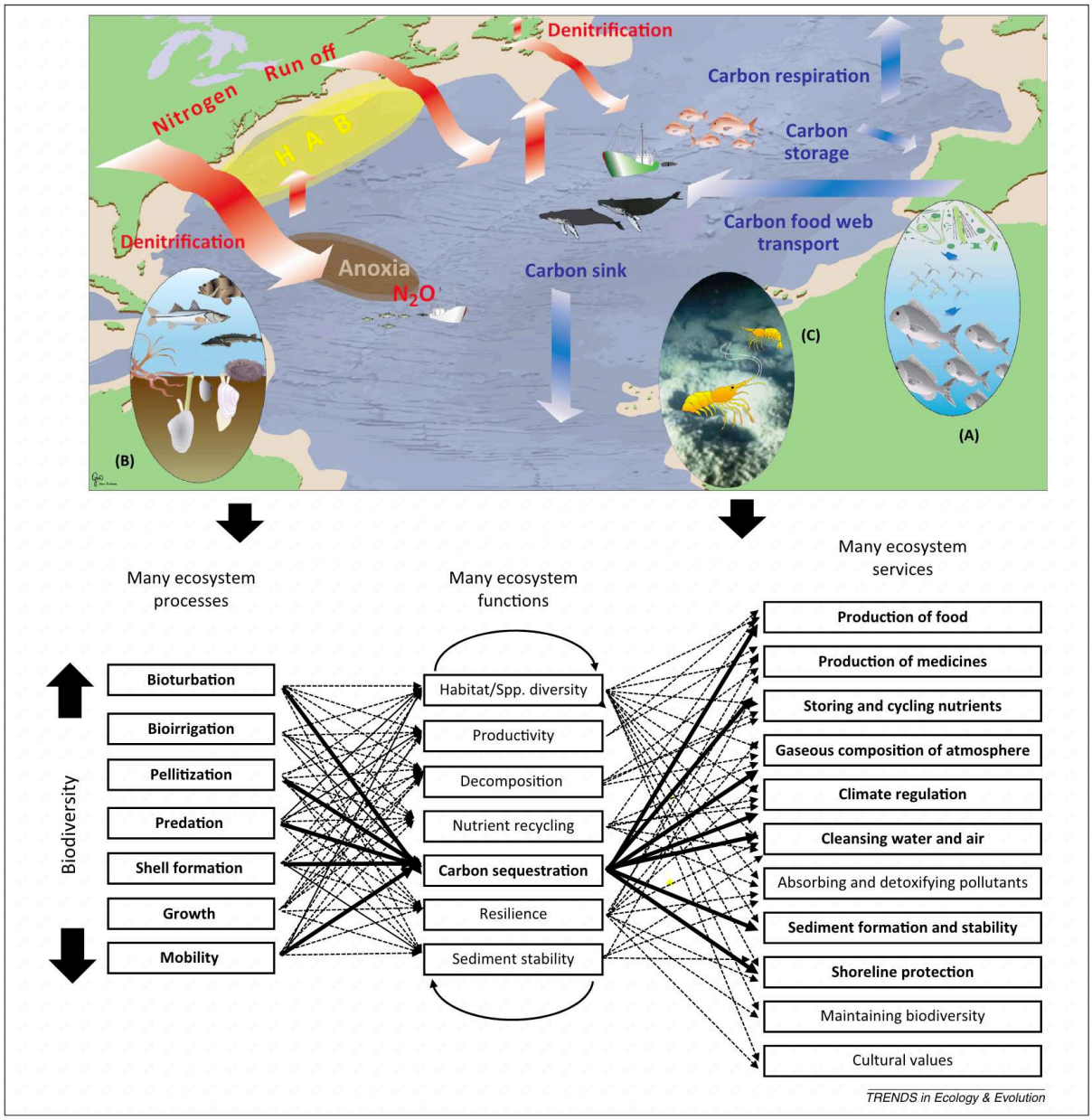


FIGURE 1: The role of marine species in multiple ecosystems functions and services. Carbon and nitrogen cycling closely link species to multiple functions and services. Top panel: nitrogen runoff from land and internal recycling results in high rates of primary production, and, thus, carbon fixation, fueling the food web and increasing respiration (A). Denitrification, particularly in coastal sediments, returns nitrogen to the atmosphere and healthy seafloor ecosystems recycle organic matter, regenerate ammonia and nitrate, and oxygenate sediment (B). Food web carbon transfer and physical processes transport organic material offshore and to the seafloor, where it may be broken down or permanently buried (C). Excess nitrogen input that cannot be denitrified leads to eutrophication, and hypoxia, anoxia, harmful algal blooms (HAB) and mortality on the seafloor. Lower panel: these and other processes show multiple links between biodiversity, ecosystem function, and the delivery of ecosystem services. Interlinkages among ecosystem processes (the precursors to functions), functions, and services complicate understanding of seafloor ecosystems. Unbroken arrows denote linkages specific to carbon sequestration. Broken lines other linkages. From Snelgrove et al. (2018).

Marine ecosystems are already under high demand and the constantly growing human population results in an increase and an acceleration of human impacts on ocean and coastal ecosystems. For example, Halpern et al. (2015) showed increases in cumulative human impacts in 66% of the ocean over only 5 years. Moreover, human activities can often change the extent, frequency and magnitude of natural disturbances. Disturbances can be defined as events that occur infrequently and temporarily affect the system (enabling it to reach a dynamic equilibrium), while stresses are events that occur at a frequency that prevent the system to return to a similar pre-event dynamic, shifting its trajectory (Borics et al. 2013). Examples of dominant disturbances can be flooding, drought or temporary vegetation removal via sedimentation (Ward et al. 2020) and examples of chronic stressors in coastal ecosystems are sea-level rise, temperature increases, ocean acidification, land-use conversion and alteration to water flow.

Anthropogenic disturbances and stressors both have direct and indirect effects that affect ecosystem structure, functions, services and are implicated in biodiversity loss (Balvanera et al. 2006; Worm et al. 2006; Lotze et al. 2006; Barbier et al. 2008). The most important human impacts that have led to the degradation of these rich, diverse and productive ecosystems are overexploitation and habitat destruction, and these are still intensifying in many regions (Lotze et al. 2006). Despite slower ocean warming, the velocity of anthropogenically driven climate change in the ocean is as high as on land (Burrows et al. 2011), and the latter can interact with local human impacts in a synergistic, antagonistic or additive manner (He and Silliman 2019; Stockbridge et al. 2020). These significant threats to coastal ecosystem structure, functions and services reinforce the need to monitor, detect, quantify or predict their forthcoming changes.

1.2. Zoom in on the benthic compartment

One of the essential components of coastal ecosystems are benthic sediments. Indeed, marine sediments cover the second largest surface of the earth after the ocean water column (the ocean covers 70% of the earth surface) (Gray and Elliott 2009). Benthos refers to the plants and animals at the bottom of the sea but also include organisms living in and on intertidal sediments (Gray and Elliott 2009). Benthic fauna can be categorized according to the size, the living position of the organisms and the tidal zone they occupy (Gray and Elliott 2009; Thrush et al. 2021a).

In this thesis, the focus is on benthic macrofauna which represents organisms larger than 1 mm and encompasses most kinds of marine invertebrates. More precisely, benthic macrofauna occupying the intertidal and the subtidal zones and living within the sediment (infauna or endofauna) is studied here, although it can be intricate to strictly separate infauna

from epifauna (i.e., sedentary or mobile species sitting or roaming on the sediment) (Thrush et al. 2021a). Macrofauna organisms are big enough to move sediment particles and pump water in and out of the sediment which gives them a strong influence on ecosystem function (Thrush et al. 2021a). Indeed, they play important roles such as nutrient cycling, bioturbation and secondary production (Snelgrove 1998). Moreover, most of these species are non-migratory (thus exposed to the local physical environment), show various life spans and exhibit different tolerances to environmental constraints, making them good indicator of ecosystem changes (Dauer 1993).

1.2.1. Biodiversity and functioning

At least partly because of the greater physical variety of benthic habitats, the number of phyla and species of benthic animals exceeds those of pelagic species (Lalli and Parsons 1997). Concerning macrofauna, polychaetas, bivalves, gastropods, amphipods, isopods and ophiuroids are among its most common constituting invertebrate taxa (Thrush et al. 2021a). Their local richness is highly determined by the regional species pool and their distribution by the availability of food resources, sediment structure (influenced by biological activities, hydrodynamical and geomorphological factors) and physical or historical disturbances (Snelgrove 1998; Gray 2002).

Soft-bottom habitats contain both autotrophic and heterotrophic organisms that can generate biomass at the base of the food web. Microphytobenthos, seagrasses and macroalgae ensure primary production but also other ecosystem functions such as habitat formation, sediment stability or nutrient cycling. This primary production supports higher trophic levels through secondary production, a key ecosystem function that reflects energy flow through the sediment ecosystems. Benthic food webs are also supported by organic matter that is produced or delivered to the sea floor. Its remineralization through microbial processes also indirectly provides carbon and nutrients (Thrush et al. 2021a).

Organisms of the macrofauna exhibit a variety of feeding modes (e.g., suspension feeders or deposit feeders) which mostly drive the modification of their physical environment and underpin much of the functionality of marine sediments (Thrush et al. 2021a). Feeding and bioturbation activity of these organisms can affect the physical and chemical (e.g., nitrogen and oxygen fluxes) properties of the sediment, increase exchanges between the sediment and the overlying water and influence local levels of benthic-pelagic coupling (Snelgrove et al. 2018). Moreover, macrofauna can facilitate sediment organic carbon processing by microbes, enhance the rates of organic matter deposition on seafloor, speed-up organic matter mineralization and

contribute to sediment oxygen uptake through respiration or bioturbation (Thrush et al. 2021a). In addition to organic matter processing and nutrient cycling, benthic macrofauna plays a major role in secondary production, either as direct food sources to human population or as major food sources for bottom-feeding species that can be commercially exploited (Snelgrove 1998).

Finally, benthic biogenic habitats structured by foundation species (i.e., organisms that provide structure, moderate local biotic and abiotic conditions, and have a large, positive effect on other species in a community; Dayton 1972) can affect multiple functions. For instance, these organisms may increase sediment stability, enhance species diversity or dampen hydrodynamics impacts on communities, which might have an effect on the resilience and stability of the ecosystems, these two aspects also being considered as functions even though they not directly link organisms to fluxes of energy (Bouma et al. 2009a; Angelini et al. 2011; Thrush et al. 2021a).

1.2.2. Soft-bottom habitats

Used loosely up to this point, the term "habitat" refers to the physical environment, that is the predominant features that creates structural complexity in the environment such as plants or geological features (Airoldi and Beck 2007) and its associated biological community. Sediments harbor a variety of different habitats, the majority of which are created by species living in or on the sediment themselves: ecological engineers that can cause biologically mediated habitat modification (Jones et al. 1994; Thrush et al. 2021a). Autogenic engineers are organisms that change the environment via their own physical structures (e.g., seagrass meadows, coral reefs) while allogenic engineers are organisms that transform living or non-living material from one physical state to another (e.g., sediment reworking by bioturbators) (Jones et al. 1994; Bouma et al. 2009a; Thrush et al. 2021a). The foundation species that structure biogenic habitats are autogenic engineers as their physical structures can affect local hydrodynamics, sediment trapping and enhance habitat complexity leading to higher biological diversity (Crooks 2002; Bouma et al. 2009a). In this thesis, four coastal soft-bottom habitats are considered: sandy beaches, subtidal soft sediments as well as intertidal seagrass beds and subtidal maerl (rhodolith) beds, two biogenic habitats structured by autogenic engineers. A brief description of each of these habitats is given below.

1.2.2.1. Sandy beaches

Sandy beaches (Figure 2A) are highly dynamic habitats defined by tides, waves and sand. They range from narrow and steep (reflective beaches, mostly prevalent in the tropics) to wide and flat (dissipative beaches, more common in temperate regions), but most beaches are intermediate between these extremes (Schlacher et al. 2008). Their coarse sediments retain little water or organic matter, making it an inhospitable habitat inhabited by species able to tolerate mobile sediments (Gray and Elliott 2009). They lack of biogenic structures and are physically controlled by the environment. Indeed, communities are more structured by the responses of species to the physical environment than by biological interactions, although these interactions may be more important in more dissipative beaches (Defeo and McLachlan 2005; Schoeman et al. 2014). Most species they harbor are not found in other environments and present key adaptation that allow them to cope with rapidly changing conditions, even though some are more adapted to harsh environments than others confined to more dissipative beaches (Defeo and McLachlan 2005; Schlacher et al. 2008). Additionally, the dissipative beach surf-zone is rich in phytoplankton and microorganisms resulting in a high productivity of these systems (Schlacher et al. 2008). Moreover, sandy beaches are important in processing large quantities of organic material, recycling nutrients back to coastal waters, filtering water and mineralizing organic matter through the porous sandy body and they serve as important nursery and foraging areas for commercial or heritage species (Schlacher et al. 2008). They also play a major role in coastal protection and erosion control and furnish recreational benefits (e.g., via tourism) (Barbier et al. 2011). Thus, they are of great socio-economic importance and provide irremediable ecosystem services. In this thesis, macrofauna samples were taken in the low intertidal zone (also called midlittoral zone).

1.2.2.2. Seagrass beds

Seagrass species (Figure 2B) are rhizomatous, clonal marine angiosperms that occupy space through the reiteration of shoots with their leaves and roots produced as a result of rhizome extension (Duarte 2002). They provide physical structure to bare sediments (hence more potential niches), enhancing community richness and diversity compared to bare sediments and potentially reducing predation and increasing community stability (Boström and Bonsdorff 1997; Hily and Bouteille 1999; Duffy 2006). They can shelter organisms that generally do not occupy sediments providing them hard substrate and refugia. They also enhance primary and secondary production (Duffy 2006). Indeed, they cover about 0.1 to 0.2% of the global ocean and are among the most productive coastal ecosystems and most valuable

ecosystems in the biosphere (Costanza et al. 1997; Duarte 2002). In addition to their high primary production, they perform a plethora of functions such as provision of food for coastal food webs, provision of oxygen to waters and sediments, organic carbon export to adjacent ecosystems, trapping and cycling of nutrients, nursery and shelter for ecologically and commercially important species, sediment stabilization, prevention of sediment resuspension, wave attenuation and carbon sequestration from atmosphere (Duarte 2002; Barbier et al. 2011). Indeed, they are an important global sink of carbon since detritus burial from vegetated coastal habitats contributes to 50% of the carbon burial in ocean and seagrasses might represent 15% of the total surplus carbon fixed in the global ocean (Duarte and Chiscano 1999; Duarte et al. 2005). In this thesis, only seagrass beds located in the intertidal zone are studied.

1.2.2.3. Subtidal soft sediments

Although they cover a large area, we generally know less about subtidal soft sediments (Figure 2C) than sandy beaches due to higher accessibility for sampling in sandy beaches (Gray and Elliott 2009). Yet, macrofauna species richness is higher in subtidal soft sediments than in sandy beaches for an equivalent sample size (Gray and Elliott 2009). Subtidal environments are also defined by the tidal currents, but in comparison to intertidal sediments, the strength of environmental stresses is lowered, with less fluctuation in abiotic factors, less wave action and less desiccation (Moran 1999). It has also been shown that subtidal communities might respond slowly to environmental changes compared to intertidal ones (Hinz et al. 2011). However, biotic interactions such as predation and competition may be relatively more important in subtidal habitats (Moran 1999). Although the literature on the functions and services delivered by subtidal soft sediments is less exhaustive than that of the other studied habitats, the species they harbor can support important functions and services. Indeed, bioturbators can change fluxes of inorganic nutrients from sediment to water column, improving conditions for production by microphytobenthos, thus increasing levels of primary production in shallow subtidal habitats (Lohrer et al. 2004). Additionally, by reworking the sediment, these allogenic engineers can maintain levels of diversity in this *a priori* homogeneous habitat (Widdicombe et al. 2000) and may contribute to an increased capacity of the system to resist invasion (Lohrer et al. 2008).

1.2.2.4. Maerl (rhodolith) beds

Maerl or rhodoliths (Figure 2D) are free-living structures composed of non-geniculate coralline algae (Foster 2001). Maerl thalli can accumulate locally forming beds, the surface of which is composed of fragments of living and/or dead maerl that can reach several km^2. Fragments are slow growing making maerl beds extremely fragile (Foster 2001). Their hard structure and complex architecture provide a range of hard habitats (depending of the size and shape of maerl) and heterogeneous soft bottom for numerous organisms usually not found on sedimentary bottom, such as free-living invertebrates living on and in the rhodoliths and underlying sediments (Foster 2001; Foster et al. 2013). Their structural complexity makes them highly biologically and functionally diverse compared to bare sediments and provide shelter for many predators with biotic interactions preventing monopolization of resources by dominant species (Grall and Glémarec 1997). These biotic interactions might be important in regulating the availability of food, refugia and production, thus influencing the diversity and productivity of this ecosystem (Barbera et al. 2003). Additionally, they support many rare species, have considerable value as nursery grounds for species of commercial interest and are also important carbonate producers with a higher carbonate production than other European coastal habitats (Barbera et al. 2003). They are of great economic importance, having been extracted, first as an enriching agent for soils for hundreds of years, then as a food supplement for livestock and for the treatment of wastewater in sewage plants, and even as a raw material entering in the composition of pharmaceutical or cosmetic products (Salomidi et al. 2012).

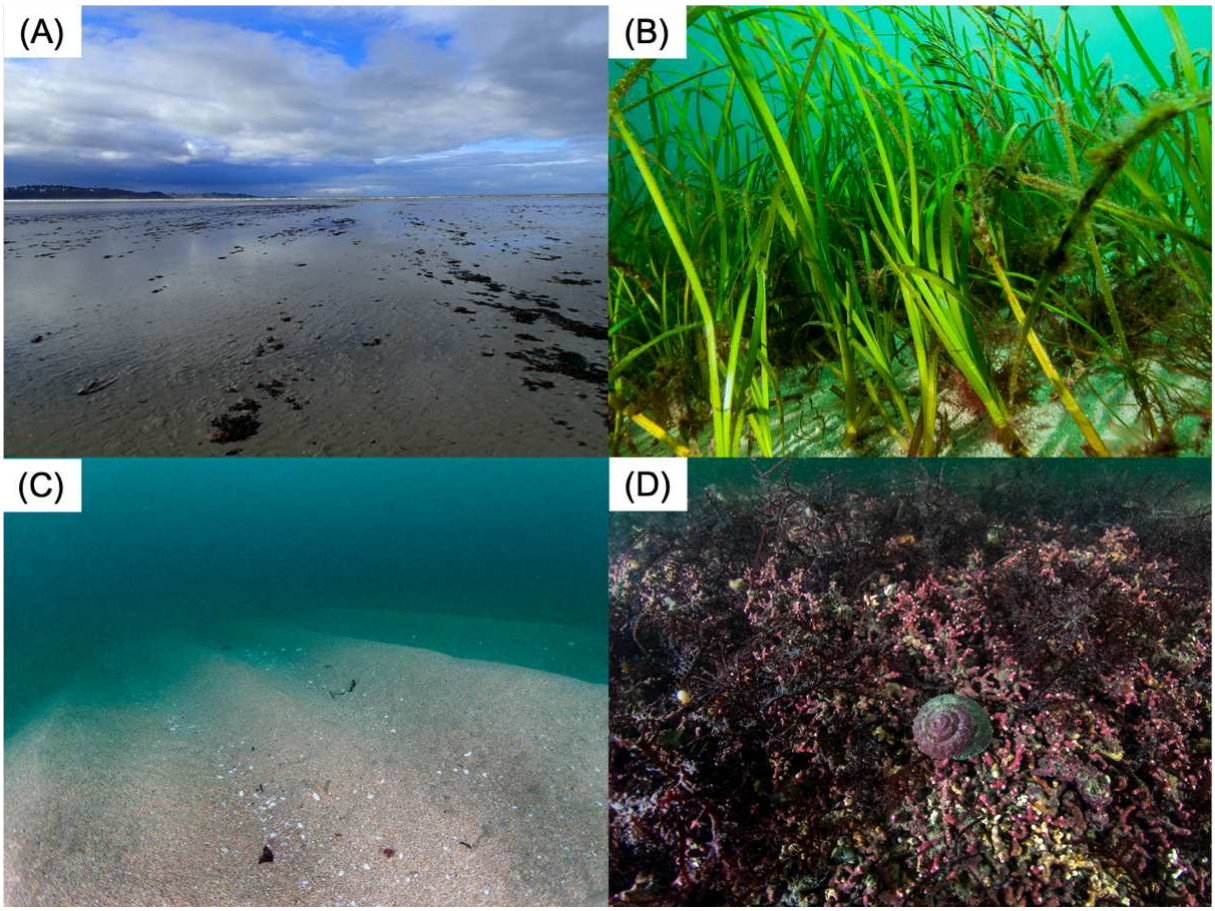


FIGURE 2: Examples of the four monitored habitats. (A) sandy beaches, (B) intertidal seagrass beds, (C) subtidal soft sediments and (D) maerl beds. Photo credits: Nolwenn Quillien (A) and Erwan Amice (B, C, D).

1.2.3. Threats

Coastal benthic ecosystems are particularly vulnerable as they are at the junction between land and sea, therefore anthropogenic disturbances and stressors can occur from users of the marine system but also from land and freshwater (Thrush et al. 2021a) (Figure 3). Indeed, human impacts to European seas were estimated to be higher in coastal areas than shelf or beyond shelf areas (Korpinen et al. 2021). Soft-bottom habitats are threatened by eutrophication, fishing activities, contaminants but also by terrestrial sediment inputs, introduction of non-indigenous species, seabed exploitation, noise and coastal development, and this list is not exhaustive (Crain et al. 2009; Harris 2020). For example, eutrophication and nutrient enrichment that result from land use and agriculture, can promote invasion by non-indigenous species (Williams and Smith 2007), lead to the development of opportunistic macroalgae or "green tides" (Cloern 2001; Quillien et al. 2018) or eliminate bioturbating macrofauna leading to intensifying anoxia and hypoxia in sediments and the water column which can change the physiology or kill macrofauna (Thrush et al. 2021a). As another example,

overfishing has strong impacts on the structure and functioning of ecosystems, as it can have direct impact on the fauna and indirect impact *via* modifying sediment characteristics (with trawling gears), which are determinant factors controlling soft-bottom fauna diversity and distribution (Hily et al. 2008). Additionally, it can remove important functional groups and change the size and structure of food-webs (Jackson et al. 2001).

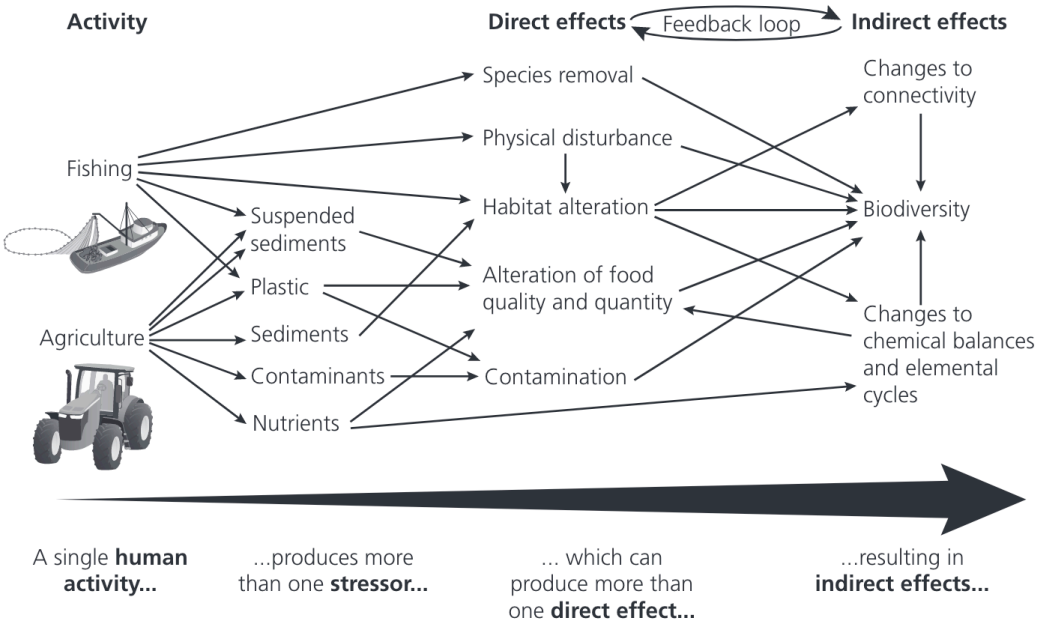


FIGURE 3: A single human activity can produce multiple stressors and affect the ecosystem in multiple ways. Moreover, different activities can produce similar stressors or interact in producing it. From Thrush et al. (2021a).

Another major threat to marine biodiversity is habitat fragmentation, homogenization and loss, mainly caused by human activities (Gray 1997). Habitat degradation leads to the loss of resident species, loss of food resources and loss of ecosystem functions (Airoldi et al. 2008). Moreover, the loss of habitat complexity frequently leads to the invasion of opportunistic species which can amplify changes to the ecosystem (Airoldi et al. 2008). The arrival of new species can increase species richness, yet habitat degradation also causes an increase in the similarity of the biological diversity across space called biotic homogenization (Olden 2006; Airoldi et al. 2008). Additionally, before complete habitat loss, habitat fragmentation can induce higher rates of species extinction, lower immigration rates and a higher difficulty to provide recruits for some species (Gray 1997; Thrush et al. 2021a). For example, the most important threats to the degradation of seagrasses are pollution, eutrophication and sedimentation (Airoldi and Beck 2007), maerl beds are particularly threatened by overexploitation, extraction and dredging (Hall-Spencer and Moore 2000; Barbera et al. 2003)

and intertidal and subtidal sediments by coastal development, fishing and eutrophication (Defeo et al. 2009; Salomidi et al. 2012).

To these anthropogenic stressors and disturbances are added the effects of climate change on benthic communities, that interact in various ways . Climate change leads to changes in environmental variables such as temperature and pH and increases the frequency of extreme events. For example, changes in temperature can cause poleward shifts in the distribution of benthic species and changes in seasonality can influence the timing of primary production and lead to match/mismatch scenarios influencing the recruitment of species, with a high potential of impact in ecosystem structure and functioning (Birchenough et al. 2015). Decrease in pH, ocean acidification, has negative effects on benthic organisms relying on carbonates for their formation. Moreover, eutrophication can interact with climate warming to exacerbate opportunistic algae leading to harmful algal blooms (He and Silliman 2019). In addition, increasing rainfall can lead to major influx of sediments, decreasing water quality and increasing habitat fragmentation (Thrush et al. 2021a).

In response to these different threats, various strategies have been set up such as restoration or bioremediation, but one of the most widely applied has been the protection of coastal ecosystems through the establishment of marine protected areas (Gray 1997). Monitoring appears as an essential tool to better understand the responses of communities to these increasing threats. Moreover, it constitutes a gateway between science and management and should allow to develop effective management strategies.

2. Monitoring biodiversity

Article 2 of the Convention on Biological Diversity (CBD) signed in Rio in 1992 defined biological diversity as “the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems”. Thus, biodiversity is multifaceted and can be measured at different scales using a variety of methods, metrics or indices that ecologists have developed over the past decades and are still developing.

2.1. Biodiversity facets

Biodiversity encompasses genetic diversity (i.e., the genetic differences between individuals and populations), taxonomic diversity (i.e., species diversity or diversity at higher levels than the species level), phylogenetic diversity (i.e., the minimum total length of all phylogenetic branches required to cover a set of taxa on the phylogenetic tree), functional diversity (i.e., the range of functions that are performed by organisms in a system) and ecosystem and habitat diversity (Gray 1997). Essential Biodiversity Variables (EBV) are a minimum set of essential measurements to capture major dimensions of biodiversity change that are complementary to one another (Pereira et al. 2013). They are divided into 6 classes: genetic composition, species populations, species traits, community composition, ecosystem structure and ecosystem function (Pereira et al. 2013).

Since all of these classes could not be assessed during this thesis, we focused on two facets of biodiversity: taxonomic diversity (i.e., community composition according to Pereira et al. 2013) and functional diversity (i.e., species traits according to Pereira et al. 2013). These two facets are related to the structure and functions of the ecosystem and enable to better understand Biodiversity-Ecosystem Functioning (BEF) relationships. These relationships can take many forms (Figure 4), for example positive relationships between the taxonomic diversity of ecosystems and their functions (e.g., Tilman et al. 2014; Gamfeldt et al. 2015) might rely on different mechanisms such as niche complementarity (species with more specialist niches might allow diverse communities to be more efficient at exploiting resources, leading to higher functionality) or functional facilitation (when the presence of a function facilitates the implantation or maintenance of another) (Hooper et al. 2005; Thrush et al. 2021a). In addition, factors such as the insurance effects (different species with similar functional roles responding differently to stressors), portfolio effects (independent fluctuations of many different species serving to lower functional variability) or compensatory dynamic effects (negative temporal covariance between species contributing to the same functions) can stabilize the functional performance of the communities (Thrush et al. 2021a).

Thus, ecosystem functioning not only relies on the diversity of taxa present in a system but also on the functional traits these taxa exhibit (Petchey and Gaston 2006; Cadotte 2017). A functional trait is defined as any morphological, physiological or phenological feature that impacts fitness via its effects on growth, reproduction and survival (Violle et al. 2007) and functional diversity as the number, type and distribution of functions performed by organisms within an ecosystem (Díaz and Cabido 2001). In addition to be an indicator of ecosystem functions, functional diversity may act as an indicator of the processes governing community

assembly and the impact of perturbations and environmental gradients on community structure (Villéger et al. 2008). Moreover, functional diversity can be less affected by large-scale geographic influences than relative taxon composition in benthic studies and can be more closely linked to small or local scale environmental conditions (Bremner et al. 2003). Because the patterns between taxonomic and functional diversity can be decoupled (e.g., Edie et al. 2018; McLean et al. 2019b), looking at these two facets can deepen our understanding of biodiversity change.

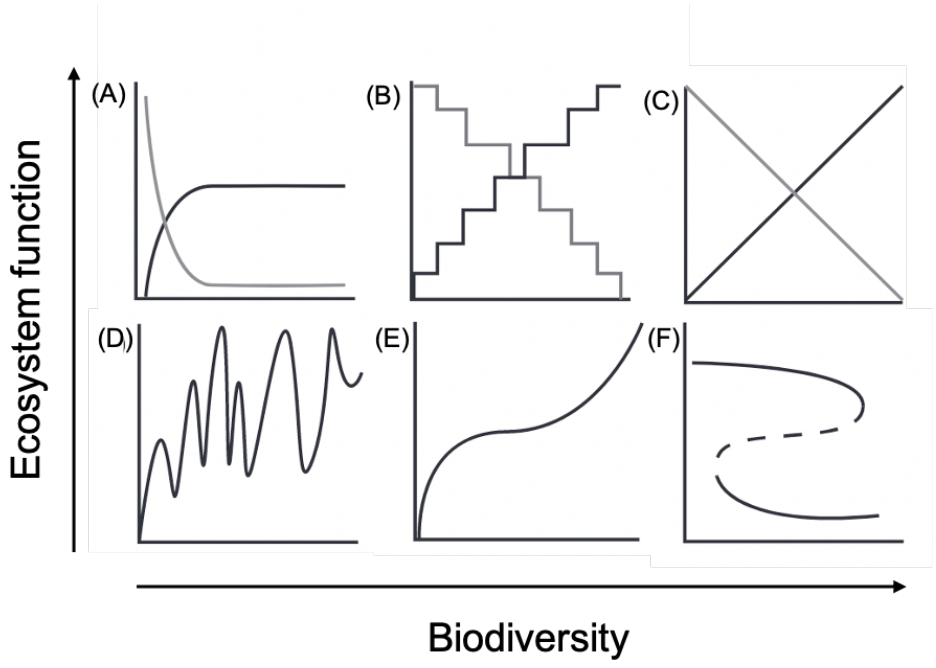


FIGURE 4: Biodiversity-Ecosystem Functioning (BEF) relationships can take many forms: (A) initial fast change followed by slower change, (B) stepwise changes, (C) linear change, (D) variable or oscillations around a trend, (E) fast change followed by slower change followed by another increase in rate of change and (F) regime shifts with tipping points and hysteresis. From Thrush et al. (2021a).

2.2. Measuring biodiversity

2.2.1. Metrics and scales

Whatever facet of biodiversity is measured, the latter can be observed at different spatial and/or temporal scales. Since most methods were firstly developed for taxonomic diversity, the following paragraphs are mainly based on it and a focus on functional diversity is given in section 2.2.4.

Whittaker (1960, 1972) was the first to describe spatial scales of biodiversity. He defined point diversity as the species richness (i.e., the number of species) of a single sample, α diversity as the number of species in samples within a habitat or ecosystem in a given region,

γ diversity as the cumulative species richness in a larger unit (e.g., landscape, island, region), and the ε diversity as the total species richness of areas of γ diversity (e.g., in a large biogeographical province). However, biodiversity not only includes richness but also aspects of identity, dominance and rarity (Hillebrand et al. 2018). Gray (2000) emphasized that species diversity is represented by species richness and also the proportional abundances of the species which he called "heterogeneity diversity". Different indices were developed to measure species diversity, the most commonly used being species richness, Shannon-Wiener's index, Simpson's index, and Pielou's evenness index (Whittaker 1972; Gray 2000).

β diversity is a different property from that of the scales of diversity previously mentioned as it was first described as the variation in the identities of species among sites and as providing a direct link between α and γ diversity in a multiplicative form $\beta = \gamma/\alpha$ (Whittaker 1960, 1972; Anderson et al. 2011). Its definition has then evolved to incorporate the abundances of species and to distinguish β diversity into the notion of "turnover" which is the measure of change in community along a spatial, environmental or temporal gradient, and the notion of "variation" in community structure among a set of sample units within a given spatial or temporal extent (Anderson et al. 2011; Figure 5). Note here the consideration of the temporal scale which was firstly minimized in favor of the spatial scale.

As for α diversity, numerous methods exist to compute these two notions of β diversity. They include multidimensional resemblance measures that can be based on species identity (e.g., Jaccard), relative abundances (e.g., Hellinger) or take into account total abundances (e.g., Bray-Curtis) (Anderson et al. 2011). Depending on their properties (Legendre and De Cáceres 2013), these similarity or dissimilarity indices can then be interpreted using different multidimensional statistical methods such as ordinations (e.g., Principal Component Analysis (PCA), Principal Coordinates analysis (PCoA), metric or non-metric multidimensional scaling (MDS or nMDS)) or clustering methods (e.g., hierarchical clustering, k-means clustering) (Anderson et al. 2011; Clarke and Warwick 2014). Furthermore, β diversity as quantified by a dissimilarity measure can be decomposed into species replacement, richness difference or nestedness to better understand how it is expressed (Legendre 2014). Interestingly, it was also proposed to estimate β diversity as the total variation of a community matrix (i.e., sample units *species matrix containing presence/absence or raw or relative abundances in the case of taxonomic diversity) (Legendre and De Cáceres 2013). This method allows to directly link community total variation to its underlying drivers through Redundancy Analysis (RDA) and variation partitioning.

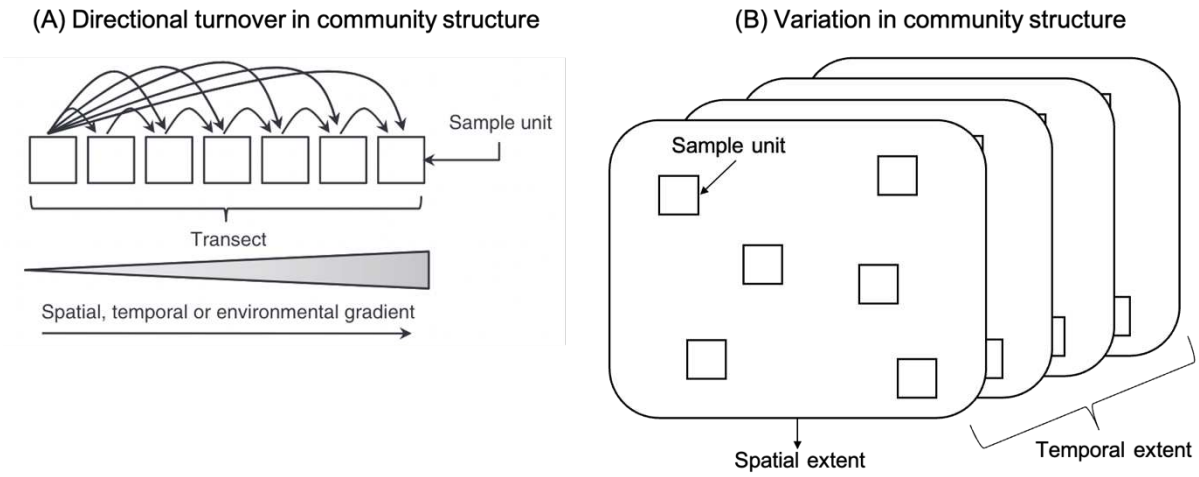


FIGURE 5: Schematic diagram of two conceptual types of β diversity for ecology: (A) turnover in community structure along a gradient and (B) variation in community structure among sample units over a spatial and temporal range. Modified from Anderson et al. (2011).

2.2.2. Biodiversity trends

Biodiversity trends are strongly dependent of the scale of observation and metrics used. McGill et al. (2015) recognized four spatial scales (local, meta-community, biogeographical and global) and four classes of biodiversity (α diversity, spatial β diversity, temporal β diversity and abundance) which yielded 15 distinct categories of biodiversity exposing different trends (Figure 6). For example, although the loss of species and biodiversity in general is reported at a global scale (e.g., the global Living Planet Index shows an average 69% decrease in relative abundance of monitored vertebrate populations between 1970 and 2018, Almond et al. 2022), this is not necessarily the case at smaller scales (Thomas 2013; Vellend et al. 2013; Vellend 2017).

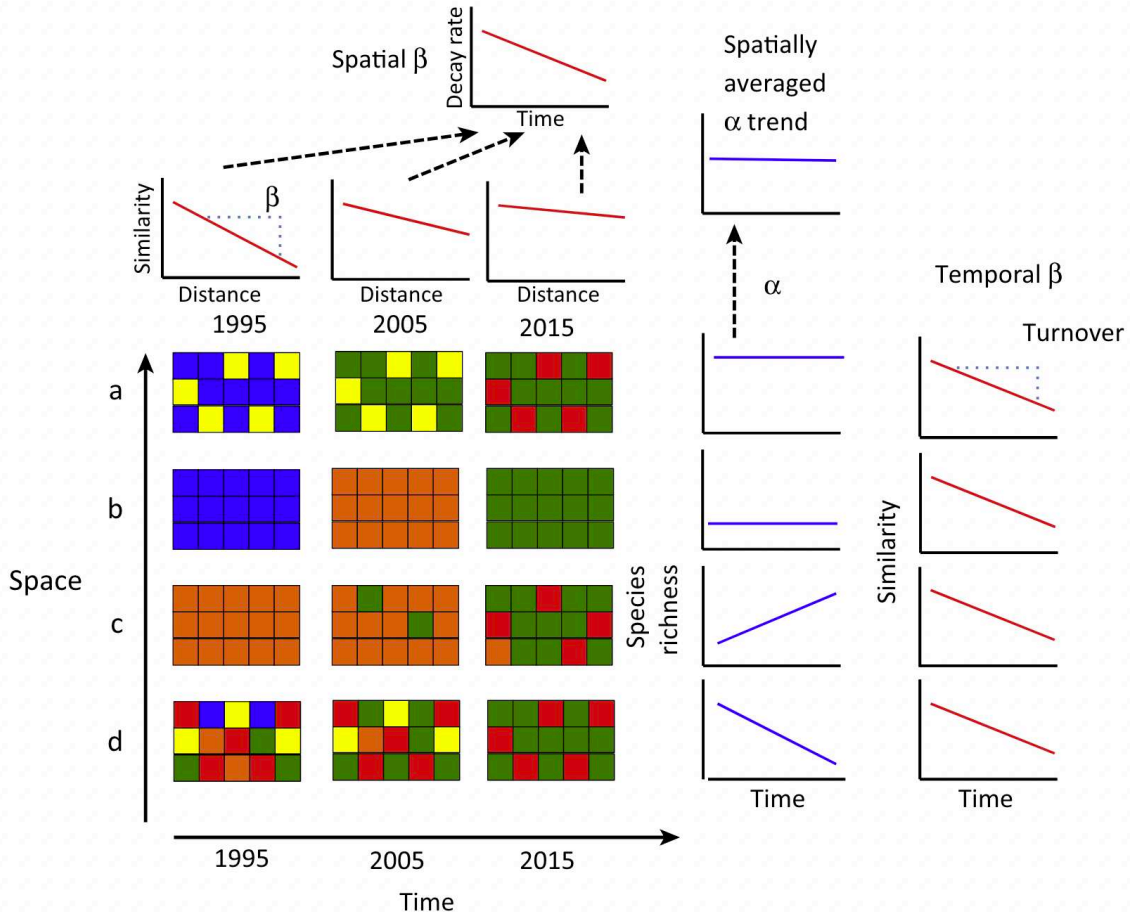


FIGURE 6: Four hypothetical communities (a–d) through three time periods (1995, 2005, 2015) (community abundance is constant, colors represent distinct species) demonstrating all of the major types of trends of α and β diversity. From McGill et al. (2015).

At regional scales (i.e., metacommunity according to McGill et al. 2015), species richness often shows an increase mainly associated with the introduction of non-native species in new regions, while at local scales, declines occur only in particular scenarios and species richness mostly remains steady (Thomas 2013; Vellend 2017). In their meta-analyses, Dornelas et al. (2014) did not detect a consistent negative trend in species richness, rather, they demonstrated that the overall slope was indistinguishable from zero. However, species temporal turnover (i.e., temporal β diversity) exhibited consistent long-term changes representing a change in community composition per decade of 10% of the species. This suggested that regional assemblages experience a substitution of their taxa rather than a systematic loss (Dornelas et al. 2014). This also highlighted that, although species richness became the most dominant measure of biodiversity as it can be easily observed and recorded, it can be insufficient to capture key changes in biodiversity (Hillebrand et al. 2018). It emphasizes the need to quantify temporal β diversity alongside α diversity to further our understanding of biodiversity change (Magurran et al. 2018). Indeed, a key challenge is to better understand the

rate of turnover in communities to report changes that are greater than those that might have happened by chance, to identify early warning signal of change and communities' capacity of resilience (Magurran et al. 2010, 2018). For example, in their meta-analyses, Gotelli et al. (2017) demonstrated that contemporary rates of temporal β diversity were greater than ecological theory predicts and Blowes et al. (2019) demonstrated that direction and magnitude of changes differ across regions with higher rates of temporal β diversity in the ocean than on land. These considerations bring to light the need to take into account β diversity more frequently and pave the way for more temporally explicit framework in community ecology (Yang 2020).

2.2.3. Analyzing spatial and temporal β diversity

Although the development of β diversity analysis methods was first concerned with spatial scales, diverse methods have been developed and used over the past 30 years in studies focusing on temporal community dynamics (Figure 7; Buckley et al. 2021b). Multivariate datasets can be more sensitive to changes in explanatory variables than univariate statistics which has led to promising developments in methods for analyzing multivariate dataset in a temporal context in recent decades, with some methods derived from the ones used in spatial β diversity analyses (Buckley et al. 2021a). The main multivariate methods used over this thesis to analyze spatial and temporal β diversity are unconstrained and constrained ordination methods (e.g., PCoA, RDA) (Chapters I to IV) and Community Trajectory Analysis (CTA) (Chapter I and III). Redundancy Analysis (RDA) coupled with variation partitioning (Chapters II and IV) and Moran Eigen Vector Maps (MEMs) (Chapter II) were used to better understand the underlying drivers of communities' β diversity.

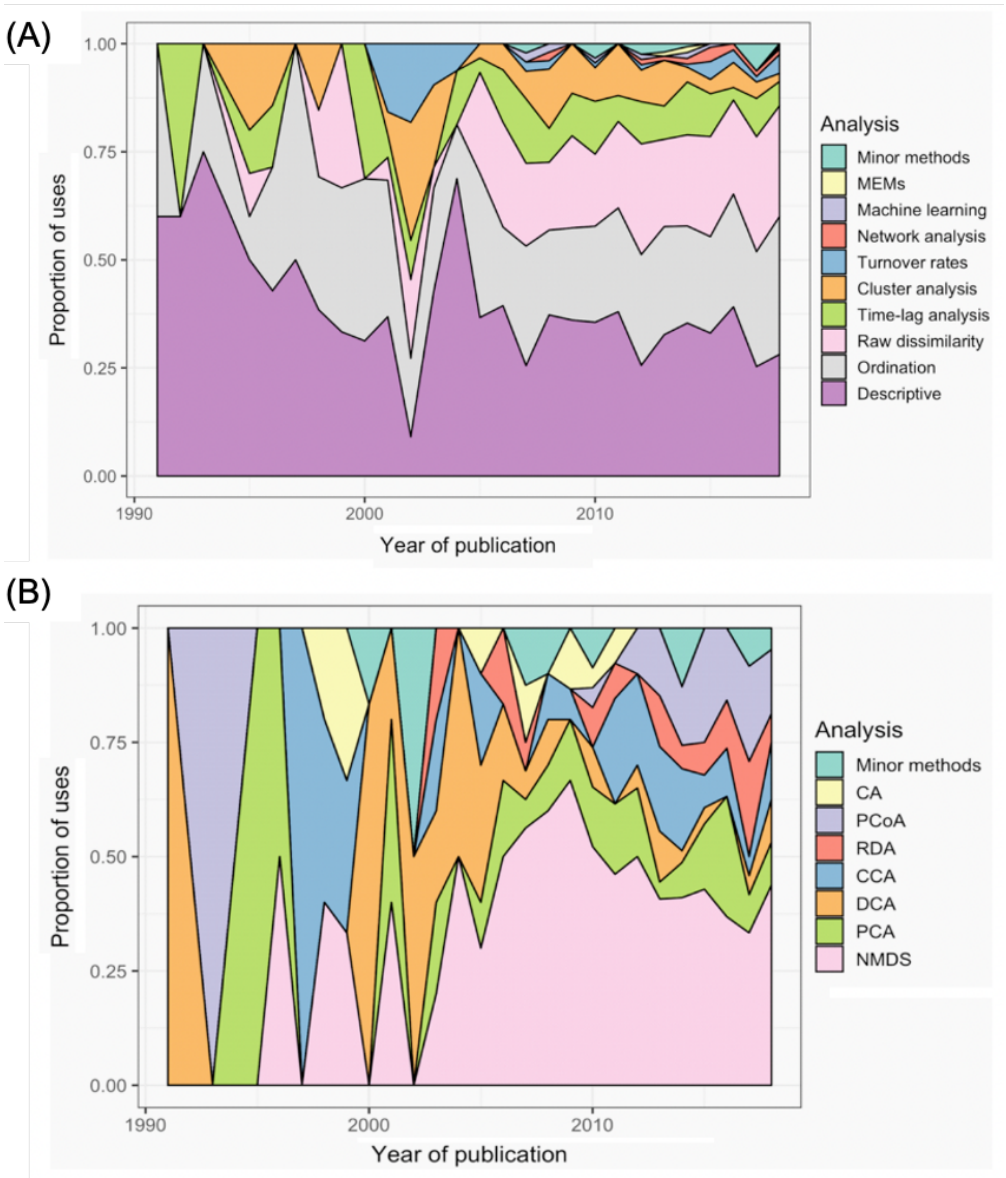


FIGURE 7: Trends in the use of different methods for the analysis of temporal community dynamics datasets, from 1990 to the end of 2018. (A) The proportion of uses of 10 categories of analysis methods across all sampled publications; 'Minor methods' include compositional pivot days, multiplicative change, multivariate regression modelling, nestedness analysis, synchrony, and temporal stability. (B) The popularity of the different ordination methods used across the 28 years. CA, correspondence analysis; PCoA, principal co-ordinates analysis; RDA, redundancy analysis; CCA, canonical CA; DCA, detrended CA; PCA, principal components analysis. 'Minor methods' are: distance-based RDA (dbRDA), detrended CCA (DCCA), partial CCA (pCCA), pRDA, Procrustes and multiple co-inertia analysis. From Buckley et al. (2021b).

PCoA, RDA and variation partitioning are now common analyses in ecology and are well described in Legendre and Legendre (2012). CTA (De Cáceres et al. 2019) is a more recent multivariate method used to understand community dynamics. It focuses on the geometrical analysis of temporal trajectories (i.e., consecutive observations linked by a segment) in a multivariate space defined by the resemblance between community observations, obtained with

the calculation of a dissimilarity coefficient (De Cáceres et al. 2019). The temporal trajectories of the communities under study are associated with geometrical properties and statistics (e.g., directionality, shape, length, net change, etc.) that can help identifying temporal patterns or variations in community dynamics (De Cáceres et al. 2019; Sturbois et al. 2021c). Another tool used here to analyze temporal β diversity, MEMs provide a matrix of uncorrelated temporal or spatial variables that can be used to model scales of temporal or spatial variation in community composition (Legendre and Gauthier 2014). Thus, they can be used in multivariate analyses such as RDA and paired with variation partitioning to show the amount of variance explained by eigenvectors representing different scales of temporal or spatial variation in composition (Legendre and Gauthier 2014; Buckley et al. 2021b).

2.2.4. Measuring functional α and β diversity

The description of the methods in the previous paragraphs relied mainly on the taxonomic diversity facet since it has received more attention to date than other facets of biodiversity. However, information on functional diversity can contribute to substantial added value to biodiversity analyses and need to be considered (Magurran et al. 2019). Methods to assess functional α and β diversity follow the same logic as taxonomic diversity methods but present some differences. Firstly, the matrices of interest do not include information on presence or abundances of taxa but on their functional traits. A list of coherent traits has to be selected and coded for each recorded taxa (Martini et al. 2021). Traits information can be measured directly from the individuals or taken from the literature. They can be coded in a quantitative, semi-quantitative or qualitative way. In our case, information on functional traits were found in the literature and we applied a fuzzy-coding method (Chevenet et al. 1994). This approach allows to capture the intraspecific variability and ontogeny since each trait is divided into modalities coded according to the affinity of the taxa to these modalities (see Chapter IV for more details).

As for the taxonomic α diversity, numerous methods and metrics exist to quantify functional α diversity (Mouchet et al. 2010). In this thesis, functional α diversity was estimated from the space occupied by species in a multidimensional trait space based on a subset of PCoA axes obtained from the distances between species' traits (Villéger et al. 2008). To correctly assess effects of the diversity of traits on ecosystem processes, it has been suggested to use a minimum combination of three indices: functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv) (Mouchet et al. 2010) (Figure 8). Additional indices were used and described in Chapter IV of this thesis.

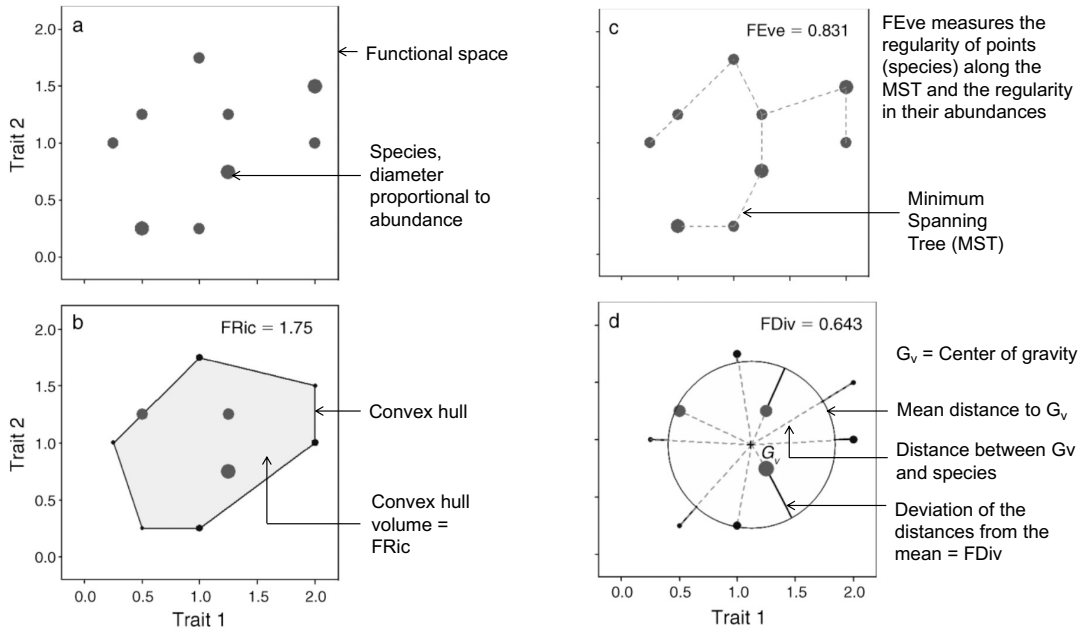


FIGURE 8: Estimation of three functional diversity indices in multidimensional functional space: functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv). Modified from Villéger et al. (2008).

To estimate functional β diversity, the Community-Weighted Mean trait value (CWM) can be used. It represents a sites*traits matrix with the average values of the weighted traits of the community. Multivariate analyses are then used on this CWM to describe spatial or temporal variability in benthic community functional structure in the same way as for taxonomic β diversity (Bremner et al. 2006; Beauchard et al. 2017). In Chapter IV, we estimated functional β diversity from a matrix of "abundance-weighted traits", which, after transformation, is equivalent to a CWM on each trait category (Figure 9).

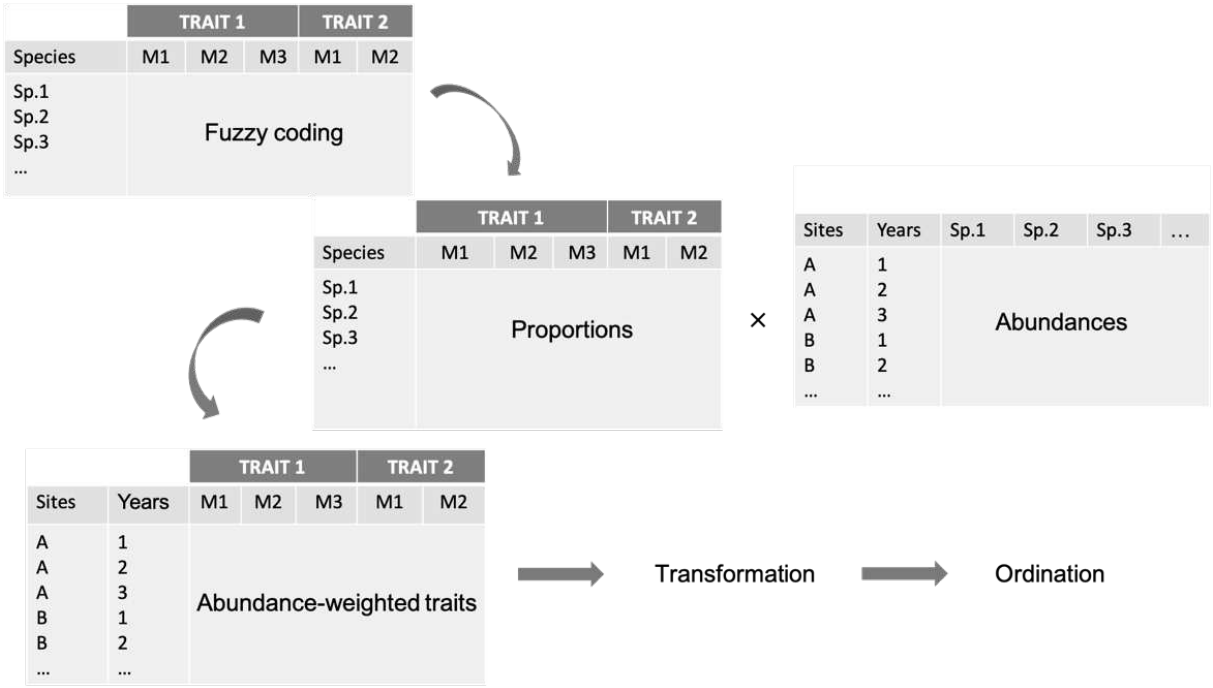


FIGURE 9: Steps to estimate functional β diversity, as used in this thesis. In the "proportion matrix" each trait modality score is converted into a relative expression so that the sum of the trait category scores for an individual trait and a given taxon equals 1. M = trait modality; Sp. = species.

2.3. The importance of long-term monitoring programs

Monitoring is defined as the process of gathering information about some system state variables (i.e., variable within the system of interest that is used to characterize the system status) at different points in time (Yoccoz et al. 2001). In the context of ecological monitoring, these variables are often information on the variety and/or abundance of species or other taxonomic units in the system (Magurran et al. 2010). Lindenmayer et al. (2012) defined "long-term" studies as those that systematically and regularly collect field data from a particular site or set of sites for more than 10 years. These monitoring programs can be used in different ways such as surveillance monitoring (i.e., assess long-term natural or anthropogenic changes), operational monitoring (i.e., related to a particular human activity or problem) or investigative monitoring (i.e., looking for explanations when deviation from perceived or required quality is detected) (Gray and Elliott 2009).

The current context of biodiversity loss at a global scale (Díaz et al. 2019) highlights the importance of long-term ecological research to better understand biological response to environmental changes but also to better evaluate the rate of natural changes in communities (Magurran et al. 2010; Sukhotin and Berger 2013). Indeed, data series arising from long-term monitoring may, ideally, help to separate long-term trends induced by climatic changes or anthropogenic influences from regular cycles and/or spontaneous fluctuations resulting from

natural environmental variability, biotic interactions or the noise induced by highly variable natural data (Sukhotin and Berger 2013). Moreover, they allow to identify rare events or tipping points and the early warning signs of these changes (Magurran et al. 2010). Long-term ecological monitoring is also instrumental in making valuable contributions for advancing ecological theory (Kominoski et al. 2018), as well as improving ecological models (Giron-Nava et al. 2017) and policy design (Hughes et al. 2017). To summarize, Lindenmayer et al. (2012) grouped the benefits of long-term ecological monitoring in 5 key-values: it allows to 1) quantify ecological responses to ecosystem changes, 2) understand ecosystem processes occurring over long period, 3) provide data that can be used in ecological models or to validate models, 4) promote collaborative and multidisciplinary study, and, 5) support decision making, policy design and management of ecosystems or evaluate results from management.

The scientific community agrees on the importance of long-term research in ecology and places greater value on long-term rather than short-term studies (Hughes et al. 2017; Kuebbing et al. 2018). Indeed, many ecosystems change slowly, thus long-term studies are more coherent to apprehend their dynamics (Lovett et al. 2007). Moreover, they may provide a more complete representation of the complexity of a system than local and short-time scale studies as it is often the case in experimental studies (Witman et al. 2015). However, and while there is also a consensus that coupling long-term studies with experimental ones is the best association to reach a better understanding of the mechanisms behind system changes (Yoccoz et al. 2001; Lovett et al. 2007; Kuebbing et al. 2018), experimentation is not always possible. In addition to a long-term temporal scale, multi-site and multi-species studies are more valuable to advance our understanding of complex dynamics of multispecies assemblages and ecosystems and to develop general theory (Hughes et al. 2017; Kuebbing et al. 2018). Unfortunately, despite the many values of long-term ecological monitoring, few ecological time-series exceed decades and the effort, fundings and personnel necessary to maintain long-term monitoring make them not particularly common (Magurran et al. 2010; Lindenmayer et al. 2012; Hughes et al. 2017).

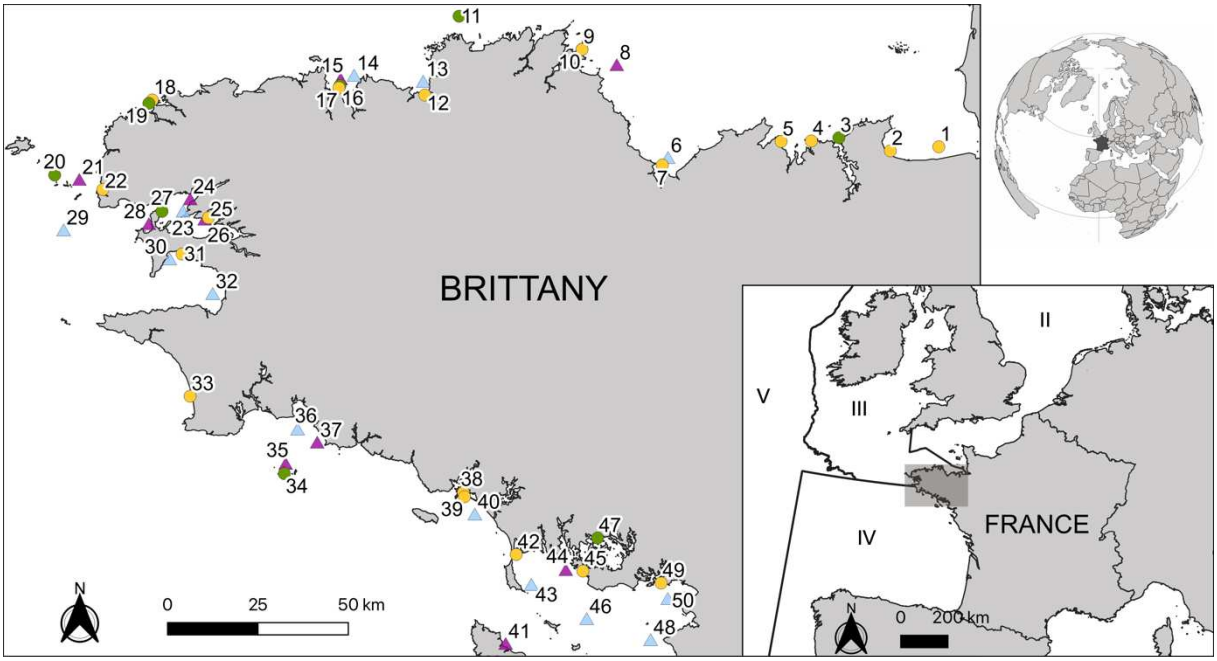
3. Context and aims of the thesis

3.1. The REBENT monitoring program

3.1.1. Location and objectives

The REBENT (RÉseau BENThique, literally Benthic Network, https://rebent.ifremer.fr/) monitoring program was established after the sinking of the oil tanker Erika off the shores of Brittany (France) in 1999. Several studies sought to identify and quantify the impact of this pollution, however, the lack of available baseline data at the regional scale made this goal difficult to achieve. The need for a perennial coastal monitoring program became apparent, and it was in this context that the REBENT monitoring program was created (Derrien-Courtel et al. 2013). The monitoring became operational in 2003 and is since conducted jointly by the observatory of the Institut Universitaire Européen de la Mer (IUEM), and the biological stations of Roscoff and Concarneau.

Brittany (France) is a biogeographic transition zone between the Northern European seas and the Lusitanian province (Spalding et al. 2007), or, according to the delimitation of the Oslo-Paris (OSPAR) commission, between the Greater North Seas, the Celtic Seas and the Bay of Biscay and Iberian Coasts (Figure 10). Thus, Brittany is an area where Nordic and Mediterranean influences meet and is inhabited by species with both “warm” and “cold” affinities (Spalding et al. 2007; Quillien 2016). It is therefore an area of great interest for monitoring in the face of climate change and changes in the distribution of species. A hydrological front separates distinct water masses between the South and the North, with more homogeneous waters in the North and more stratified ones in the South (Derrien-Courtel et al. 2013). In Southern Brittany, the Gulf of Morbihan and the Vilaine and Loire estuaries bring increased turbidity while the waters of the English Channel, the Iroise Sea, and southwestern Brittany are less turbid (Derrien-Courtel et al. 2013). Moreover, Brittany’s shoreline shows a macrotidal regime which ranges from 5 to 13 m (Quillien 2016). This region also covers a variety of topographic and hydrodynamic conditions from very sheltered to exposed sites (Derrien-Courtel et al. 2013), enabling the existence of a high diversity of benthic habitats and making it a hotspot for macrobenthic richness (Gallon et al. 2017).



Sandy beaches	Intertidal seagrass beds	Subtidal soft sediments	Maerl beds
1. Baie du Mont Saint-Michel	3. Saint-Malo	6. Saint-Brieuc	8. Baie de Saint-Brieuc
2. Saint-Benoît	9. Arcouest	13. Lannion	15. Morlaix
4. Saint-Briac	11. Sept-îles	14. Pierre Noire	21. Molène
5. Saint-Cast	16. Callot	23. Rade de Brest - Larmor	24. Rade de Brest - Keraliou
7. Baie de Saint-Brieuc	19. Sainte-Marguerite	29. Mer d'Iroise	26. Rade de Brest - Rozegat
10. Arcouest	20. Molène	30. Baie de Douarnenez Nord	28. Camaret
12. Saint-Efflam	27. Roscanvel	32. Baie de Douarnenez Sud	35 Glénan
17. Callot	34. Glénan	36. Concarneau	37. Trévignon
18. Sainte-Marguerite	47. Arradon	40. Lorient Etel	41. Belle-île
22. Blancs Sablons		43. Quiberon	44. Meaban
25. Rade de Brest		46. Vilaine Large Nord	
31. Plage de l'Aber		48. Vilaine Large Sud	
33. Audierne		50. Vilaine Côte	
38. Gâvres			
39. Erdeven			
42. Plouharnel			
45. Kerjouanno			
49. Damgan			

FIGURE 10: Map of the sites sampled in the four studied habitats, in the context of the REBENT monitoring program. II = Greater North Sea, III = Celtic Seas, IV = Bay of Biscay, V = wider Atlantic (OSPAR commission). Sources: OpenStreetMap, European Environment Agency, OSPAR commission.

The objectives of the REBENT project are to collect, format and store data on habitats and associated benthic biocenoses in the coastal zone in order to provide scientists, managers and the public with relevant and coherent data to better understand the existing situation of these different habitats and detect spatiotemporal changes. These observations, including the faunistic and floristic composition of the habitats, are common to different needs: accidental pollution detection and monitoring, Water Framework Directive, integrated management. Cartographic data collections are carried out at zonal and sectoral scales but this thesis will focus on more localized monitoring ("station" approach) and short-term frequency monitoring

(1 year interval or less, Pereira et al. 2013) of biological variables (specific composition and abundance) on selected regionally important habitats. This level allows a detailed estimation of the changes in habitats and associated biodiversity.

3.1.2. Sampling of soft-bottom habitats

The REBENT program encompasses both sediments and rocky habitats but we only focus on the four soft-bottom habitats described above (section 1.2.2.), more precisely for the two biogenic habitats, monospecific seagrass beds composed of *Zostera marina* and maerl beds principally composed of *Lithothamnion corallioides* and *Phymatolithon calcareum*. Observations within each habitat were conducted yearly at two seasons: during spring (more precisely between the end of February and the beginning of May) and during fall. Fall sampling concerned all the sites for the first years, then was continued only for sites located within the Zone Atelier Brest-Iroise (ZABrI, www.iuem.univ-brest.fr/zabri/fr). In this thesis, only data collected in late winter/early spring are used. This sampling takes place before the spring recruitment period of the majority of benthic species in the region (Dauvin et al. 2007) and corresponds to the period of minimum density and faunal richness (Grall 2002). In addition, this sampling takes place before the onset of the seasonal growth phase of eelgrass, at the period of minimal development of the seagrass bed (Moore and Short 2006). Thus, the acquisition of data at this time allows us to understand the inter-annual variations of the communities without the confounding factors that might be brought by inter-annual variations in the recruitment of species or the seasonal development of the meadow.

Each monitored site includes three fixed sampling points distributed ~ 200 m apart. At each point, three faunal samples are taken using 0.03 m^2 cores in the intertidal and 0.1 m^2 Smith-McIntyre grabs in the subtidal, making a total of 9 faunal samples per site. In seagrass beds, the collection of vagile epifauna is also carried out, yet this thesis only focuses on endofauna samples. Retrieved samples are sieved over a 1 mm mesh and fixed in 4% formalin in the laboratory until sorting, counting and morphological identification of the specimens to the lowest taxonomic levels possible. Additional biological variables on the plant itself are measured for the *Zostera marina* beds. For all four habitats, an additional sample (core or grab accordingly) is taken at each point and used to estimate grain size distribution and organic matter content at the time of the faunal sampling (Figure 11). Details on the acquisition of these variables are given in the appendices of Chapter II. Additionally, proxies for anthropogenic pressures, environmental and biological (life history traits) variables were also acquired *a*

posteriori. The methods for acquiring and processing these data are described in the chapters concerned with their use (i.e., Chapter II and IV).

Since the acquisition and identification of specimens were not all carried out by the same teams (i.e., IUEM for data on sandy beaches, seagrass beds and maerl beds and Roscoff Biological Station for data on subtidal soft sediments), or by the same people over the years of the monitoring program, we proceeded to a taxonomic homogenization. Indeed, differences in taxonomic identification between experts and/or over time can induce an erroneous source of variation in the data. To avoid this, each recorded taxon was scrutinized by experts in benthic taxonomy and their names were checked thanks to the World Register of Marine Species (WoRMS Editorial Board 2021) to ensure a consistent taxonomic resolution. This work was performed on the whole database before conducting analyses.

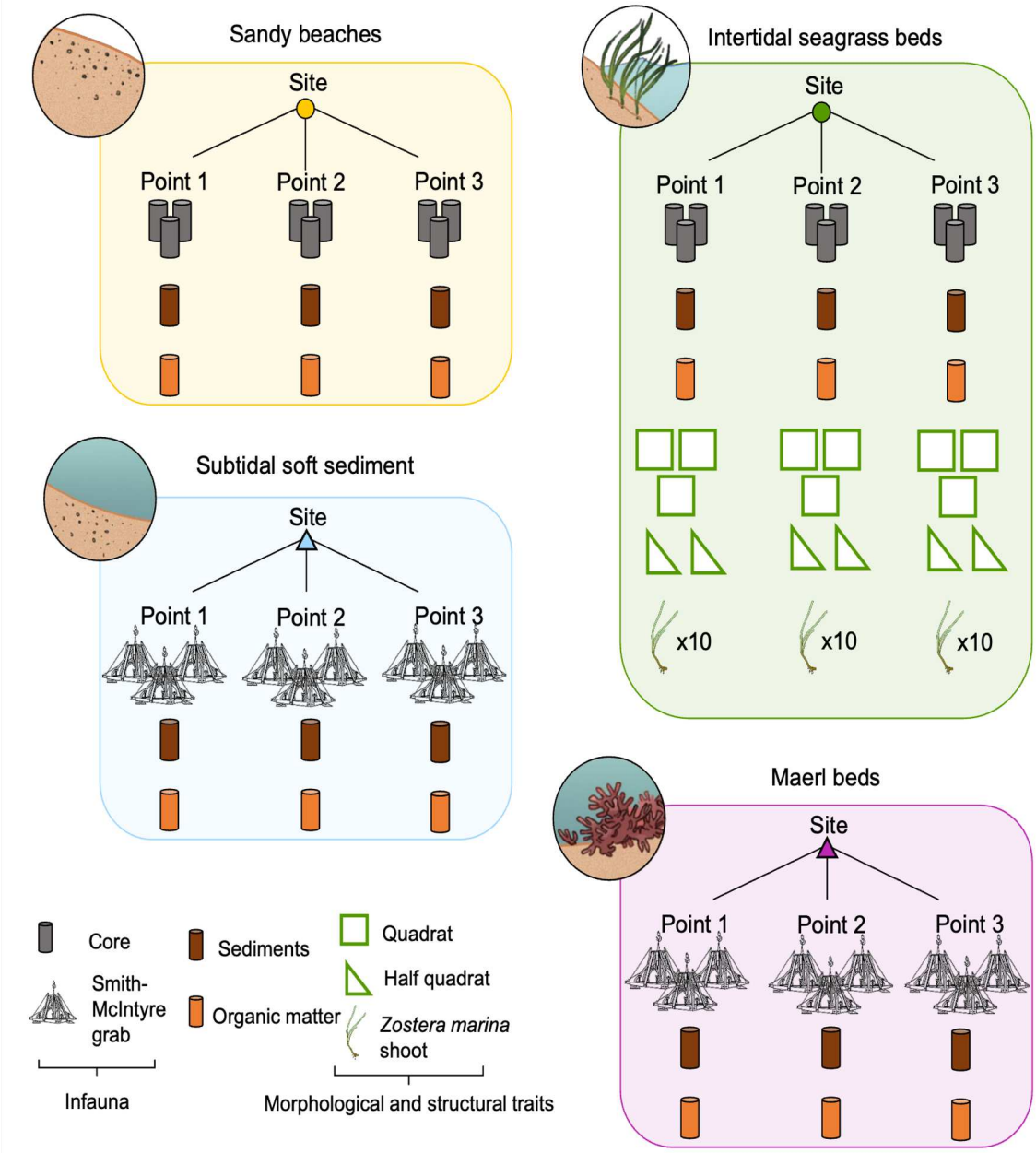


FIGURE 11: Schematic representation of sampling methods in each of the four monitored habitats. In the subtidal habitats, cores for sediment and organic matter analyses are sampled in an additional grab. Quadrat, half quadrat and *Zostera marina* shoots are used to count and measure the plants.

3.2. Aims of the thesis

The main objective of this thesis is to determine the role of the habitats on the spatial and temporal dynamics of the structure and functioning of their benthic macrofauna communities and to identify the main drivers behind such dynamics. It provides knowledge on the ecology of these different habitats and aims at making the link between observations and theoretical ecology. The final objective is to better predict the potential fate of these habitats in the face of forthcoming degradation. In order to meet these objectives, the thesis was divided in four chapters addressing different questions (Figure 12). Moreover, α and β diversity (more precisely spatiotemporal β_{ST} or temporal β_T diversity) of benthic communities taxonomic or functional structures were apprehended over the chapters, either within different sites of a given habitat (β1) or between sites from different habitats in a given tidal level (β2) (see Figures 13, 14, 15, 16).

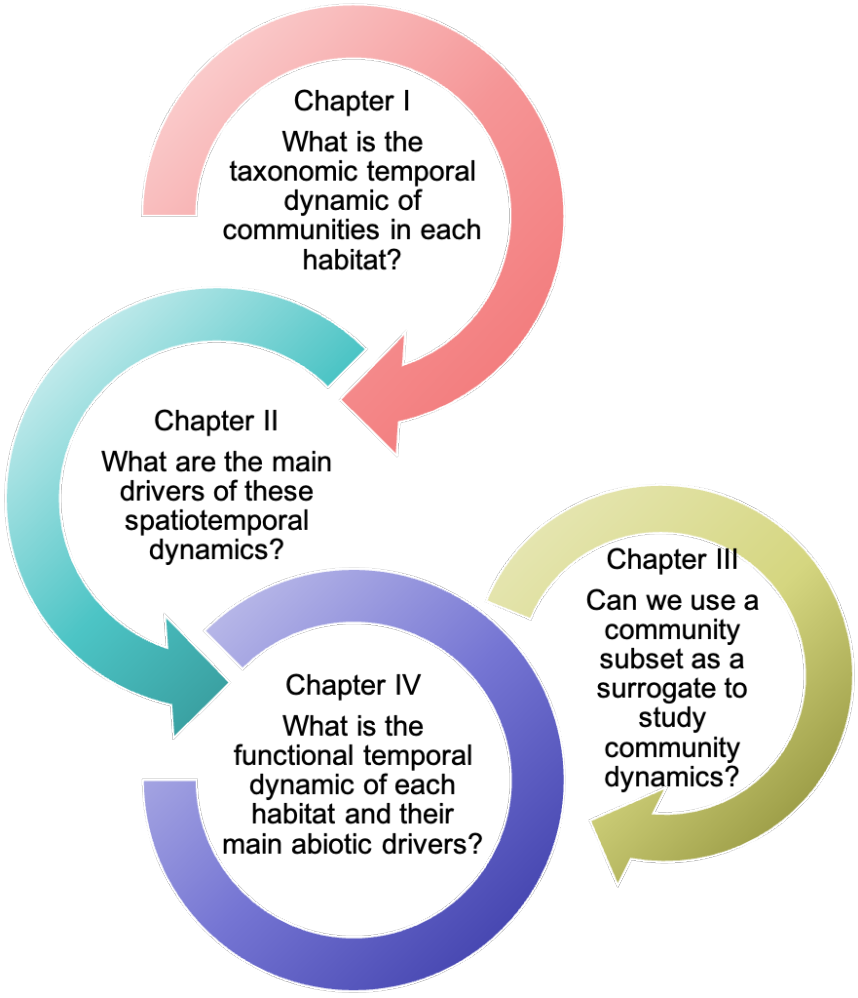


FIGURE 12: Main questions addressed in the four chapters of the thesis and how they interact.

In Chapter I, I mainly focused on the temporal dynamics of the macrofauna community of each habitat and their spatial differences using CTA. I characterized the temporal dynamics of each habitat and sought for similarities or dissimilarities between the temporal patterns of the habitats, especially between biogenic and bare ones in the same tidal level. I also evaluated the potential influence of rare/transient species on the temporal dynamics of the habitats. I finally developed hypotheses linking the ecology of the habitats to the temporal dynamics observed (Figure 13).

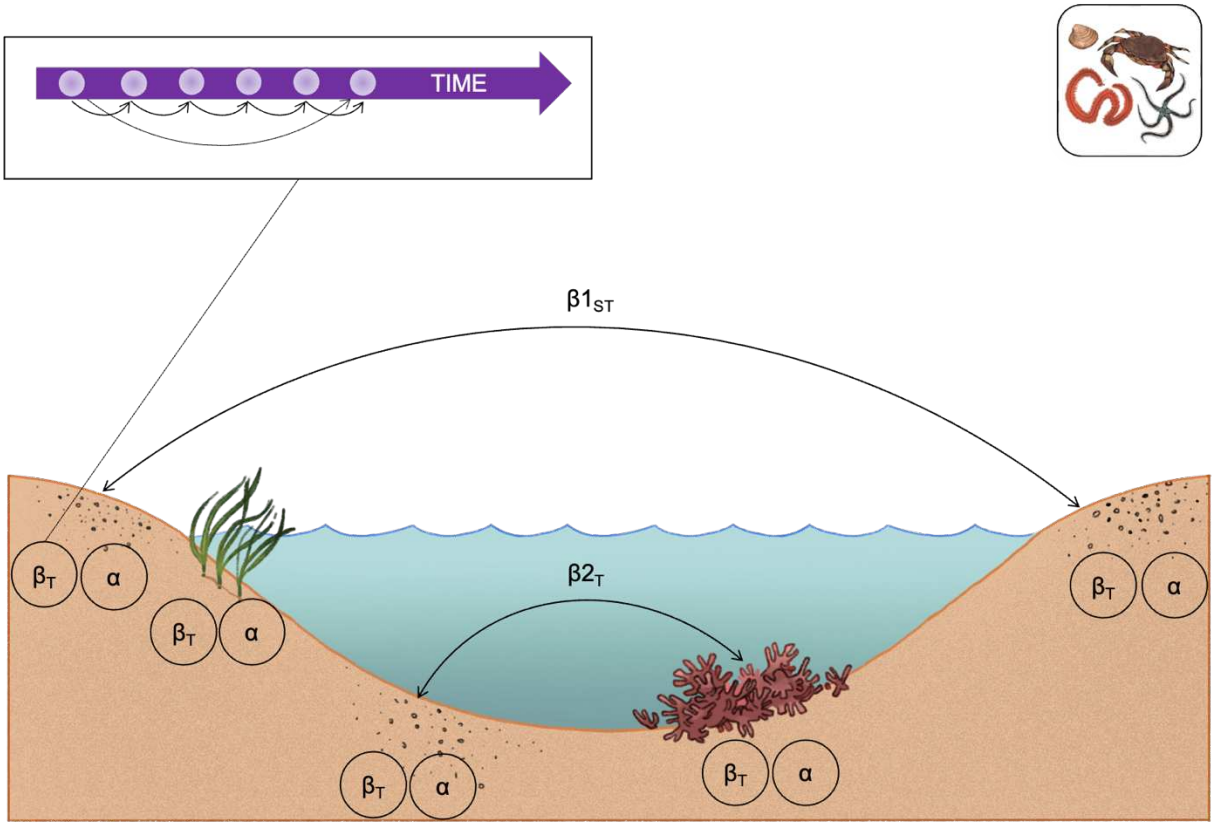


FIGURE 13: Chapter I focuses on the temporal β diversity of the macrofauna community of each site within each habitat (β_T) and between sites of different habitats of a same tidal level ($\beta 2_T$) using CTA. Moreover, CTA allowed to quantify the spatiotemporal β diversity within a same habitat ($\beta 1_{ST}$). α diversity of each habitat was also estimated.

In Chapter II, I evaluated the main drivers of the spatial and temporal dynamics in each habitat and their relative importance in the response of their communities. To do so, I used environmental variables, proxies of anthropogenic pressures and MEMs as spatial and temporal variables. This approach allowed to better understand how the nature of the different habitats and the tidal level influence the response of the macrofauna communities to varying environment which allowed to draw hypotheses on their responses to potential increasing disturbances or stresses (Figure 14).

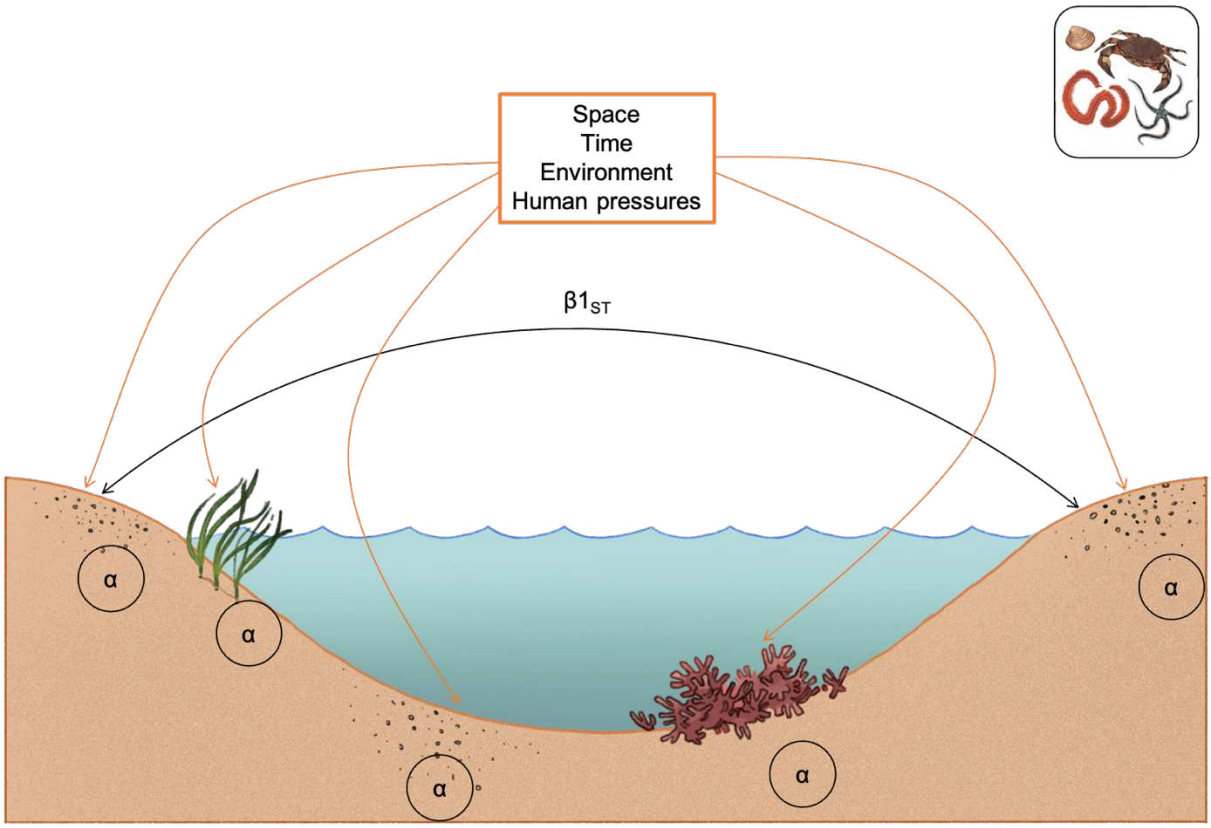


FIGURE 14: Chapter II focuses on spatiotemporal β diversity between sites of a same habitat ($\beta 1_{ST}$) and its underlying drivers. It takes into account all macrofauna community and species richness in each habitat was also estimated.

In Chapter III, I compared the temporal dynamics of 3 subsets of the community (Polychaeta, Crustacea and Mollusca) to the temporal dynamic of the overall community using CTA. It allowed to test whether this method is effective for summarizing long-term overall community dynamics in the four different soft-bottom habitats but also to test if one taxon would better perform as a surrogate for community dynamics. Such approach could serve to restrain the analyses to a single high-level taxon of the community therefore lowering costs, time and efforts needed to maintain monitoring programs over the long term (Figure 15).

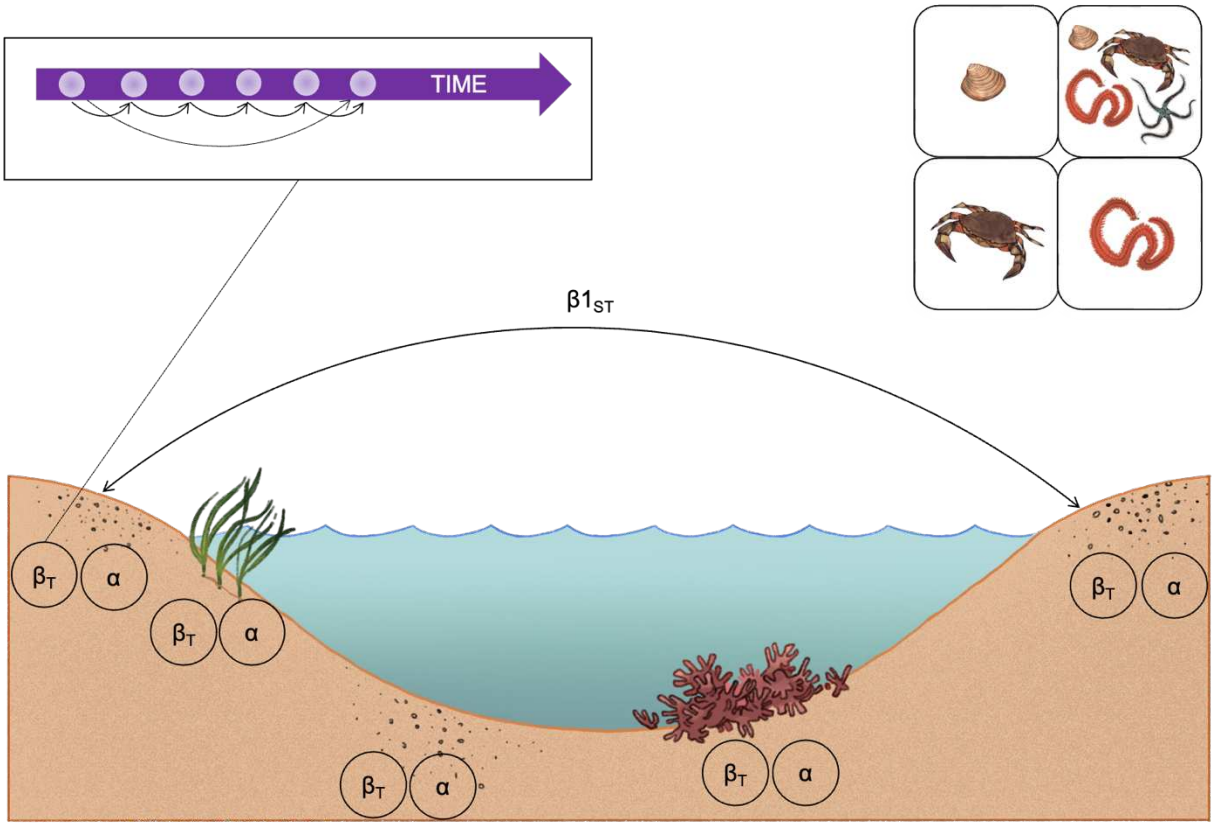


FIGURE 15: Chapter III compares the spatiotemporal β ($\beta 1_{ST}$) and α diversity between the overall macrofauna community and 3 subsets of the community (Polychaeta, Crustacea and Mollusca) using CTA.

In Chapter IV, I described and compared the spatiotemporal patterns and variation in the functional traits' distribution and diversity between the four habitats. It allowed to identify the main drivers of these variations as well as the most structuring traits-environment relationships. This was achieved by focusing on the functional traits of Polychaeta assemblages while I used environmental variables and proxies for anthropogenic pressures as explanatory variables. I mainly focused on variations within a tidal level in order to better understand the role of the habitat type itself (bare or biogenic) in the functioning of the communities. It allowed to reinforce our understanding of the links between the ecological processes and the dynamics and responses of the communities observed in the precedent chapters (Figure 16).

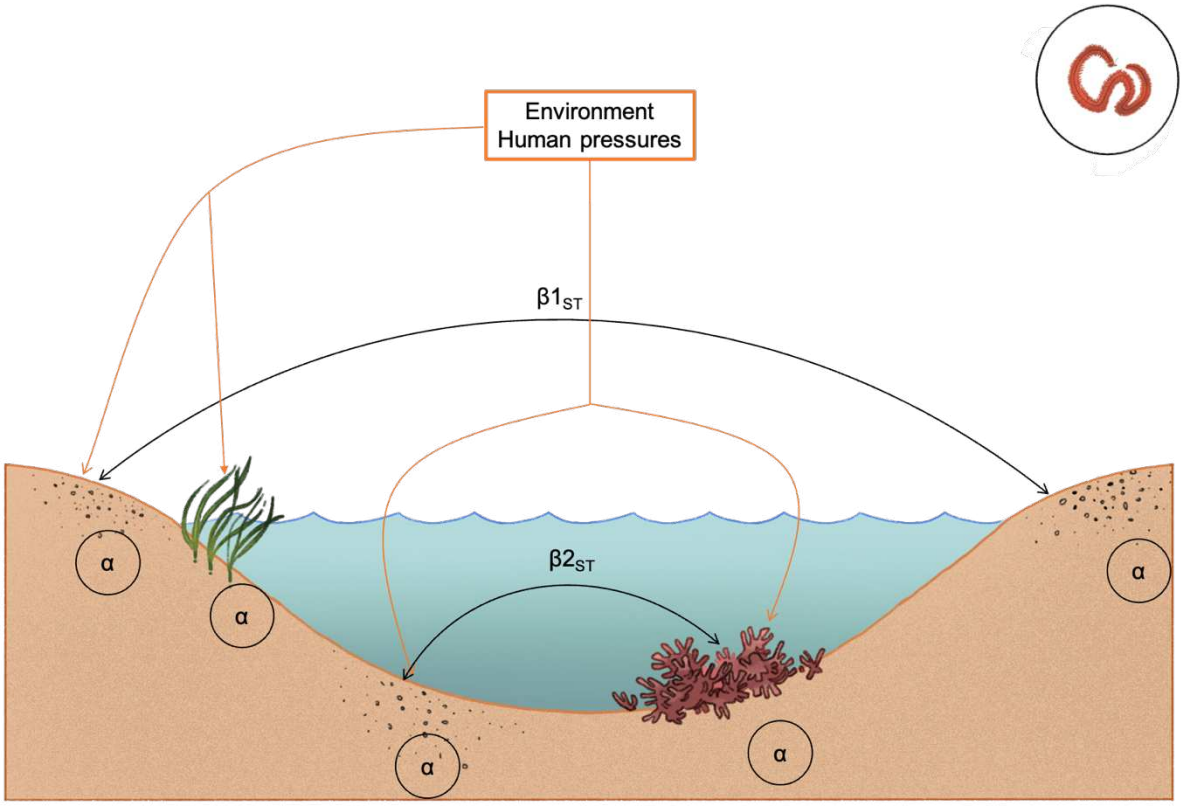


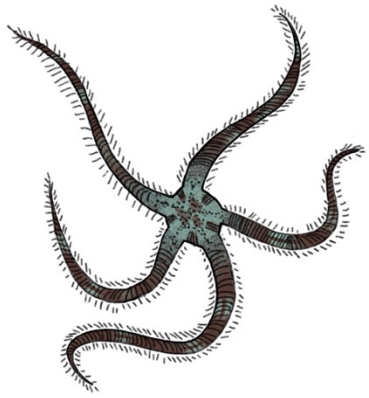
FIGURE 16: Chapter IV focuses on functional α diversity of the different habitats and functional spatiotemporal β diversity within a same habitat ($\beta 1_{ST}$) or between different habitats within a same tidal level ($\beta 2_{ST}$) and its underlying drivers. Only the functional traits of Polychaeta were taken into account.

Throughout the different chapters, sandy beaches, intertidal seagrass beds, subtidal soft sediments and maerl beds were renamed respectively “intertidal bare habitat” (IBAR), “intertidal biogenic habitat” (IBIO), “subtidal bare habitat” (SBAR) and “subtidal biogenic habitat” (SBIO). Moreover, different number of sites and time scale were selected according to the chapters as summarized in Table 1.

TABLE 1: Summary of the biodiversity facet, macrofauna assemblage and temporal and spatial coverage used in each chapter.

	Chapter I	**Chapter II**	**Chapter III**	**Chapter IV**
Biodiversity facet	Taxonomic diversity	Taxonomic diversity	Taxonomic diversity	Functional diversity
Fauna	All community	All community	All community *vs* Polychaeta *vs* Crustacea *vs* Mollusca	Polychaeta
Temporal coverage	14 years (2005-2018)	15 years (2005-2019)	13 years (2007-2019)	15 years (2005-2019)
Spatial coverage	26 sites (5 IBAR, 7 IBIO, 8 SBAR, 6 SBIO)	38 sites (12 IBAR, 8 IBIO, 9 SBAR, 9 SBIO)	32 sites (9 IBAR, 8 IBIO, 8 SBAR, 7 SBIO)	38 sites (12 IBAR, 8 IBIO, 9 SBAR, 9 SBIO)

Chapter I



Résumé en français

Les suivis à long-terme sont des outils essentiels afin de détecter des changements dans les écosystèmes mais également affiner notre compréhension des processus écologiques fondamentaux. Dans le contexte actuel de pressions anthropiques croissantes sur les écosystèmes côtiers, il est essentiel de comprendre la dynamique et la réponse de la biodiversité à ces changements. Dans ce chapitre, qui a fait l'objet d'un article publié dans la revue Ecography, nous avons utilisé des données issues du suivi à long-terme des communautés de macrofaune benthique réalisé à une échelle régionale dans le cadre du REBENT. Les données couvraient un total de 14 années (2005-2018) et 26 sites répartis dans 4 habitats côtiers distincts, pour un total de 979 taxons. Les quatre habitats étudiés sont ceux décrits dans l'Introduction et comprennent donc deux habitats biogéniques situés dans les zones intertidale et subtidale et deux habitats sédimentaires nus associés à ces mêmes zones respectives. À travers la méthode de l'Analyse des Trajectoires des Communautés (CTA en anglais), nous avons quantifié et comparé les dynamiques des communautés. Dans la mesure où ne disposions pas de trajectoires de « référence » auxquelles comparer les trajectoires des communautés observées, nous avons créé un modèle nul de trajectoires non directionnelles. En outre, nous avons comparé les trajectoires des communautés avec et sans les espèces « rares » (présentant à la fois une faible abondance et une faible occurrence sur les 14 années du suivi dans chacun des habitats). Cela a permis de caractériser l'effet de ces espèces sur les trajectoires temporelles des communautés. Malgré des différences marquées en termes de structure et composition des communautés entre les sites et les habitats, les résultats ont révélé que les communautés ont suivi des dynamiques non directionnelles à l'échelle des 14 années de suivi. Cependant, les formes géométriques des trajectoires montraient plus de similitudes entre sites d'un même habitat qu'entre sites d'habitats différents pour un étagement similaire, ce qui suggère un rôle important du type d'habitat considéré sur la dynamique des communautés qu'il abrite. Ainsi, les communautés de macrofaune ont montré une dynamique stable à l'échelle régionale mais avec des patrons dépendant clairement des habitats. Cependant, une variabilité accrue durant les 5 premières années du suivi dans l'habitat intertidal nu apparait tandis que les résultats soulignent l'importance des habitats biogéniques dans le maintien de la stabilité des communautés benthiques dans le temps. Les variations dans l'habitat intertidal nu pourraient être dues à des changements de dominances d'espèces principalement liés à la nature instable des conditions environnementales dans cet habitat. En revanche, l'habitat intertidal biogénique montre une forte stabilité qui pourrait être déterminée par son effet tampon sur les variations environnementales et hypothétiquement les faibles interactions avec des espèces transitoires.

L’habitat subtidal biogénique montre quant à lui une hétérogénéité temporelle supérieure qui pourrait trouver son origine dans sa forte richesse et la proportion élevée d’espèces rares que l’on y trouve (espèces qui pourraient néanmoins participer à la résilience des communautés). Enfin, l’habitat subtidal nu présentait un patron de stabilité intermédiaire entre les deux habitats biogéniques, potentiellement dû à l’effet plus mitigé des variations environnementales dans la zone subtidale.

Long-term coastal macrobenthic Community Trajectory Analysis reveals habitat-dependent stability patterns

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Abstract

Long-term monitoring programs are fundamental to detect changes in ecosystem health and understand ecological processes. In the current context of increasing anthropogenic threats on marine ecosystems, understanding the dynamics and response of communities becomes essential. We used data collected over 14 years in the REBENT benthic coastal invertebrates monitoring program, at a regional scale in the North-East Atlantic, covering a total of 26 sites and 979 taxa. Four distinct habitats were studied: two biogenic habitats associated with foundation species in the intertidal and subtidal zones and two bare sedimentary habitats in the same respective tidal zones. We used Community Trajectory Analysis, a statistical approach that allows for quantitative measures and comparisons of temporal trajectories of ecosystems. We compared observed community trajectories to trajectories simulated under a non-directional null model in order to better understand the dynamics of the communities, their potential drivers, and the role of the studied habitats in these dynamics. Despite strong differences in the community compositions between sites and habitats, the communities followed non-directional dynamics during the 14 years monitored, which suggested stability at the regional scale. However, the shape, size, and direction of the trajectories of benthic communities were more similar within than among habitats, also suggesting the influence of the nature of the habitat on community dynamics. Results showed a higher variability in community composition the first years of the monitoring in the intertidal bare habitat and confirmed the role of biogenic habitats in maintaining temporal stability. They also highlighted the need to apprehend the role of transient and rare species and the scale of observation in temporal β diversity analyses. Finally, our study confirmed the usefulness of Community Trajectory Analysis to link observed trajectory patterns to fundamental ecological processes.

1. Introduction

A key challenge in community ecology is to monitor, detect, quantify and predict temporal changes in biodiversity (Dornelas et al. 2013; Buckley et al. 2021a). Indeed, biodiversity is a key driver of ecosystem functions (Gamfeldt et al. 2015; Duffy et al. 2017) providing essential services to society (Kremen 2005). Moreover, understanding the drivers and consequences of changes in biodiversity is necessary to set up management strategies (Palumbi et al. 2008). Long-term monitoring programs allow for detecting changes in ecosystem health, and understanding fundamental ecological processes, community dynamics and their responses to environmental constraints (Giron-Nava et al. 2017; Kominoski et al. 2018). Species abundances and community composition are examples of Essential Biodiversity Variables that arise from monitoring programs and serve as indicators of ecosystem change (Pereira et al. 2013). Indeed, species richness variations are insufficient to capture changes in biodiversity (Dornelas et al. 2014; Hillebrand et al. 2018; Blowes et al. 2019). Nonetheless, temporal alpha diversity has received more attention than temporal β diversity or the shift in the identity and/or abundance of named taxa in communities over time (Magurran et al. 2019).

The methods applied in temporal community ecology have grown over the past decades, from descriptive (e.g., bar graphs, ordinations) to more computationally complex methods (e.g., Moran Eigenvector Maps, machine learning methods) (Buckley et al. 2021b). Community Trajectory Analysis (CTA) is a multivariate method specifically tailored to study temporal community dynamics (De Cáceres et al. 2019). Starting from a classical ordination, it performs a geometric analysis of temporal trajectories that allows for identifying temporal patterns and variations in community dynamics (De Cáceres et al. 2019; Sturbois et al. 2021c). CTA allows for describing single trajectories by quantifying the changes between consecutive observations, the direction of these changes or the overall dynamics of the community. Additionally, it allows for comparing trajectories and apprehending the spatial variability of community dynamics and their underlying drivers (Legendre and De Cáceres 2013; De Cáceres et al. 2019). This is fundamental as community responses are diverse and not consistent across locations and scales (Hewitt and Thrush 2009; Blowes et al. 2019). Matthews et al. (2013) followed by Lamothe et al. (2019) proposed a theoretical framework linking temporal trajectory patterns and ecological processes. Following Van Meerbeek et al. (2021), a system is considered stable if it retains its reference conditions (state or dynamic) under changing conditions. In CTA, subsequent temporal observations very close to each other would imply stable communities that follow

non-directional and gradual changes. Directional (i.e., trajectory following a particular direction) or saltatory changes (sudden and abrupt change between consecutive observations) would imply succession or regime shifts after a disturbance (Matthews et al. 2013; Lamothe et al. 2019).

In marine ecosystems, macrobenthic species are useful to measure ecosystem changes as they are not very mobile, show various life span and a large range of sensitivity to disturbance (Bessa et al. 2014; Dauvin et al. 2017). Changes in structure and composition of these communities are mostly the result of interactions between drivers acting at different temporal and spatial scales (e.g., Schückel and Kröncke 2013; Kröncke et al. 2019; Thrush et al. 2021a). Interestingly, long-term stability with little changes has been observed in macrobenthic communities (Hinz et al. 2011), even in areas under continuous anthropogenic pressures (Bacouillard et al. 2020). Habitat-dependent factors could also drive heterogenous responses. For example, intertidal communities – subject to repetitive physical stresses – may be more often reset than subtidal ones (Defeo and McLachlan 2005; Gray and Elliott 2009; Quillien et al. 2018; Boyé et al. 2019). Previous research has focused on communities' response after a particular disturbance to study their recovery potential (e.g., Fromentin et al. 1997; Gilkinson et al. 2005). These studies highlighted that the removal of habitat-forming species and ecosystem engineers lowers community resilience (Cimon and Cusson 2018). Indeed, biogenic habitats with high levels of recruitment or connectivity promote resilience (O'Leary et al. 2017). Moreover, they increase community stability through the multiplicity of niches they create, promoting species richness, populations stability and asynchronous fluctuations across species (Lamy et al. 2020), but also through the attenuation of physical disturbances (e.g., thermal buffering) (Jurgens and Gaylord 2018). Other factors might influence the temporal dynamics of the communities. For example, marine ecosystems show more singletons and more transient species than terrestrial ones because of more open and less isolated communities (Raffaelli et al. 2005; Snell Taylor et al. 2018). Low Occurrences and Low Abundances Species (hereafter referred to as LOLAS) are frequent in marine communities, but it is mostly impossible to distinguish *rare* (always present but not always sampled because of sampling effort) from *transient* species (observed occasionally as a result of dispersal from adjacent habitats). LOLAS do not interact with their biotic and abiotic environment as do core species (Snell Taylor et al. 2018). As such, LOLAS may have a real ecological impact on community trajectories or they may simply make the signal noisier and hinder our ability to analyze trajectories.

Temporal trajectories have already been used in studies on changes in macrobenthic communities, but the interpretation of the shapes of the trajectories was mostly subjective. Indeed, the multidimensional space used to display and interpret trajectories has most often been the output from a non-metric multidimensional scaling (nMDS) analysis which is not suited for geometric and quantitative comparisons (e.g., Fromentin et al. 1997; Warwick et al. 2002; Beuchel et al. 2006). Here, we used CTA to study the dynamics of macrobenthic communities in 26 sites monitored for 14 years. Sites were located in biogenic and bare benthic habitats in the intertidal and subtidal zones of the coast of Brittany (France). A null model was used as a reference for non-directional dynamics and analyses were conducted with and without LOLAS to better understand their influence on the dynamics of ecosystems. Given the hypotheses that biogenic habitats enhance stability and resilience of their associated communities and that intertidal and subtidal communities would show different dynamics, we investigated the following questions: 1) How did macrobenthic communities of biogenic and bare habitats in the intertidal and subtidal zones change over 14 years? 2) Were there any similarities in community dynamics of the different habitats at the regional scale? 3) How did removing LOLAS influence the inferred temporal dynamics of the communities? We hypothesized that i) temporal trajectories of communities associated with biogenic habitats would show gradual changes and short trajectories or rapid return towards a stable point after a potential perturbation whereas communities from bare habitats would have more directional dynamics and/or saltatory changes following a potential perturbation, ii) temporal trajectories of communities in subtidal areas would show less variability (e.g., shorter trajectory or segment lengths) compared to the intertidal, iii) temporal trajectories would show similar features (e.g., in the direction of changes) at the regional scale as large-scale environmental changes may outweigh local ones, iv) LOLAS would induce larger stochasticity in trajectories through higher species turnover.

2. Methods

2.1. Study area

At the northwestern tip of France, Brittany is a biogeographic transition zone between the English Channel and the Bay of Biscay. It is a hotspot for macrobenthic fauna richness, characterized by a high diversity of benthic habitats (Gallon et al. 2017). Brittany harbors habitats associated with foundation species, the most common being intertidal seagrass beds (*Zostera marina* and *Zostera noltei*) and subtidal maerl (or rhodolith) beds (principally *Lithothamnion corallioides* and *Phymatolithon calcareum*).

2.2. Sampling

Benthic communities have been monitored yearly since 2003 along the coast of Brittany (France) within the REBENT program (http://www.rebent.org). We focused on four habitats: intertidal seagrass beds (only *Zostera marina* beds are monitored within the REBENT), intertidal sandy beaches, subtidal maerl beds and subtidal soft sediments (respectively referred to as intertidal bare habitat (IBAR), intertidal biogenic habitat (IBIO), subtidal bare habitat (SBAR) and subtidal biogenic habitat (SBIO) from this point forward).

At each site three faunal samples were taken at each of three fixed sampling points distributed 200 m apart (0.03 m^2 cores in the intertidal and 0.1 m^2 Smith-McIntyre grabs in the subtidal; see Boyé et al. 2019), except for Pierre Noire (8) where up to 10 grabs were taken at the sampling site. Sampling was performed between the end of February and the beginning of May, before recruitment of most species occurs in the region (Dauvin et al. 2007; Boyé et al. 2019). In the laboratory, specimens were sorted, counted and identified to the lowest possible taxonomic level (usually species). Since the acquisition and identification of specimens were not carried out by the same people over the years of the monitoring program, we proceeded to a taxonomic homogenization: each recorded taxon was scrutinized by experts in benthic taxonomy and their names were checked thanks to the World Register of Marine Species (WoRMS Editorial Board 2021) to ensure a consistent taxonomic resolution.

In order to minimize the prevalence – and potential effect – of missing data as much as possible, we only selected sites with complete time series and with at least 3 core or grab samples in any particular year. Samples were pooled to estimate abundances at the site level. In the end, this led to a selection of 26 sites monitored from 2005 to 2018 while keeping a spatial resolution covering the coasts of Brittany and encompassing most of the environmental

settings found in this region (Boyé et al. 2017, 2019). Of these 26 sites, 5 were in IBAR, 7 in IBIO, 8 in SBAR and 6 in SBIO (Figure 1). We conducted the analyses at the habitat level or within a same tidal level because it may not be relevant to run analyses including two different tidal levels since sampling gears differ between intertidal and subtidal sites.

Hereafter, the term "site" refers to a given location in a given habitat and the term "observation" refers to a sampling occasion at a given site in a given year (here there were 364 observations in total over the 26 sites and 14 years monitored).

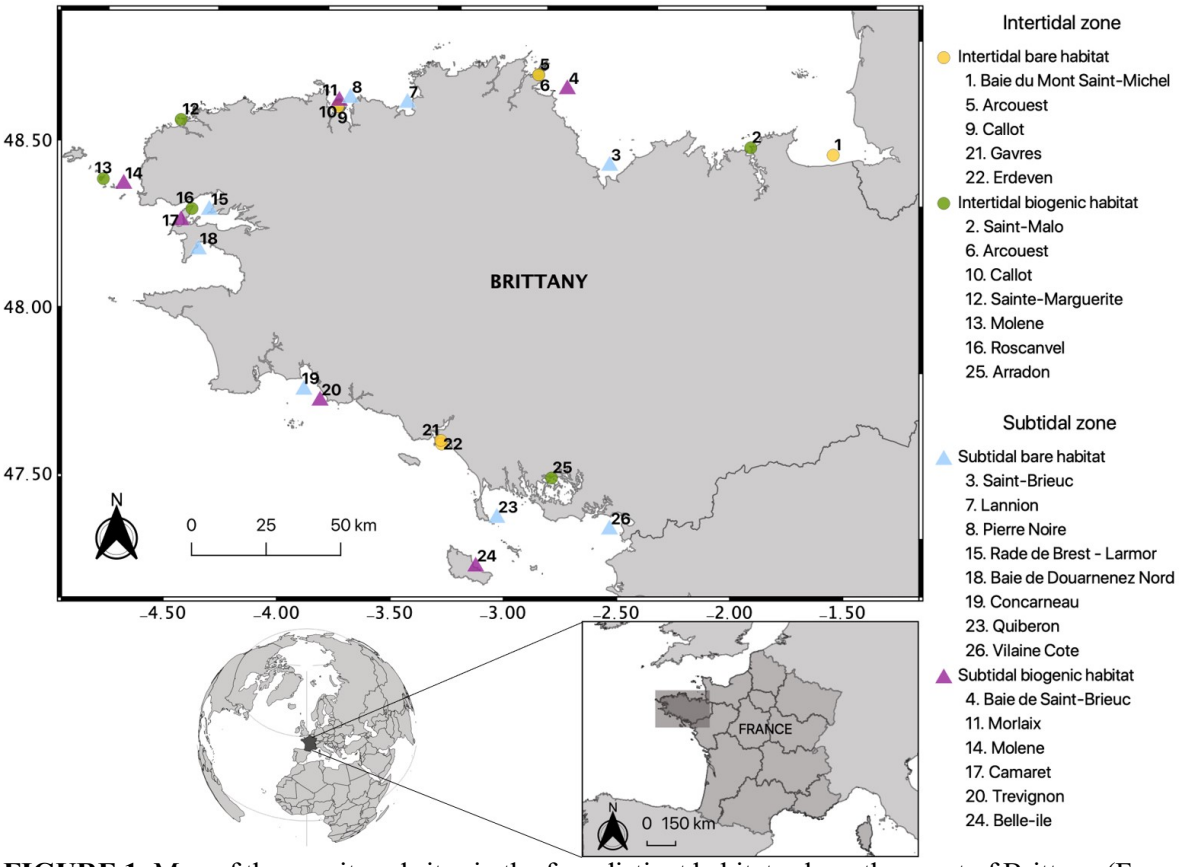


FIGURE 1: Map of the monitored sites in the four distinct habitats along the coast of Brittany (France), (sources: OpenStreetMap, European Environment Agency).

2.3. Numerical analyses

2.3.1. Community Trajectory Analysis (CTA)

CTA is based on the dissimilarity between pairs of community observations in space and time (De Cáceres et al. 2019). We defined the multivariate space of resemblance between community observations using species abundances and the Hellinger distance coefficient, which is equivalent to the Euclidean distance computed on the square root of species relative abundances. It does not give an excessive weight to rare species and has the advantage of

fulfilling the metric and Euclidean properties (Legendre and Gallagher 2001; Legendre and De Cáceres 2013). We used a Principal Coordinates Analysis (PCoA) to display trajectories and compute CTA metrics without any distortions, for each habitat or each tidal zone separately. Each observation is represented in the multivariate space by its coordinates. Two consecutive observations of a same site are linked by a segment, the ensemble of the segments of a site representing its temporal trajectory. Geometrical metrics computed on site trajectories describe their ecological dynamics (see De Cáceres et al. 2019; Sturbois et al. 2021c, for the detailed formulas). Trajectories are usually represented on the first two axes of the ordination, but CTA can compute these metrics using all dimensions. Here we computed the following metrics for the whole multidimensional space:

- *segment length* or the distance between two consecutive observations. With the Hellinger distance, the maximum value between two observations is $\sqrt{2} \approx 1.41$,
- *trajectory length* or the total path length of the trajectory which is the sum of all the segment length of the trajectories. With the Hellinger distance, the maximum value of the trajectory length is $(n-1) \times \sqrt{2}$, where *n* is the number of observations in a site. Here 14 observations give trajectories of 13 segments and a maximum trajectory length of $13 \times \sqrt{2} \approx 18.38$,
- *net change* or the distance between the first and the last observations. Here it is the distance between the observations made in 2005 and 2018 at a given site. With the Hellinger distance, the maximum value remains $\sqrt{2} \approx 1.41$,
- *angle* θ between two consecutive segments takes values from 0° to 180°: 0° indicates three observations completely aligned with no change in direction, whereas 180° indicates two vectors with the same orientation but opposite directions,
- *overall directionality* of the trajectory considers the angles between consecutive segments and their lengths. It reflects the degree to which the community is consistently moving in a particular direction. Directionality takes values between 0 and 1, with 1 representing a trajectory following a completely directional pathway,
- *resemblance* between a pair of trajectories is assessed using the symmetrized directed segment path dissimilarity (D_{SDSP}) (Besse et al. 2016; De Cáceres et al. 2019) which takes into account shape, size, direction and position of the trajectories. Because positions of the trajectories are highly influenced by species compositions at each site, we centered the trajectories prior to the calculation of trajectory distance to focus on compositional dynamics rather than spatial variation of species composition. After

computing D_{SDSP} between all centered trajectories of sites in each habitat, we assessed the overall variation of community dynamics in each habitat using the total dynamic Beta Diversity (dBD_{tot}) (Legendre and De Cáceres 2013; De Cáceres et al. 2019).

Analyses were repeated focusing on the core species of the communities of each of the four habitats by removing the LOLAS. Core species are defined as the most abundant and persistent ones whereas LOLAS occur more infrequently and often have low abundance (Magurran and Henderson 2003). To achieve a compromise between the maximum abundance of each taxon and the number of observations in which they were detected, we set an arbitrary occurrence threshold (corresponding to 1/5 of the maximum occurrence in each habitat) under which species were classified as LOLAS and removed (Appendix 1). This led to the removal of 50 to 75 % of the species of each site in each habitat, as LOLAS were preponderant in the studied communities (Appendices 1 and 2). However, removing LOLAS resulted in datasets containing from 79 % to 96 % of original total abundance.

We also tested the influence of habitat type (i.e., bare *vs*. biogenic) on the dynamics of the communities by performing a PERMANOVA (Anderson 2017) on the symmetric matrix of distances between trajectories (i.e., with D_{SDSP} values computed on centered trajectories of sites). For this, trajectories were first recomputed within tidal levels.

Finally, we were interested in comparing directionality values of sub-trajectories in IBAR especially because we identified two periods of time which seemed to show different dynamics (see Results section). Sub-trajectories were obtained by splitting the trajectories into two or more sub-trajectories to compare time periods within the overall trajectory. The coordinates of the observations in the multidimensional space are the same as for the whole trajectories but the directionality metric is computed on each sub-trajectory independently.

2.3.2. Simulations

We simulated communities under a pure non-directional dynamic to create a null model allowing for comparison with observed CTA metrics. Communities were simulated for each habitat separately while preserving the following habitat-specific properties:

- Species pool composed of all species recorded in the habitat during the 14 years,
- The empirical distribution of species abundances, based on species abundances recorded for each observation in the habitat,
- The empirical distribution of species occurrences, based on the number of observations each species was recorded in the habitat,

- The empirical distribution of total abundances, based on the total abundance recorded for each observation in the habitat,
- A fixed mean extinction rate, i.e., the average proportion of species lost between consecutive years (0.46 for IBAR, 0.41 for IBIO, 0.38 for SBAR, 0.39 for SBIO).

The simulation procedure is detailed in the Appendix 3 and was designed to break the temporal dependency between consecutive observations except for the identity of the species kept. CTA metrics were computed on 100 trajectories of simulated communities in each habitat, with a 14-year dynamic as the observed communities. CTA metrics used to compare simulated and observed community dynamics were the directionality of trajectories, the net change, the total length of trajectories and the length of the consecutive segments. We used two-sided Kolmogorov-Smirnov tests to compare the simulated and observed distributions of the different metrics.

All analysis and simulations were conducted with the R programming language version 4.1.2 (R Core Team 2021) and packages ‘ecotraj’ (De Cáceres et al. 2019; Sturbois et al. 2021c) and ‘adespatial’ (Dray et al. 2021).

3. Results

3.1. Regional scale non-directionality

Community trajectories on the first two axes of the PCoA represented from 35% (SBAR) to 49% (IBAR) of the total variance (Figure 2). Site trajectories occupied clearly different positions, reflecting sites-specific composition and structure within each habitat that were also reflected by high habitat-wise total Beta Diversity which represents the variance of the community matrix and takes a maximum value of 1 (Legendre and De Cáceres 2013): BDtot = 0.70 for IBAR, BDtot = 0.55 for IBIO, BDtot = 0.60 for SBAR and BDtot = 0.59 for SBIO. In addition to their different composition, the four habitats had different species richness: a total of 299 taxa was recorded over the 14 years in IBAR, 493 in IBIO, 527 in SBAR and 665 in SBIO. Overall, directionalities of sites trajectories were very similar even between habitats, and ranged from 0.34 to 0.39. These low values indicated a weak directionality in all monitored sites as did mean angles higher than 90° (Table 1). Trajectories rotated on themselves or oscillated around a point and can therefore be qualified as non-directional.

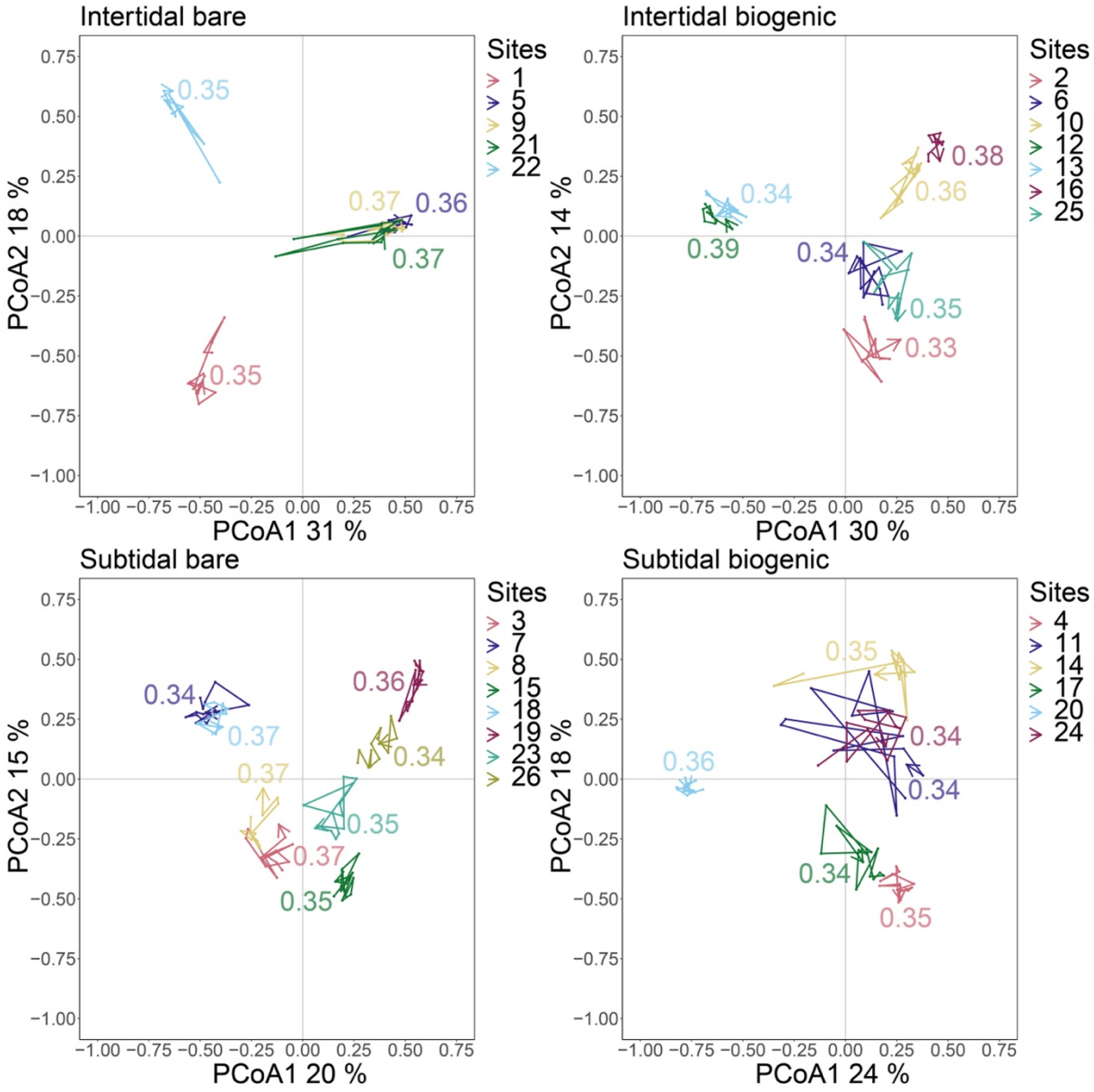


FIGURE 2: Representation of community trajectories (with LOLAS) on the first two PCoA axes with their directionality values associated for each site in the four habitats monitored from 2005 to 2018. One point represents the community state of a site in a given year (one observation). Site specific consecutive community states are linked by a segment and taken together depicts the site trajectory. The arrow represents the final community state of a trajectory (i.e., the community state of a given site in 2018 here).

3.2. Habitat-dependent dynamics

Mean trajectory length in IBIO was somewhat shorter than that of other habitats but all fell within the same range (Table 1). These shorter trajectories mean that community composition in IBIO was more similar and less variable from year to year. IBIO and SBIO had the smallest net changes across the survey period and thus a high similarity between their states in 2005 and 2018. On the contrary, IBAR trajectories exhibited the highest net changes, with high variability in community structure and composition between the first and last survey.

Interestingly, IBAR also possessed the highest dBDtot meaning that there was more variability between the dynamics of IBAR sites compared to the other habitats.

PERMANOVA computed on trajectories dissimilarity (D_{SDSP}) between centered trajectories for the subtidal and the intertidal zones separately showed that 10% of the variance of trajectories shapes can be attributed to habitat type (intertidal: $F = 1.115$, $R^2 = 0.10$, $p = 0.046$; subtidal: $F = 1.228$, $R^2 = 0.093$, $p = 0.001$), lending support to a habitat-dependent influence on the temporal dynamics of communities.

As expected, removing LOLAS and focusing on core species reduced dBDtot, net change and trajectory length (Table 1). However, directionality remained low (Appendix 4) and angles were greater than 90° (Table 1), with sites still tending to return to their previous state. IBAR still presented the highest values of dBDtot, trajectory length and net change while IBIO allowed for similar or higher levels of stability than in the subtidal with or without LOLAS.

TABLE 1: Mean and standard error values of sites' trajectory metrics in the four habitats monitored from 2005 to 2018, considering the community with and without LOLAS. dBDtot = the total dynamic Beta Diversity computed on the dissimilarity D_{SDSP} between centered trajectories, length = the total path length of the trajectory, net change = the distance between the starting point and the final point of the trajectory, angle = the mean angle between two consecutive segments of the trajectory. IBAR = intertidal bare habitat, IBIO = intertidal biogenic habitat, SBAR = subtidal bare habitat, SBIO = subtidal biogenic habitat.

	Global community				Without LOLAS			
Habitat	dBDtot	Mean length±se	Mean angle±se	Mean net±se	dBDtot	Mean length±se	Mean angle±se	Mean net±se
IBAR	0.21	8.61±0.42	114.83±1.90	0.94±0.06	0.18	7.84±0.75	114.16±2.30	0.84±0.07
IBIO	0.15	7.68±0.51	115.88±0.96	0.76±0.03	0.09	5.63±0.5	114.21±1.63	0.58±0.02
SBAR	0.18	8.34±0.41	117.73±1.43	0.82±0.04	0.11	6.72±0.35	117.44±1.92	0.56±0.03
SBIO	0.19	8.31±0.91	117.23±1.35	0.74±0.07	0.10	6.22±0.6	118.30±1.88	0.58±0.07

3.3. Stability despite variability

Distributions of directionality values of the simulated and observed trajectories were not significantly different (Kolmogorov-Smirnov test; $D < 0.37$, $p > 0.05$ in all habitats), with directionality values oscillating around 0.36 in observed and simulated communities: both had a weak directionality (Figure 3). Overall, trajectory lengths, net changes (Figure 3) and segment lengths (Figure 4) of simulated communities were higher, with the exception of net change in IBAR (Figure 3). Simulated distributions of net change and trajectory lengths were more symmetric and less spread out than observed ones (Figure 3). In IBAR, simulated and observed

distributions of CTA metrics had more similar distributions (Kolmogorov-Smirnov test; net change: D = 0.48, $p > 0.05$; trajectory length: D = 0.7, $p < 0.01$) than in the three other habitats (Kolmogorov-Smirnov test; D > 0.87, $p < 0.001$), confirming that IBAR trajectories were the most temporally variable among the studied habitats.

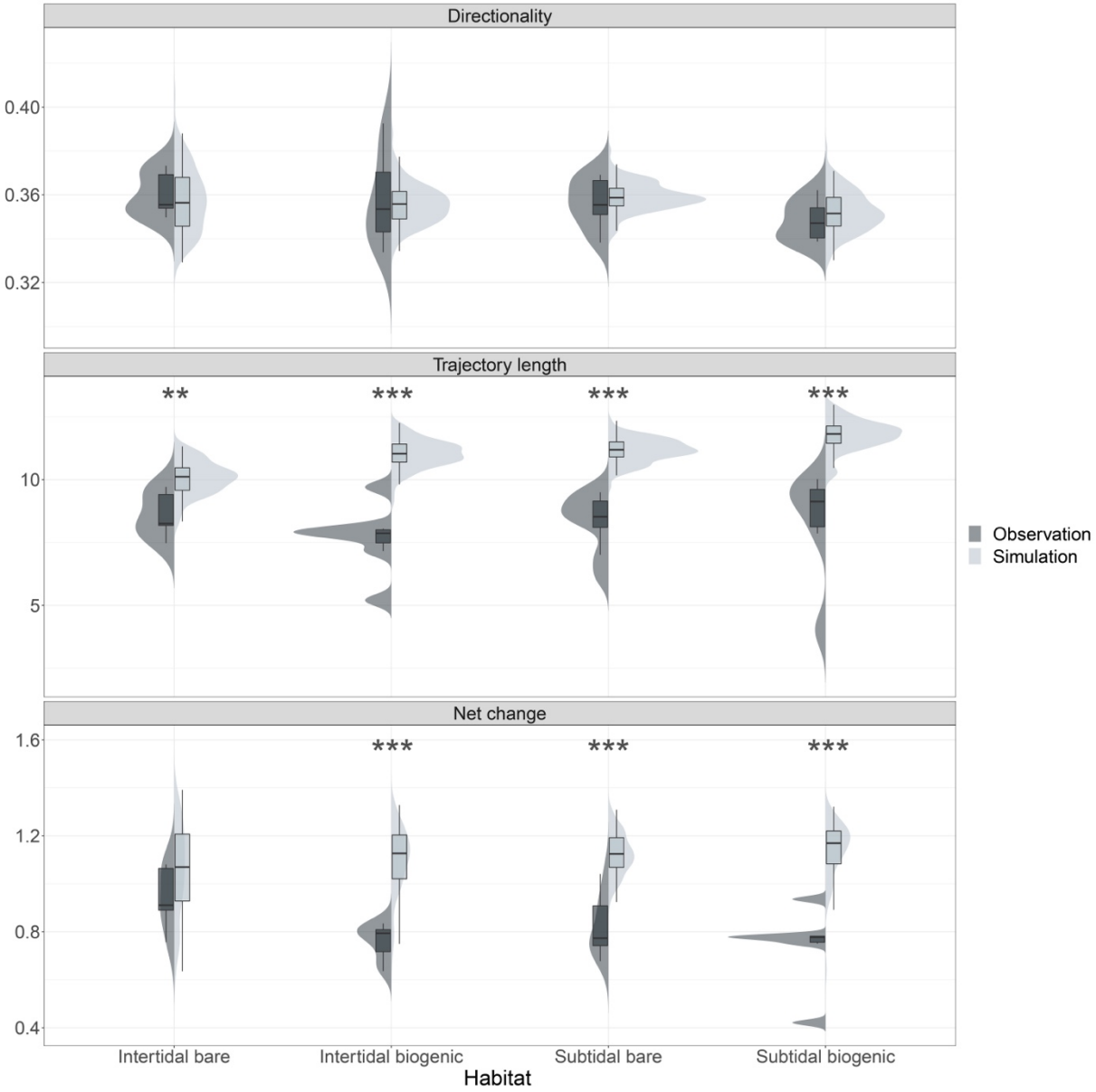


FIGURE 3: Comparison of three CTA metrics (Directionality, Trajectory length and Net change) computed on the observed communities of the four habitats monitored from 2005 to 2018 and the communities simulated under the non-directional null model. Differences between observed and simulated distributions were tested by a two-sided Kolmogorov-Smirnov test (significance code: absence of code = p > 0.05, * = p < 0.05, ** = p < 0.01, *** = p < 0.001).

As expected, simulated segment lengths showed no particular trend and simulated segment length distributions were very similar from year to year regardless of habitat (Figure 4). Simulated trajectories presented longer segments than observations, reflecting higher variability in community compositions between consecutive years. Some differences appeared between habitats in simulations: for example, the simulated segment lengths in IBAR were more variable than in SBAR. As simulations were based on habitat-wise observed distributions, this might reflect the observed heterogeneity of segment lengths in IBAR. The stability in the simulated segment lengths diverged from the observed trajectories, especially for IBAR. Indeed, in IBAR the first four observed segments (2005-2009) were longer than the following 9 (2009-2018), revealing a more stable dynamic of the communities these last nine years (Figure 2, Figure 4). However, we did not find a corresponding change in directionality for these sub-trajectories (2005-2009: 0.35; 2009-2018: 0.34).

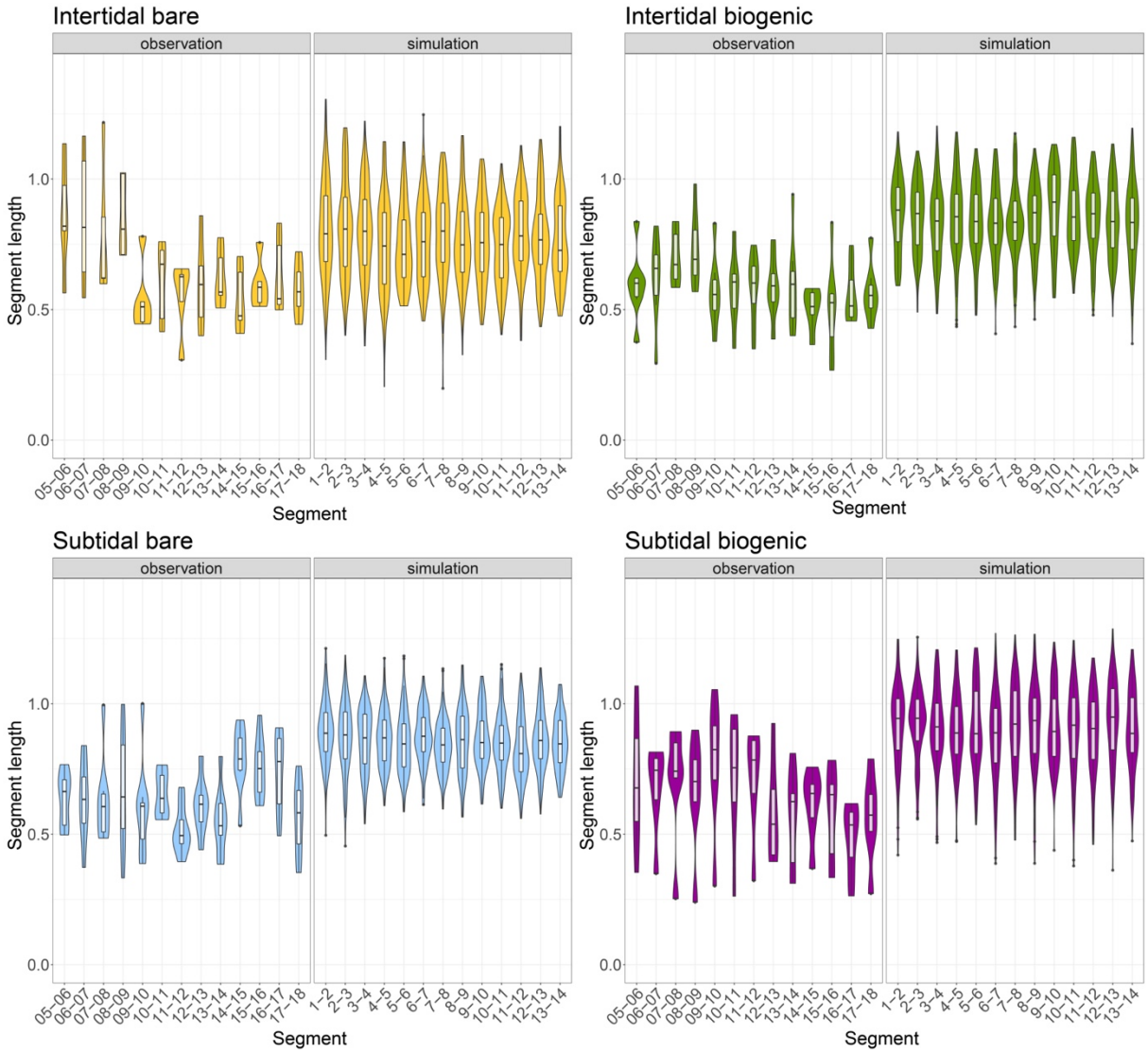


FIGURE 4: Comparison of trajectory segment lengths of the communities observed in the four habitats monitored from 2005 to 2018 and the simulated ones.

4. Discussion

4.1. Non-directional regional dynamic

We used CTA to describe and understand 14 years of ecological dynamics of macrobenthic communities located in four distinct coastal habitats. Results suggested a global stability of the system at the regional scale with non-directional temporal trajectories. The low directionality observed is perhaps due to the nature of the considered systems. CTA was firstly applied on plant communities (De Cáceres et al. 2019), with more persistent and fewer species than expected in marine systems that have higher diversity and higher temporal turnover, and present less ordered ecological succession (Raffaelli et al. 2005; Henderson and Magurran 2014). The low directionality could also be due to the frequency of sampling in our study. It is likely that some ecological processes in the benthic macrofauna communities monitored are faster than our sampling frequency (i.e., seasonal variations). Furthermore, macrobenthic communities can exhibit different multi-year cycles (e.g., 3-9 years, 5-7 years, 10-12 years; Thrush et al. 2021a) that could not be detected within a 14-year time series.

Long-term stability of macrobenthic communities has already been demonstrated in the English Channel (e.g., Fromentin et al. 1997; Bacouillard et al. 2020). Recently, CTA was used on intertidal communities monitored in a single bay, and results also demonstrated stability at the scale of the study area with changes mainly reflected by random population dynamics of structuring prevalent species under strong natural pressures (Sturbois et al. 2021b). CTA conducted on phytoplanktonic communities of the Eastern English Channel also demonstrated an overall stability in community composition (Lefran et al. 2021). Brittany is a biogeographic transition zone with a high diversity of benthic habitats (Gallon et al. 2017) and its geographical location makes it a very open system. This might enable large-scale transport of propagules from outside source patches (Ayata et al. 2010) and multiple sources of colonists thanks to the multiplicity of habitats. These factors could enhance recovery or persistence of communities in the region (Ellis et al. 2000). Moreover, Brittany is a hotspot of biodiversity (Gallon et al. 2017) and this could also have a stabilizing effect on communities (Downing et al. 2014; Craven et al. 2018), especially if species show asynchronous responses to environmental fluctuations and differences in the speed at which they respond to perturbations (Loreau and de Mazancourt 2013). However, the diversity-stability debate is still ongoing in ecology (Ives and Carpenter 2007; Kéfi et al. 2019).

Trajectory length and net change mostly had higher values in simulated communities compared to observed ones. Simulations smoothed out site-specific effects on trajectories: for instance, in observed communities, Trévignon (20) in SBIO expressed the lowest net change and trajectory length (Appendix 5), since this site was largely dominated by a single and temporally persistent taxon (*Porcellanidae spp*.) (Appendix 6). Moreover, temporal autocorrelation may be lower in simulated compared to observed communities: temporal turnover should be higher in simulated communities given the simulation procedure with abundances resampled at each step. Indeed, the within-site year-to-year BDtot was higher in simulated communities. However, the proportion of Replacement and Difference of Richness (see Legendre and De Cáceres 2013; Legendre 2014) were fairly homogeneous between simulated and observed communities in IBIO and SBAR but not in IBAR and SBIO (Appendix 7). With habitat-scale constraints, the simulation did not only remove autocorrelation, but also broke co-occurrence patterns and site-specific constraints, making it a regional-scale neutral model. This also suggests that biotic or abiotic factors (which were not considered in the simulations), such as characteristics of the habitat itself, could act as filters preventing observed communities from adopting the dynamic produced in the simulation (especially the higher temporal turnover), and thus enhance stability at the regional scale.

4.2. Habitat-dependent dynamics

4.2.1. Biogenic *vs* Bare

Despite non-directional regional scale dynamics, results revealed habitat-dependent community dynamics. First, within tidal zone differences exist between biogenic and bare habitats. In the intertidal, all CTA metrics were lower in IBIO compared to IBAR, translating a higher temporal stability in this former habitat. Hily and Bouteille (1999) demonstrated that the development of eelgrass meadows enhances abundances and biomasses and increases specific and functional diversity compared to IBAR. Indeed, the shelter created by seagrass patches can improve the recruitment, survival and diversity of species (Boström and Bonsdorff 2000). Moreover, their physical structures enhance habitat heterogeneity and complexity, increasing shelters and food resources availability and promoting biodiversity (Thomaz and Cunha 2010), hence stability given the mechanisms suggested by Loreau and de Mazancourt (2013). Biogenic habitats can also act as environmental buffers: in an environment facing harsh conditions, such as the intertidal zone, habitat-forming species can sustain biodiversity and ecosystem functioning through the reduction of physical stress (Bulleri et al. 2018), for example

by altering local hydrodynamic conditions and sediment dynamics or reducing thermal stresses for inhabitant taxa thanks to their physical structures (Peterson et al. 2004; Bouma et al. 2009a; Jurgens and Gaylord 2018).

In the subtidal zone, we expected more stable trajectory patterns in SBIO than SBAR. Indeed, the high architectural complexity of maerl beds may reduce predation stress in communities (Bouma et al. 2009a), increase specific (Grall and Glémarec 1997; Grall and Hall-Spencer 2003) and functional diversity and redundancy (Boyé et al. 2019) which allow ecosystems to resist disturbances because multiple species could take on critical roles (Palumbi et al. 2008). SBIO communities had non-directional dynamics and the lowest average net change but not the lowest average trajectory length. Long trajectories returning toward their initial ecological state could make us lean toward a resilience hypothesis. However, here the low net change was strongly affected by an atypical site: Trévignon (20), the single site with the lowest net change and segment lengths, which presented a nearly persistent community (Gray and Elliott 2009; Thrush et al. 2021a) (Appendix 6). Contrary to our expectations, removing this site from the analyses resulted in increased average net change and mean trajectory length in SBIO, the latter becoming the highest of all habitats (Appendix 5). However, this did not radically change the observed patterns of segment lengths in SBIO (Appendix 8). We hypothesized that the higher species richness, and hence the higher number of LOLAS, increased temporal turnover in SBIO because each LOLAS was only present over a small fraction of the time series (Magurran and Henderson 2010; Snell Taylor et al. 2018). Removing LOLAS decreased net change and trajectory length in all habitats. However, a high species diversity with numerous LOLAS could support the insurance hypothesis, where LOLAS can be more resistant or well suited to environmental change (Hewitt et al. 2016b; Thrush et al. 2021a) with asynchronous responses of species to fluctuations (Yachi and Loreau 1999). Core species could maintain local stability because they are suited to existing environmental conditions whereas LOLAS could maintain regional and long-term stability by replacing core species following an environmental change (Coyle et al. 2013; Henderson and Magurran 2014; Vermeij and Grosberg 2018).

4.2.2. Intertidal *vs* Subtidal

Biogenic habitats did not have a consistent effect on community dynamics in the two tidal zones, supporting the existence of different underlying mechanisms:

- Foundation species and stress levels: the positive effect of foundation species on biodiversity can be emphasized in stressful environments (e.g., intertidal zone) and can be dampened in mild environments (e.g., subtidal zone) (Watt and Scrosati 2013).
- Different foundation species: the high diversity of seagrass beds seem to be more dependent on transient species (Boyé et al. 2017) while we posit that it stems more from rare ones in maerl beds. Transient species can have a strong effect on the long-term return of communities through the insurance hypothesis (Arnoldi et al. 2018). However, transients rarely interact with other members of the community (Snell Taylor et al. 2018), thus weaker species interactions are expected in seagrass beds communities. Community composition might be temporally less variable with community dynamics governed by weak interactions (van Nes and Scheffer 2005; Magurran and Henderson 2010; Thrush et al. 2021a) as illustrated in IBIO.
- Richness artifact: shorter trajectories in IBIO compared to SBIO might be an artifact of their large difference in species richness (493 in IBIO *versus* 665 in SBIO). Higher species richness with a higher proportion of LOLAS in SBIO might induce a higher variability in community composition between years.

The two bare habitats also had distinct dynamics with SBAR being less variable in structure and composition of communities than IBAR (Appendix 6). Subtidal macrobenthic communities have previously been shown to have heterogeneous dynamics. Some studies reported changes and shifts in community composition mostly linked to environmental changes (Warwick et al. 2002; Frid 2011; Ghodrati Shojaei et al. 2016; Bonifácio et al. 2019), but results are inconsistent across spatial and temporal scales. Indeed, other studies demonstrated temporal stability of subtidal communities even under environmental or anthropogenic pressures (e.g., Hinz et al. 2011; Quillien et al. 2018; Bacouillard et al. 2020). In contrast to SBAR, sandy beaches (IBAR) are physically dynamic environment: instability is characteristic of this habitat where temporal environmental variability is a key driver compared to biotic interactions that are considered less important (Defeo and McLachlan 2005; Schlacher et al. 2008; Schlacher and Thompson 2013). Even if competition and predation in beach ecosystems are limited compared to all other littoral ones (Schlacher and Thompson 2013) which could have induced a higher stability (Loreau and de Mazancourt 2013), in this habitat the physical environment and habitat conditions are the main controlling factors (Defeo and McLachlan 2005; McLachlan and Dorvlo 2005). Our results showed that compositional dynamics of IBAR can be described as non-directional with saltatory changes in the first five years of the monitoring program. Directional saltatory changes usually translate into a shift of the community from one stable

state to a different one (Scheffer and Carpenter 2003; deYoung et al. 2008; Lamothe et al. 2019). However, directionality of the first four segments was indistinguishable from that of the last nine segments, suggesting that the system did not shift from one regime to another. Non-directional saltatory changes could occur when systems are facing multiple short term and delineated disturbances (Lamothe et al. 2019). Gray (1977) suggested that soft-bottom systems have multiple stable-states and tend to return to an equilibrium point after any perturbation of limited extent. Gray and Elliott (2009) also argued that marine benthic communities can exhibit poly-climax and neighborhood stability with several alternate dominant species. Interestingly, communities in IBAR presented greater changes in dominant taxa during the monitored period than any other habitats (Appendix 6). This could be an artifact of the low number of IBAR sites. Indeed, global stability is mostly observed when measures are conducted over large spatial scales while neighborhood stability is a more appropriate model over relatively small spatial scales (Gray and Elliott 2009). Notwithstanding, other habitats had similar number of sites (only one more for SBIO compared to IBAR) and we observed more of a global stability pattern, hence we assume the neighborhood pattern observed is not an artifact of the number of sites.

Because in IBAR an ecological change is mainly the result of an environmental change (Schoeman et al. 2014), we hypothesized that, along the first five years of the survey, communities had to face multiple pulse disturbances that led to changes in taxa dominance reflected in the observed trajectory patterns (saltatory changes between consecutive years). Moreover, CTA metrics from observed and simulated communities were the most similar in IBAR. The effect of pulse perturbations could break temporal autocorrelation in the observed communities as in the null model, because communities with low species richness can often be reset when facing harsh environmental conditions (Boyé et al. 2019). dBD_{tot} was the highest in IBAR suggesting that temporal dynamics differed more between sites: either the same type and frequency of disturbance on different sites produced different responses at the community level (because of the different species composition or history between sites) or the sources and timing of disturbances may be different (which is often the case in intertidal habitats where natural and anthropogenic disturbances are confounded) (Whomersley et al. 2010). Indeed, there seemed to be site-specific effects on community dynamics in each habitat and maybe even more in IBAR: distributions of CTA metrics were always more heterogenous compared to simulations where the sites characteristics and differences are not taken into account. To verify whether the observed variability could be linked to greater environmental variability during the beginning of the monitoring (e.g., alternating colder winters and warmer summers; Beukema and Dekker 2020) we looked at temperature, wind speed and precipitation anomalies (Appendix 9) for each

year of the time series and every site in IBAR. We could not detect any trend changes between 2005-2009 and 2009-2018, nor any pulse perturbations that could explain the observed trajectories. However, partitioning the components of β diversity (Legendre and De Cáceres 2013; Legendre 2014) revealed a higher proportion of species replacement between 2006 and 2007 than ever observed over the whole time series (Appendix 9). This peak in replacement is followed by consecutive years of higher richness differences from 2007 to 2009, and a lower mean species richness after 2009. Interestingly, temperature and wind speed anomalies started to oscillate between positive and negative values from 2006. One hypothesis could be that the system changed from a system with relatively stable environmental conditions to a system with a varying environment. This might have led to a loss of intolerant species and colonization of species benefiting the empty space (high replacement), followed by a stabilization phase with competitive exclusion and disappearance of opportunistic species (high richness differences), leading to a new non-directional stable state constituted of species more tolerant to a varying environment. This hypothesis is coherent with the neighborhood stability hypothesis with alternate dominant species. However, we would have expected the succession of replacement and richness differences would lead to a higher directionality of the trajectory for the first four segments which was not the case. It raises the perspective to look at the different β diversity components to better apprehend the changes in trajectory metrics in further work, and also to look at community changes preceding the observed trajectory changes because of a potential lag in species response and dynamics.

4.3. Linking trajectory shapes to ecological dynamics

To summarize, community state can be represented as the position of a ball in a cup-shaped landscape (Lamothe et al. 2019; Dakos and Kéfi 2022). In such a landscape, the ball represents the current state of the system, the cup represents its current domain of attraction. Communities showing high stability are portrayed as balls within deep cups with steep walls. In this case, important perturbations are needed to change the community state, and the community will quickly revert to its previous state. In our study:

- Observed variations in IBAR could correspond to a neighborhood stability (Gray and Elliott 2009): within a wide cup, community state alternates between shallow neighboring cups – each corresponding to a different dominant taxon – during the first five years of the survey and stays in another cup for the remaining 9 years (Figure 5). Such a landscape can be pictured by multiple narrow and shallow attraction basins in the ball-and-cup analogy (Figure 5a).

- SBAR showed more of a general stability pattern with moderate variability between consecutive years compared to SBIO or IBIO. Such a moderate variability stability landscape can be pictured by a deep attraction basin in the ball-and-cup analogy (Figure 5b).

- IBIO showed a general stability pattern with the lowest variability of communities between consecutive years among all the studied habitats. This may be due to the influence of transient species, which weaken the role of species interactions in community dynamics, thus narrowing the attraction basin. Such a low variability stability landscape can be pictured by a narrow and deep attraction basin in the ball-and-cup analogy (Figure 5c).

- SBIO showed a general stability pattern with a high variability between consecutive years compared to SBAR and IBIO. We hypothesize that the high diversity and number of rare species promote long term stability in this habitat but that they are also factors that can induce a higher temporal turnover, thus a wider attraction basin. Such a high variability stability landscape can be pictured by a wide and deep attraction basin in the ball-and-cup analogy (Figure 5d).

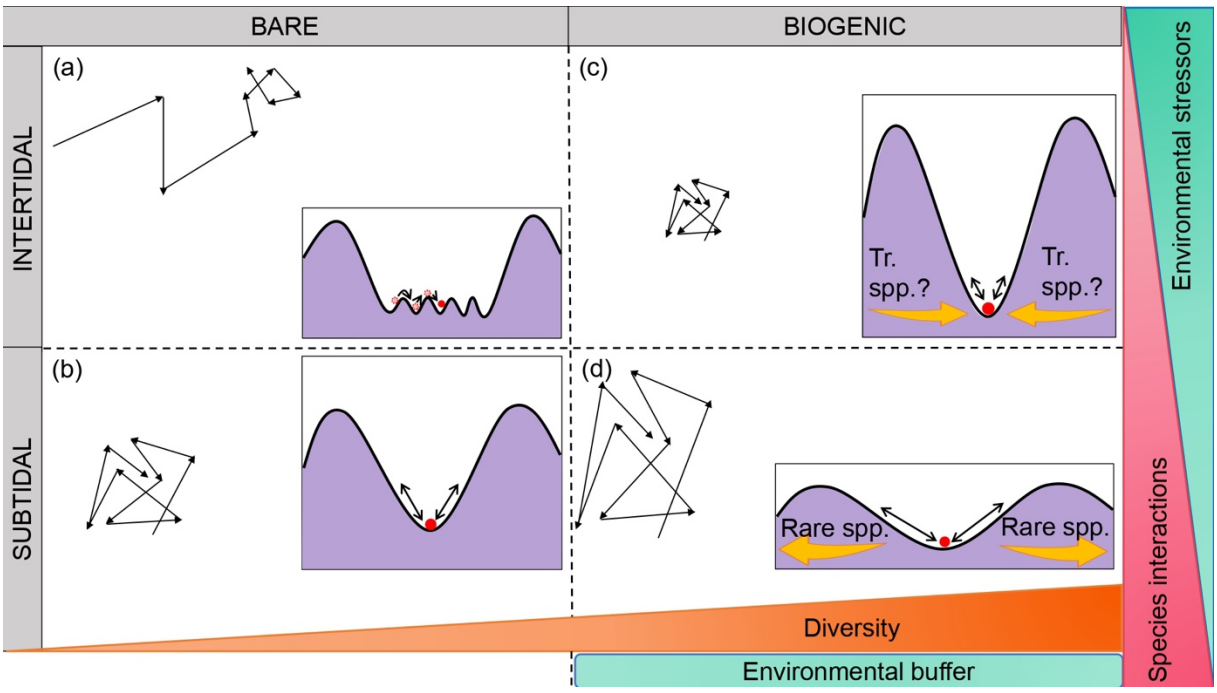
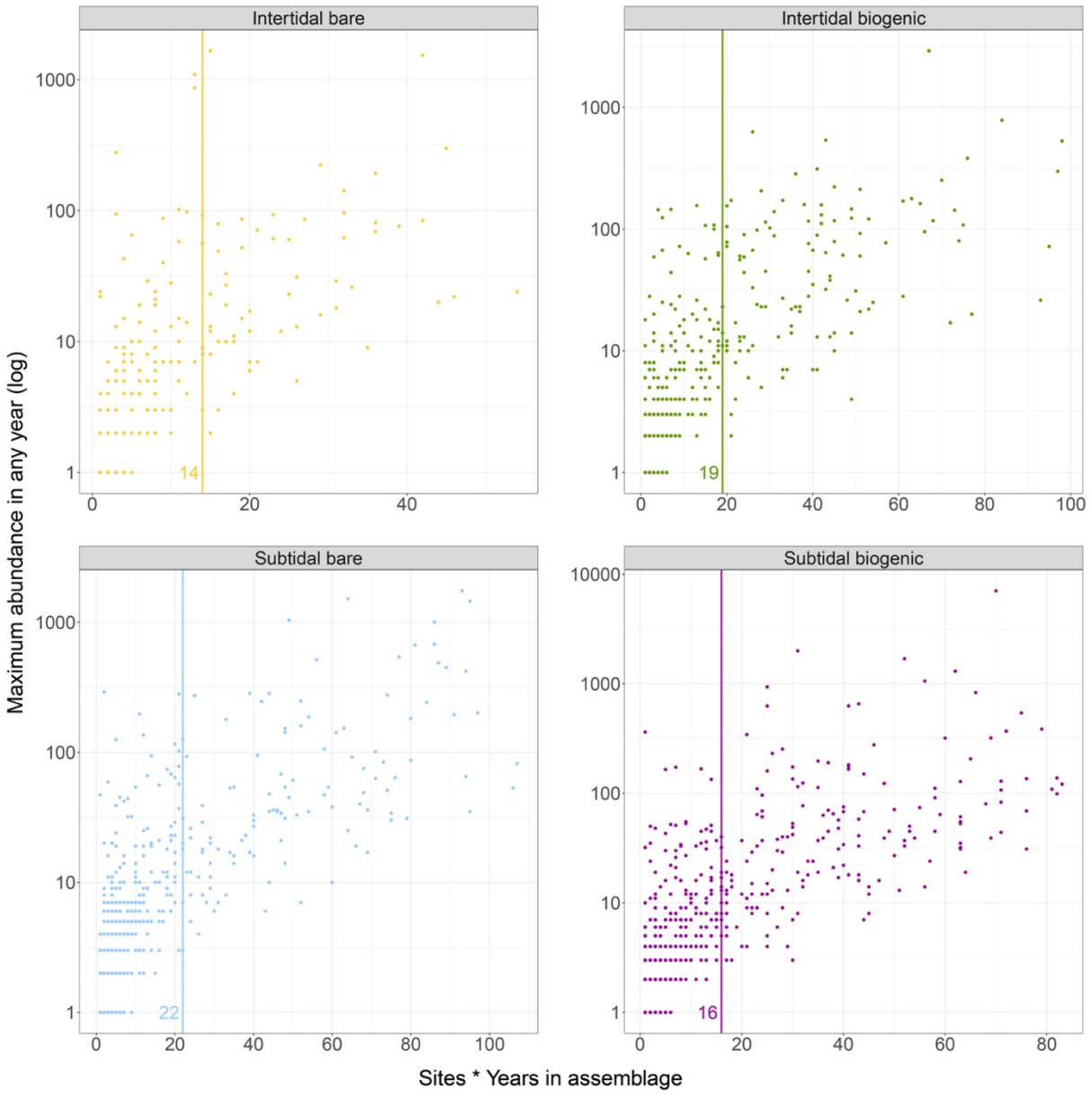


FIGURE 5: Synthetic figure of the global pattern of temporal trajectories (on the left in each box) translated into a ball and cup representation (on the right in each box) and the hypothetic drivers of the patterns observed for each of the four habitats monitored. The red ball represents the community state of a given observation and the arrows indicate the directionality of movement across the cup-shaped landscape (i.e., all possible states the community could take in this landscape). Tr. spp. stands for Transient species and Rare spp. for Rare species.

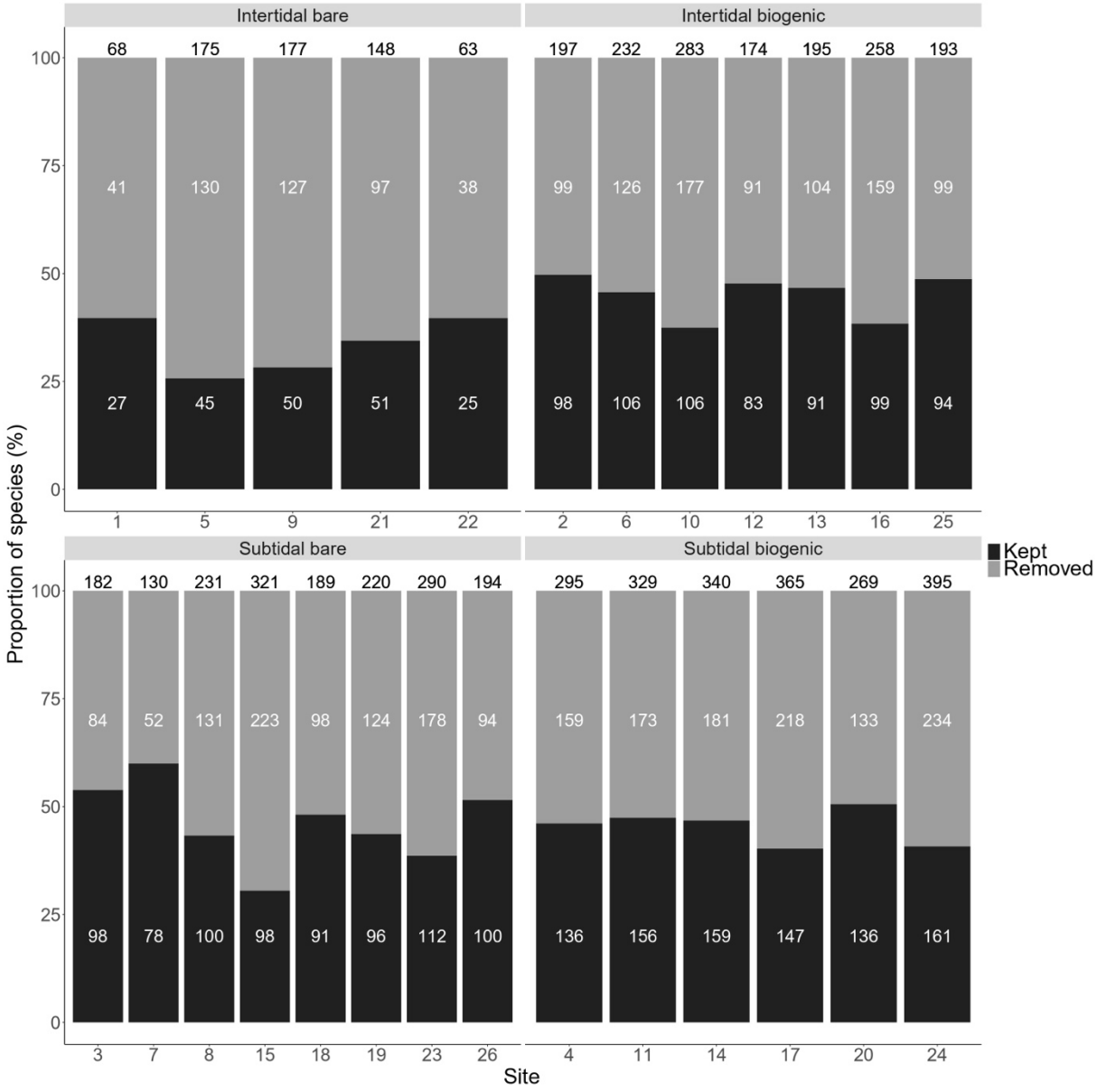
4.4. Conclusions

Our study demonstrated that habitat-dependent dynamics exist despite a general stability of macrobenthic communities at the regional scale. Indeed, the four monitored habitats could be matched to four different patterns of stability and we hypothesize (1) that these are driven by different mechanisms, related to biotic and abiotic factors involved such as habitat characteristics and (2) that the presence of numerous LOLAS can maintain the long-term stability of the systems even if it increases the temporal turnover of communities compared to the dynamics of core species only. Our study corroborates that community dynamics are not consistent across habitats and scales, which could have important consequences in the context of global change. Thus, it highlights the importance of taking the scale of observation into account in temporal studies because an observed local heterogeneity can be part of a system that is fairly homogeneous (Gray and Elliott 2009). It would be interesting in future works to investigate the threshold of variability in communities beyond which change would be of concern and fall outside the basin of attraction. Finally, our study confirmed the usefulness of CTA, coupled to null models, in order to describe, understand and draw hypotheses or conclusions on ecological dynamics of long-term monitored macrobenthic communities. Still, further work needs to be done in order to better understand and discriminate the biotic and abiotic drivers of the different temporal dynamics observed as well as the dynamic of communities when looking at other dimensions of diversity (e.g., functional or phylogenetic diversities) which are fundamental to better assess temporal β diversity in ecological communities (Magurran et al. 2019).

Appendices



Appendix 1: Representation of the maximum abundance of each taxon recorded during the monitoring program according to their persistence during the monitoring program (the number of sites and years, i.e, the number of observations, they are detected) in each habitat. The vertical line represents the threshold under which species were considered as LOLAS and upper which the species were considered as core species.



Appendix 2: Proportion of species kept (core species) and removed (LOLAS) in each site of each habitat. Numbers in white give the total number of species kept or removed in each site over the 14 years. Numbers in black at the top of each bar give the total species richness in each site over the 14 years.

Appendix 3: Simulation procedure of the non-directional null model.

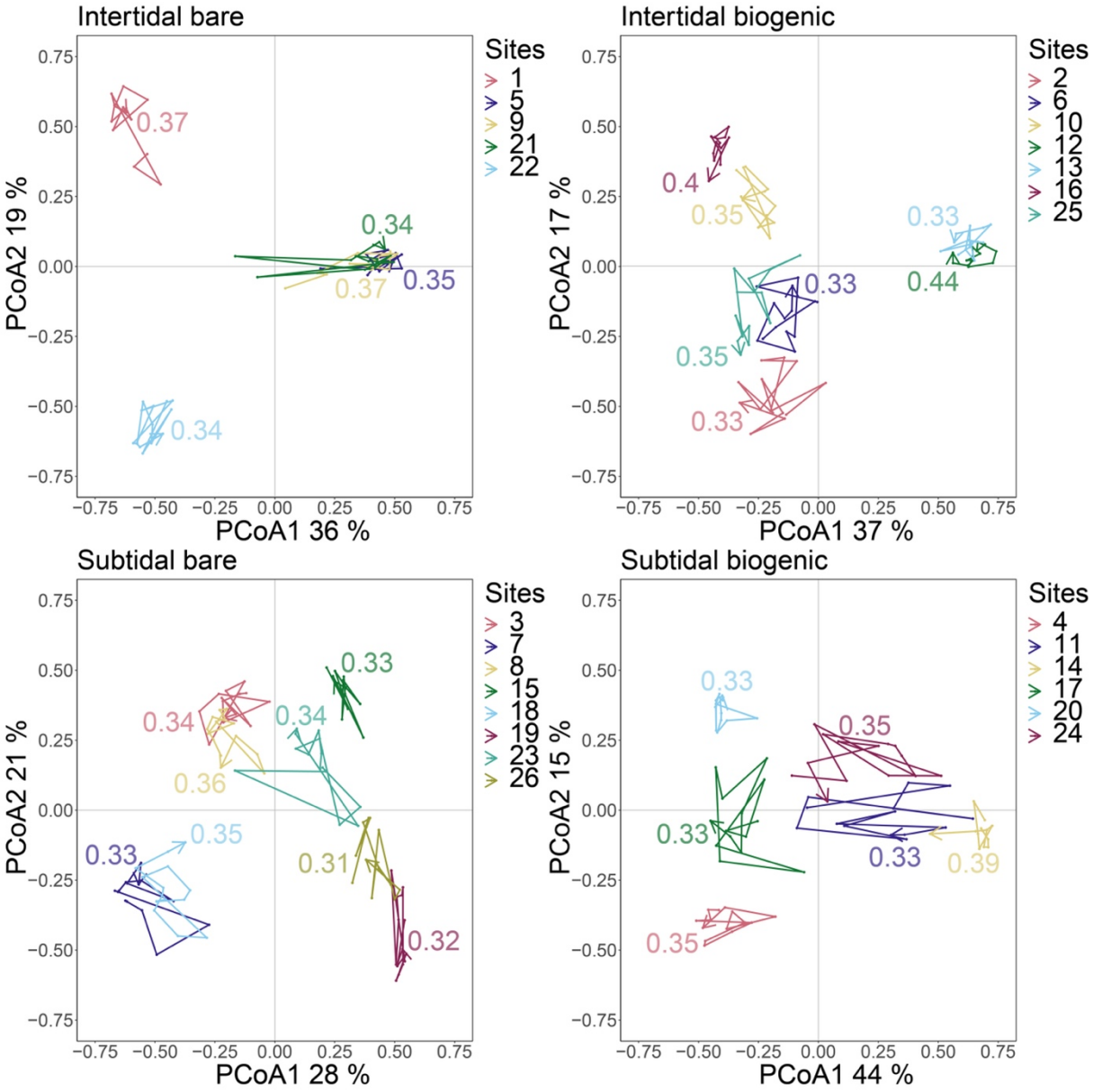
For each habitat, steps of the simulation were as follows:

1. At $t = 0$, the community is generated by sampling n_0 species from the species pool with their occurrence frequency as weights, where n is a number of species sampled from the empirical distribution of observed values of species richness.
2. For each species of the generated community, a value of abundance is sampled from the empirical distribution of observed abundances of the corresponding species.
3. The abundances are then rescaled to match a value of total abundance also sampled from the empirical distribution of total observed abundances, keeping relative abundances constant.
4. For each following time step, a new value n_t of species richness is sampled with the following constraints:
    - Limiting species loss: the new species richness n_t should not have a value $n_t < n_{t-1} \times (1 - extinction\ rate)$to maintain the fixed extinction rate.
    - Limiting species gain: $n_t - n_{t-1}$ should not have a value greater than the maximum difference of species richness observed at any site between two consecutive years in the habitat.
5. If $n_t < n_{t-1}$, a proportion of species equal to the value of the set extinction rate is removed from the community present at $t - 1$. The lower the abundance of species the more likely they are to be removed.
6. If $n_t > n_{t-1}$, a proportion of species equal to the value of the set extinction rate is removed from the community present at $t - 1$. The lower the abundance of species the more likely they are to be removed. Species from the species pool are sampled (with their frequency of occurrence as weights) until the value n_t is reached. Only species that have not been removed between t and $t - 1$ and species that are not

already in the community can be sampled from the species pool and added to the community.

7. The abundances of each species are then sampled and rescaled as in steps 2 and 3.

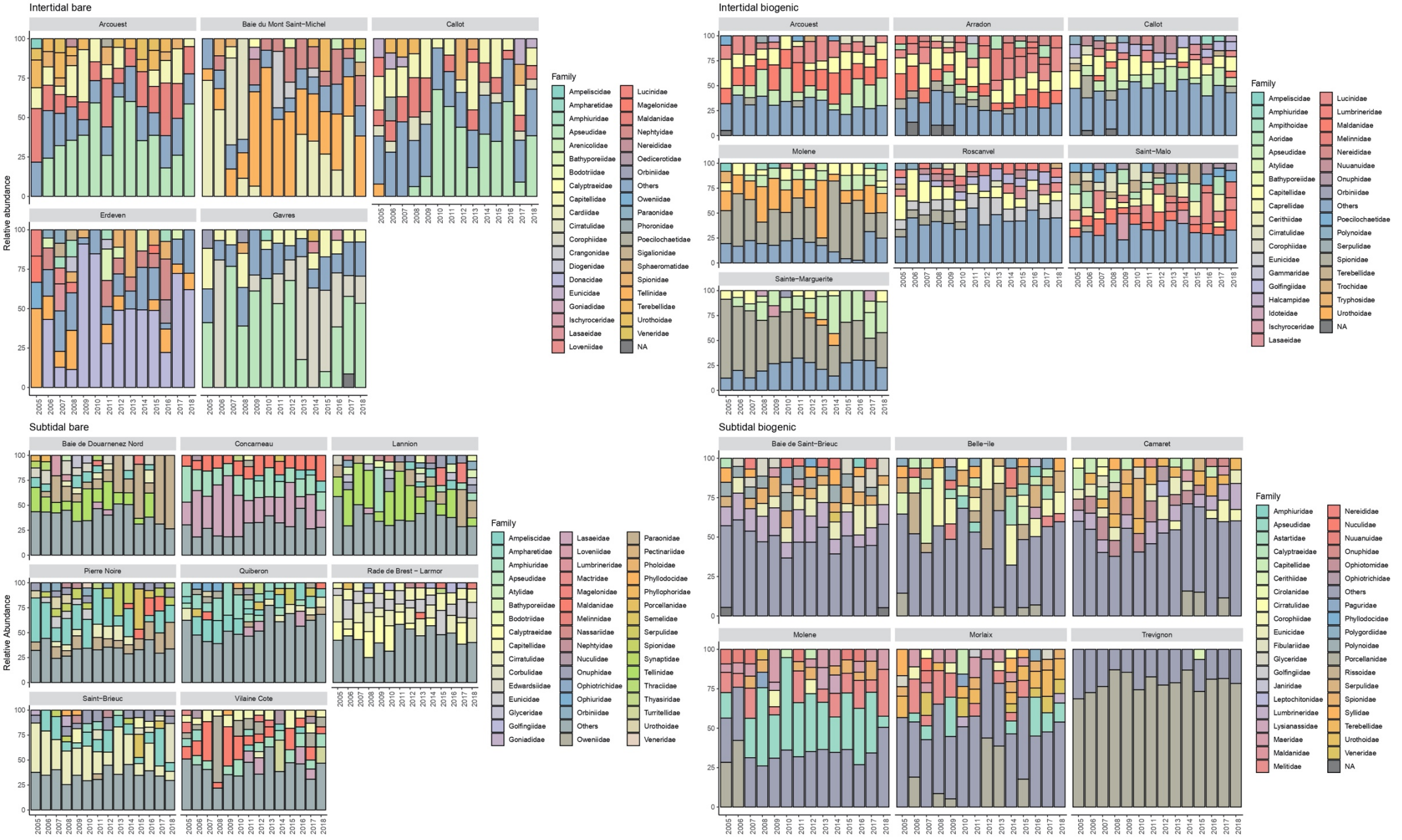
We generated 15 years of community dynamics 100 times (i.e., in 100 virtual sites) for each habitat. The communities at t=0 were removed because the initial set of species is not generated in the exact same way as the communities in the other time steps. CTA metrics were then computed on the trajectories of the simulated communities with a 14 years dynamic to have the same number of surveys as the observed communities.



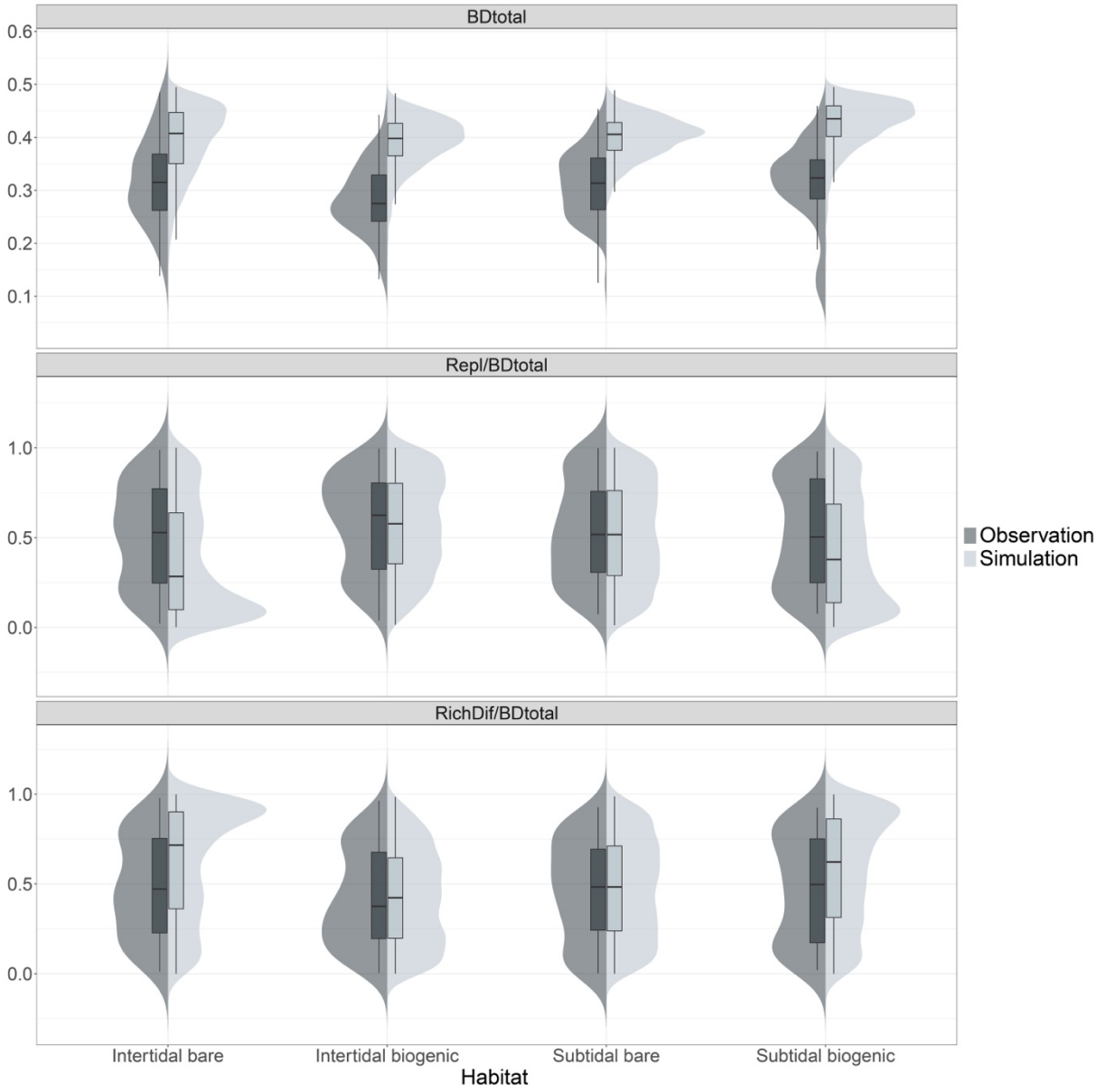
Appendix 4: Representation of community trajectories without LOLAS on the first two PCoA axes with their directionality values associated for each site in the four habitats monitored from 2005 to 2018. One point represents the community state of a site at a given year (one observation). Site specific consecutive community states are linked by a segment and taken together depicts the site trajectory, the arrow represents the final community state of a trajectory (i.e., the community state of a given site in 2018 here).

Appendix 5: Mean and standard error (se) values of sites' trajectory metrics in the subtidal biogenic habitat monitored from 2005 to 2018, with and without the site of Trevignon (20) and considering the community with and without LOLAS. dBDtot = the total dynamic Beta Diversity computed on the dissimilarity D_{SDSP} between centered trajectories, length = the total path length of the trajectory, net change = the distance between the starting point and the final point of the trajectory, angle = the mean angle between two consecutive segments of the trajectory. SBIO = subtidal biogenic habitat.

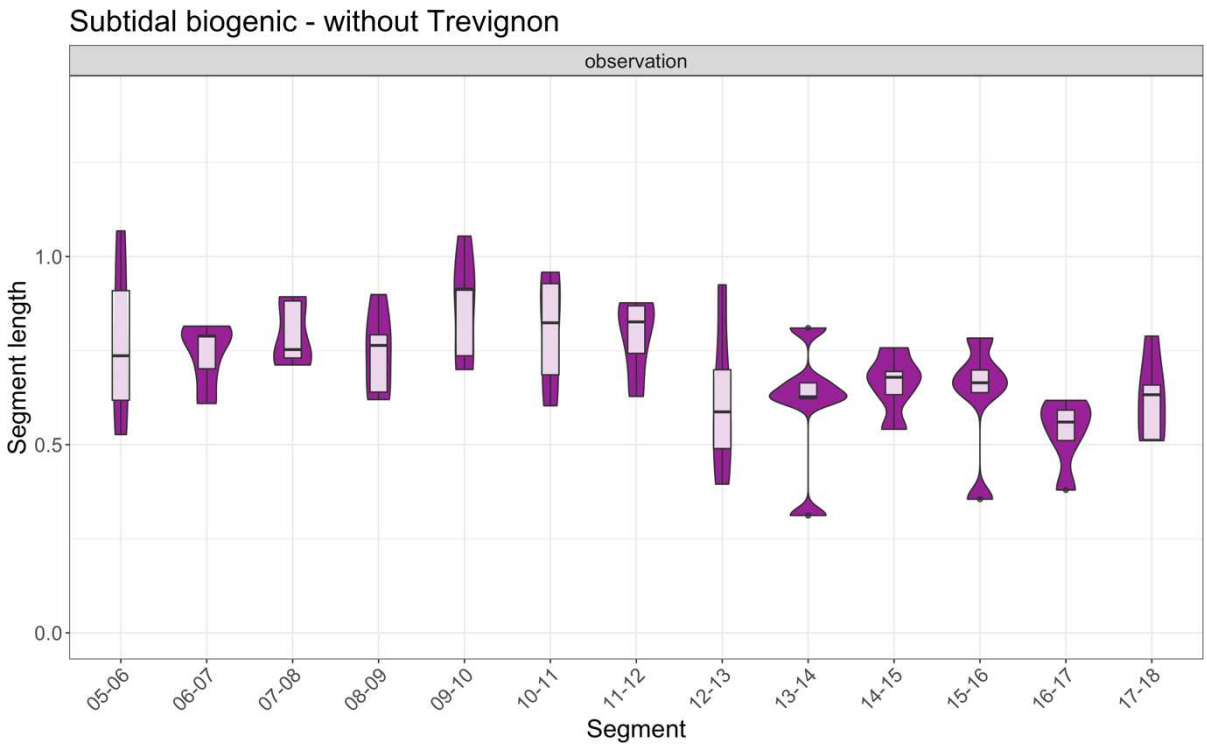
	Global community				Without LOLAS			
Habitat	dBDtot	Mean length±se	Mean angle±se	Mean net±se	dBDtot	Mean length±se	Mean angle±se	Mean net±se
SBIO	0.19	8.31±0.91	117.23±1.35	0.74±0.07	0.10	6.22±0.6	118.30±1.88	0.58±0.07
SBIO without Trevignon (20)	0.22	9.17±0.38	116.98±1.42	0.8±0.03	0.10	6.36±0.71	117.87±2.15	0.62±0.07



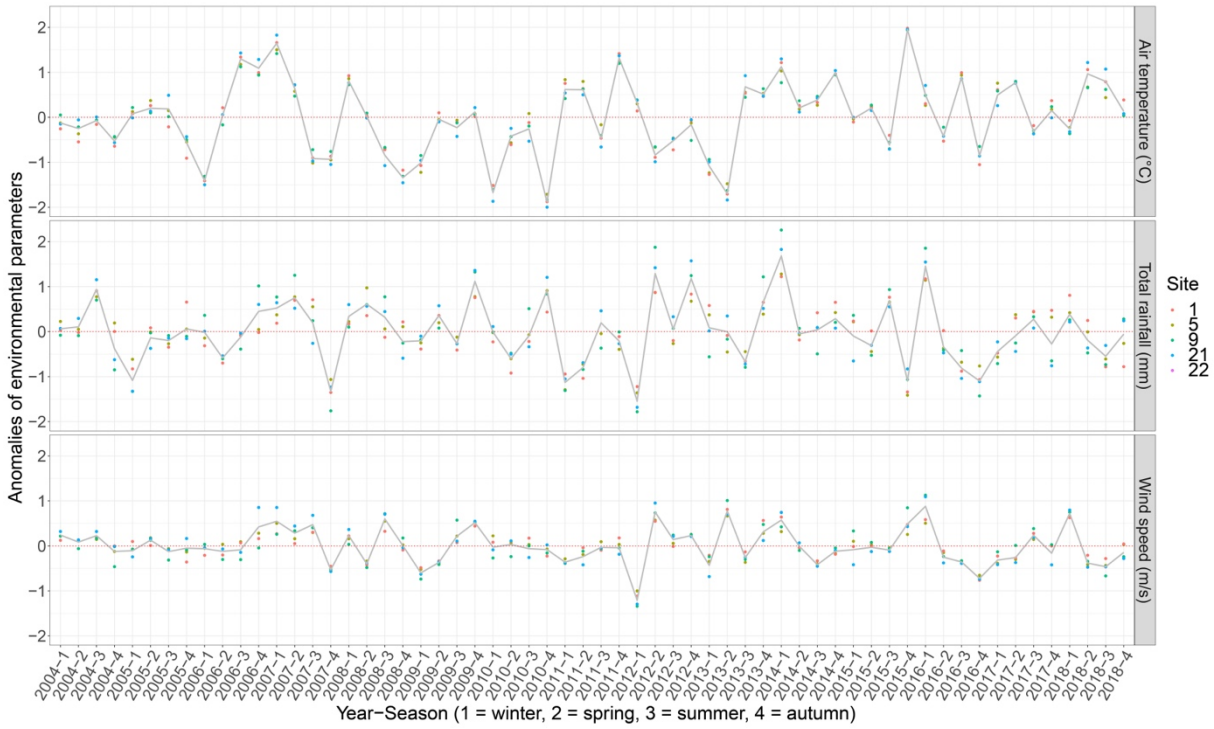
Appendix 6: Percentage of relative abundances of the taxa (taxonomic level of the family) present at each year and each site of each habitat monitored. Others = all taxa under a relative abundance of 5%. NA = taxa whose family could not be identified.



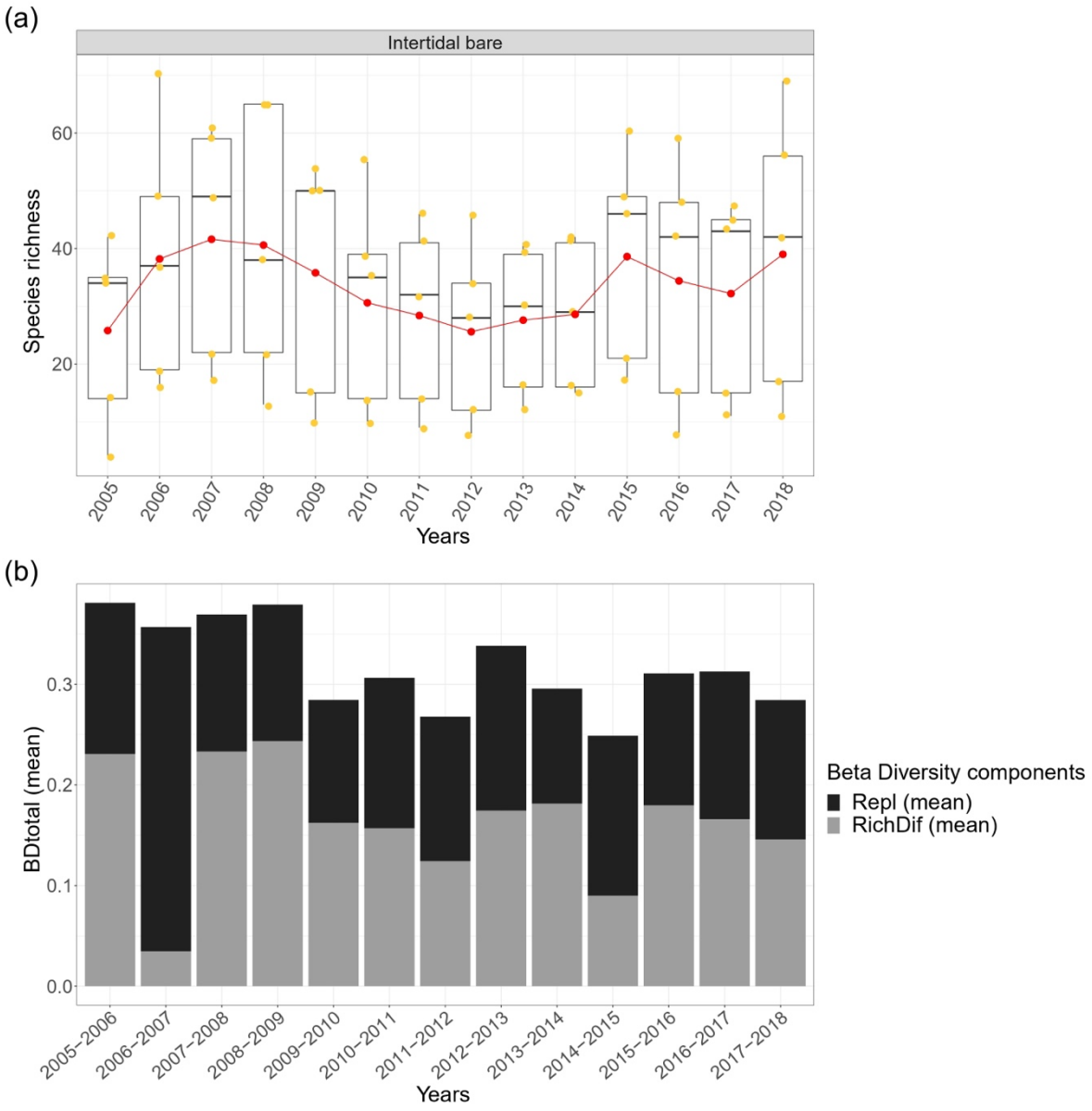
Appendix 7: Comparison of the distributions of total Beta Diversity (BDtotal) values and its two components in proportion: Replacement (Repl/BDtotal) and Richness Difference (RichDif/BDtotal) (Podani family – Ružička) (see Legendre and De Cáceres 2013, Legendre 2014), computed between each two consecutive years of each site in each habitat in the observed communities and the simulated ones.



Appendix 8: Trajectory segment lengths of the communities observed in SBIO without Trévignon (20), monitored from 2005 to 2018.



Appendix 9: Seasonal anomalies of environmental variables in the Intertidal bare habitat over the period of 2004–2018 (grey line: median value between all sites). Seasonal anomaly is computed as the difference between the mean value of the environmental variable measured during the season considered and the reference value of the environmental variable during this season (average value of the environmental variable during the season considered between 2004 and 2018). Daily air temperature (°C), total rainfall (mm) and windspeed (m/s) were extracted from the SIM2-SAFRAN model of METEO-FRANCE (8km resolution). The values of the cells included in 8km radius buffers around the points of each site were average to minimize edge effect. Values at the site level were estimated by averaging values of the three points of each site.



Appendix 10: (a) Evolution of the species richness of each site (one yellow point) of the Intertidal bare habitat from 2005 to 2018 (red points: mean values between all sites). (b) Evolution of the total Beta Diversity (BDtotal) values and its two components: Replacement (Repl) and Richness Difference (RichDif) (Podani family – Ružička) (see Legendre and De Cáceres 2013, Legendre 2014) computed between each two consecutive years of each site in the Intertidal bare habitat (here the mean values between all sites are represented).

Chapter II

Résumé en français

Après nous être penchés sur la caractérisation des dynamiques temporelles des communautés de macrofaune dans chacun des habitats dans le Chapitre I, le Chapitre II vise à mieux comprendre quels sont les facteurs contrôlant les dynamiques spatiotemporelles de ces communautés. Pour ce faire, nous avons estimé l'importance relative de facteurs environnementaux et anthropiques dans le contrôle de la diversité β macrobenthique dans les quatre habitats côtiers étudiés. Considérant que, d'après les résultats du Chapitre I, la variabilité spatiale au sein d'un habitat semble non négligeable, nous avons explicitement inclus dans les analyses les effets de l'espace et du temps afin d'en évaluer leurs importances respectives dans la diversité β. Ici, nous avons utilisé 15 années (2005-2019) de données issues du suivi de la macrofaune benthique acquises dans le cadre du REBENT, couvrant un total de 38 sites dans les quatre habitats. Ces données ont été combinées avec des variables environnementales qui étaient soit mesurées sur le terrain dans le cadre du REBENT soit issues de modèles numériques, ainsi que des proxys de pressions anthropiques tels que le nombre d'habitants, le type d'occupation du sol à proximité des sites et les pressions de pêche. Via des RDAs simples et partielles, nous avons estimé l'importance relative de chaque variable abiotique (c'est-à-dire environnementale et proxys des pressions anthropiques) dans la structuration de la diversité β macrobenthique. Ensuite, nous avons ajouté des descripteurs spatiaux et temporels grâce à la méthode de « distance based Moran Eigenvector Map » (cartes de vecteurs propres de Moran basés sur les distances) qui permet de modéliser les structures spatiales et temporelles, et nous avons testé l'importance de chaque fraction par des méthodes de partitionnement de variation classique et hiérarchique. Les résultats ont montré que les variables environnementales et les proxys de pressions anthropiques expliquaient une plus grande proportion de la diversité β macrobenthique que l'espace et le temps. De plus, l'espace jouait un rôle plus important et significatif comparé au temps. Les pressions de pêche, les variables sédimentaires et les variables décrivant les conditions hydrodynamiques ressortaient comme des variables abiotiques importantes structurant la diversité β macrobenthique dans les quatre habitats. L'analyse des résidus des modèles a indiqué que les habitats biogéniques sont susceptibles d'atténuer l'effet des événements environnementaux extrêmes plus efficacement que les habitats nus. En effet, les résidus des modèles étaient les plus élevés (donc ces modèles parvenaient moins bien à expliquer la β diversité observée) dans l'habitat intertidal nu exposé à un environnement instable. D'ailleurs au sein de cet habitat, les années dont les résidus étaient les plus élevés correspondaient aux quatre premières années du suivi ce qui est en cohérence avec les résultats du Chapitre I. Dans le partitionnement hiérarchique, les proxys de pressions

anthropiques ont montré une grande importance individuelle sur le contrôle de la diversité β de la macrofaune benthique, en particulier dans les habitats intertidaux. Notre étude souligne l'importance d'incorporer des proxys des pressions anthropiques et de mieux les caractériser dans de futurs travaux sur la diversité macrobenthique afin de mieux comprendre leurs effets et interactions et de développer des stratégies de suivi et de gestion adéquates.

Disentangling the effect of space, time and environmental and anthropogenic drivers on macrobenthic β diversity over 15 years of monitoring along 500 km of coastline

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Abstract

Coastal zones are biodiversity hotspots and deliver essential ecosystem functions and services, yet they are exposed to multiple and interacting anthropogenic and environmental constraints. Long-term monitoring programs allow for identifying ecological responses to these drivers and better estimating the relative importance of the different processes controlling changes in species abundances in space and time. We estimated the relative importance of environmental and anthropogenic drivers in controlling macrobenthic β diversity in four distinct coastal habitats: two biogenic habitats in the intertidal and subtidal zones and two bare sedimentary habitats in the same tidal zones. We used data collected over 15 years (2005-2019) in the REBENT benthic coastal invertebrates monitoring program, covering a total of 38 sites in these four habitats, at a regional scale in the North-East Atlantic, combined with environmental data and proxies of anthropogenic pressures. Using simple and partial redundancy analyses, we estimated the relative importance of each abiotic variable (i.e., environmental and proxies of anthropogenic pressures) in structuring macrobenthic β diversity. Then, we added spatial and temporal descriptors modelling spatial and temporal structures and we tested the importance of each fraction with variation and hierarchical partitioning. Results showed that environmental variables and proxies of anthropogenic pressures explained a higher proportion of macrobenthic β diversity than descriptors of spatial and temporal variability. Proxies of anthropogenic pressures had a high individual importance especially in intertidal habitats. Fishing pressures, sedimentary and hydrodynamics variables stood out as important abiotic variables structuring macrobenthic β diversity. Analysis of models' residuals indicated that biogenic habitats might mitigate the effect of extreme environmental events compared to bare ones. Our study emphasizes the importance of characterizing and incorporating proxies of anthropogenic pressures in studies on macrobenthic diversity in order to better understand their functioning and develop adequate monitoring and managing strategies.

1. Introduction

Coastal zones accommodate a large proportion of human population (Burke et al. 2001) and the ecosystems they support provide a variety of resources and valuable services (Costanza et al. 1997). However, they harbor some of the most threatened natural systems (Lotze et al. 2006; Halpern et al. 2008) since intensified human activities lead to degradation of key coastal habitats and thus the biodiversity, functions and ecosystem services they provide (Barbier et al. 2011; Bernhardt and Leslie 2013). In addition to local human impacts, anthropogenically induced climate change is an increasing threat to coastal marine ecosystems where its velocity is higher than on land (Burrows et al. 2011). Therefore, the interactions between local and global human impacts need to be considered to set up effective coastal management strategies (He and Silliman 2019). Coastal ecosystems are exposed to multiple and interacting stressors and their responses are diverse, such as linear and nonlinear trends or abrupt changes of system state (Cloern et al. 2016; Hewitt et al. 2016a; Thrush et al. 2021b). In this context, long-term studies allow for detecting and quantifying ecological responses to drivers of ecosystem change and better understanding ecosystem processes (Lindenmayer et al. 2012), as already reported from various monitoring programs in coastal waters over the past decades (Cloern et al. 2016).

Benthic macrofauna is often used in monitoring programs of coastal marine ecosystems as indicator of changes, since most macrobenthic species are non-migratory (thus exposed to the local physical environment), show various life spans and exhibit different tolerances to environmental stresses (Dauer 1993). Moreover, they play important roles in marine ecosystems such as nutrient cycling, bioturbation and secondary production (Snelgrove 1998). Many studies focusing on marine benthic ecology aimed to identify the different drivers responsible for spatial patterns structuring the communities and disentangle human impacts from natural gradients (e.g., Dutertre et al. 2013; Silberberger et al. 2019). However, we still have a limited understanding of the relationships between temporal and spatial variation in abiotic variables and the biological patterns in macrobenthic assemblages, and how they change over time (Ysebaert and Herman 2002; McArthur et al. 2010). One central topic in community ecology is the estimation of the relative importance of the different processes controlling the changes in species abundances in space and time (Anderson and Cribble 1998). Using canonical analyses, the total variation of a species abundance matrix can be explained by partitioning it in different fractions (e.g., environmental variation, environmental variation without the spatial component, temporal variation etc.) (Borcard et al. 1992; Anderson and Cribble 1998). Each of these fractions can be linked to different ecological processes (i.e., species sorting, mass-effect,

neutral model or patch dynamics) (Leibold et al. 2004; Cottenie 2005; Soininen 2014; Legendre and Gauthier 2014). The environmental fraction has often been shown to be the most structuring fraction of community variation compared to other fractions (e.g., spatial). Moreover, it can be exacerbated in marine ecosystems compared to others (Cottenie 2005; Soininen 2014).

The environmental drivers mostly structuring the distribution of macrobenthic organisms are productivity, temperature and sediment composition (McArthur et al. 2010). Many studies have shown that sedimentary variables often explained most of the community variation although other variables clearly structure macrobenthic communities depending on the habitat considered, such as bathymetry, hydrodynamic conditions or physico-chemical properties of the water column (Ysebaert and Herman 2002; Dutertre et al. 2013, 2015; Veiga et al. 2017; Couce et al. 2020). These environmental variables vary spatially and temporally and their relationship with biological patterns and processes in macrobenthic communities still need to be assessed (Ysebaert and Herman 2002; McArthur et al. 2010). In addition to these variables, the type of habitat also has a significant influence on the variation of macrobenthic assemblages, as it is a major factor determining the occurrence of benthic species (Cottenie 2005; Couce et al. 2020). For example, the presence of a foundation species can modify the extent of species niches through facilitation (Bulleri et al. 2016).

Anthropogenic pressures can also play a major role in macrobenthic β diversity as they can strongly modify their structures through direct or indirect effects (Thrush et al. 2021a). For example, fishing pressures can induce changes in community composition through the direct removal or species or by affecting food webs and sediment characteristics (Hily et al. 2008; Sciberras et al. 2018). Increasing human density and activity can induce an increase in human waste and sewage and land development for industrial and agricultural activities, leading to pollution, habitat destruction and eutrophication (He and Silliman 2019). Causes of coastal eutrophication are often bound within coastal ecosystems and their watersheds (Duarte et al. 2009) and can for example result in the development of green tides affecting macrofauna communities (Cloern 2001; Quillien et al. 2018). Thus, human population density and activity have been widely used a reasonable proxy of the relative magnitude of local human impacts (He and Silliman 2019). Moreover, these human activities can change the extent, frequency and magnitude of natural disturbances.

Brittany (France) is a biogeographic transition zone between the Northern European seas and the Lusitanian province (Spalding et al. 2007), which is characterized by a high diversity of benthic habitats and as a hotspot for macrobenthic richness (Gallon et al. 2017), although subject to different aspects of global change and anthropogenic threats (e.g., Quillien

et al. 2015, 2018; Ragueneau et al. 2018). It harbors widely distributed bare sedimentary habitats and more spatially limited biogenic habitats created by foundation species but nonetheless important for the taxonomic and functional diversities of macrobenthic assemblages (Boyé et al. 2019). Maerl and seagrass beds are two biogenic habitats that can be found along the coasts of Brittany. They are both fragile and complex biotopes providing resources and shelters for a large variety of biota while being threatened by human activities (Airoldi and Beck 2007). These habitats may mitigate the strength of abiotic factors effects on macrobenthic communities by dampening environmental variation, through the reduction of physical stress for example (Bulleri et al. 2018). Thus, we expect differential community responses to the same abiotic conditions in biogenic *versus* bare soft bottom habitats. Moreover, as intertidal communities are exposed to both terrestrial and marine constraints (Helmuth et al. 2006), we expect differential responses of benthic communities over the past 15 years between intertidal and subtidal environments (Hinz et al. 2011). Disentangling the different factors controlling the changes in macrobenthic communities of these habitats is essential to better understand how these communities spatially and temporally vary in the current context of global changes and guide management strategies for the future.

We used 15 years of benthic macrofauna monitoring in 38 sites distributed along 500 km of Brittany coasts and located in four different soft-bottom habitats exposed to different abiotic constraints: two biogenic habitats associated with foundation species (i.e., seagrass and maerl beds) in the intertidal and the subtidal zones respectively, and two bare sedimentary habitats also in these two different tidal zones. To our knowledge, this is the first study of such spatial and temporal coverage using variation and hierarchical partitioning of macrobenthic communities between space, time, environmental and anthropogenic fractions. The main objectives were to (1) identify and compare spatial and temporal patterns of benthic communities' structure between four different habitats and (2) identify and disentangle the importance of the different environmental and anthropogenic variables that drive the spatiotemporal dynamics of the benthic communities of the different habitats.

2. Material and Methods

2.1. Macrofauna sampling

Benthic communities have been monitored yearly since 2003 along the coasts of Brittany (France) within the REBENT program (http://www.rebent.org). We focused on four habitats: intertidal sandy beaches, intertidal seagrass beds (formed by *Zostera marina*), subtidal soft sediments and subtidal maerl (or rhodolith) beds (principally formed by *Lithothamnion corallioides* and *Phymatolithon calcareum*). These four habitats are respectively referred to as intertidal bare habitat (IBAR), intertidal biogenic habitat (IBIO), subtidal bare habitat (SBAR) and subtidal biogenic habitat (SBIO) from this point forward.

At each site three faunal samples were taken at each of three fixed sampling points distributed ~ 200 m apart (using 0.03 m^2 cores in the intertidal and 0.1 m^2 Smith-McIntyre grabs in the subtidal; see Boyé et al. 2019), except for the Pierre Noire site where 10 grabs were taken at each visit. For all habitats, an additional (core or grab accordingly) was taken at each point and used to estimate grain size distribution and organic matter content at the time of the faunal sampling. Sampling was performed between the end of February and the beginning of May, before the recruitment of most species in the region (Dauvin et al. 2007; Boyé et al. 2019). In the laboratory, specimens were sorted, counted and identified to the lowest possible taxonomic level (usually species). Since the acquisition and identification of specimens were not systematically carried out by the same people over the years, we proceeded with taxonomic homogenization: each recorded taxon was scrutinized by experts in benthic taxonomy and their names were checked thanks to the World Register of Marine Species (WoRMS Editorial Board 2021) to ensure for taxonomic resolution consistency.

To minimize the impact of missing data on the analyses, we selected sites that both had at least 3 core or grab samples in any particular year and less than 4 sampled years missing (out of 15). Samples were pooled to estimate abundances at the site level. This led to a selection of 38 sites monitored from 2005 to 2019 while keeping a spatial resolution covering the coasts of Brittany and encompassing most of the environmental settings found in this region (Boyé et al. 2017, 2019). Of these 38 sites, 12 were in IBAR, 8 in IBIO, 9 in SBAR and 9 in SBIO (Figure 1).

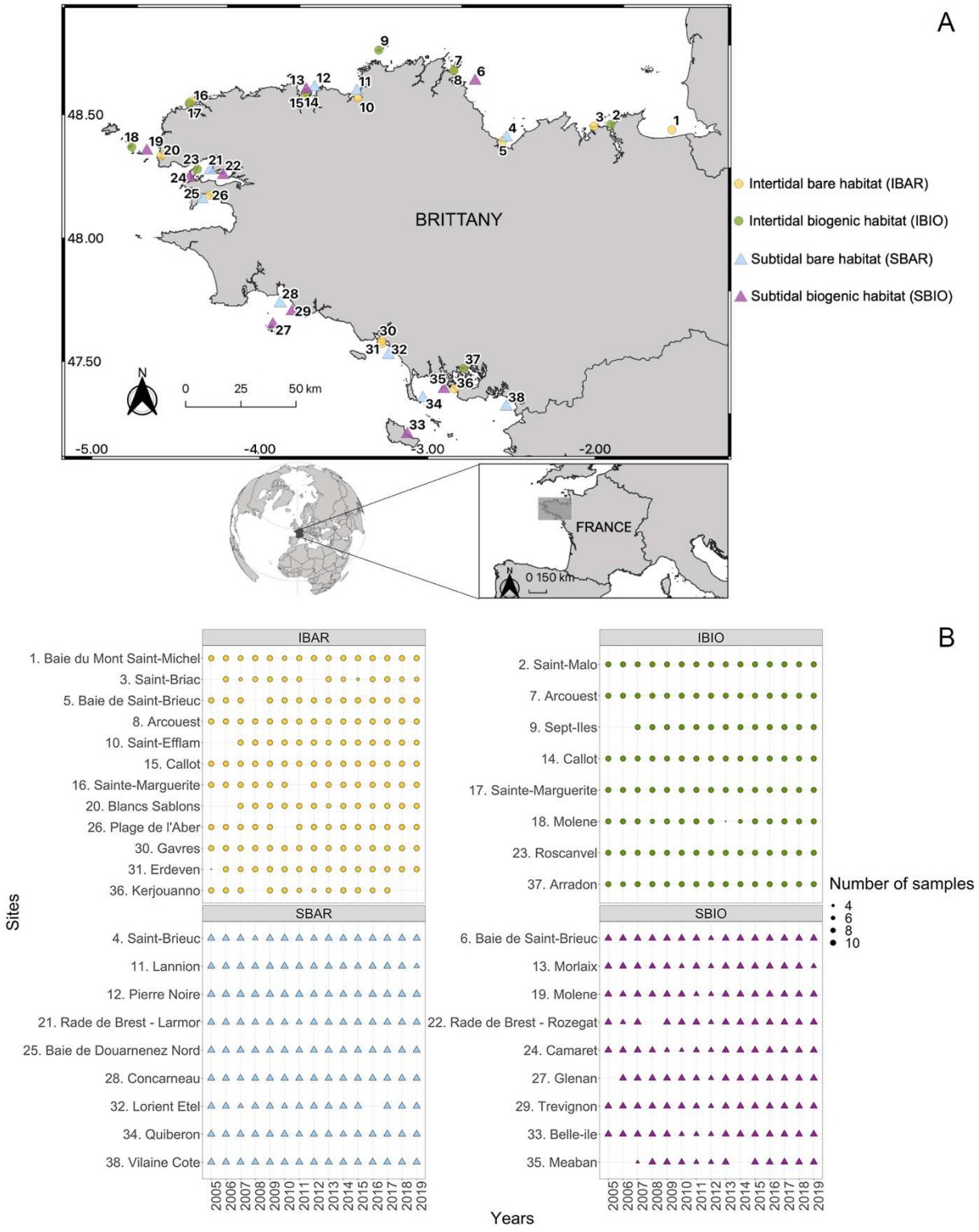


FIGURE 1: A) Map of the sites in the four monitored habitats along the coast of Brittany (France). (Sources: OpenStreetMap, European Environment Agency). B) Data availability for each site in each habitat from 2005 to 2019. The size of the points is proportional to the number of samples (cores in the intertidal and grabs in the subtidal) that were aggregated to estimates taxon abundances at the site level.

2.2. Explanatory variables

2.2.1. Spatial and temporal patterns

To model spatial patterns, we used distance-based Moran's Eigenvector Maps (dbMEM) which are linearly independent spatial descriptors that allow for modeling spatial structures over a wide range of spatial scales (Borcard and Legendre 2002; Dray et al. 2006). For dbMEMs computation, distances among sites were calculated as the shortest paths along the coast following the methodology described in Appendix 1. We also modeled a spatial linear trend using the shortest distance along the coast from the northernmost site at each site consecutively to the southernmost site. Similarly, temporal patterns were modeled using dbMEMs on the temporal coordinates of the sampling dates among the 15 years monitored (Legendre and Gauthier 2014). Because the temporal linear trend was not significant, we did not include it in the final models. In both cases we only selected the dbMEMs accounting for positive spatial or temporal correlation (Borcard et al. 2018; see for example Appendices 2 and 3).

2.2.2. Abiotic variables

Abiotic variables included environmental variables and proxies of anthropogenic pressures that were extracted *in situ* at the time of the REBENT macrofauna sampling, or numerically computed *a posteriori* (see Appendix 1). All data were estimated at the site level, some varying in time (spatiotemporal variation) and others not (spatial variation only) (Table 1).

Environmental variables included sediment characteristics (grain-size distribution), morphometric data of *Zostera marina* beds (*Zostera marina* morphological and structural traits), sea water properties and hydrodynamics variables (hydrology and hydrodynamics), climate data on land (meteorology), a proxy of wave exposure (fetch) and bathymetry (depth) (Table 1).

Proxies of anthropogenic pressures included the number of inhabitants in the vicinity of sites, the land surfaces covered by artificial or agricultural areas in the vicinity of sites or in watersheds in the vicinity of sites (see Appendix 1 for details), and fishing pressures according to the type of fishing carried out in each of the four habitats (Table 1). The number of inhabitants stood as a proxy for human frequentation of the sites and activities in their vicinity as well as urbanization of the coastline, while land use and watersheds stood as a proxy for potential

runoffs from industrial and agricultural areas, but also human activity in the vicinity of sites and potential eutrophication processes.

The *in situ* data had an annual temporal resolution since they were collected every year at the occasion of the macrofauna sampling. Spatiotemporal data from numerical models (i.e., hydrology & hydrodynamics and meteorology data sets, see Table 1) had a daily resolution. In order for these data to have the same temporal resolution as the macrofauna and *in situ* environmental data (i.e., one value per year), while taking into account their variability in the months preceding the sampling dates, we calculated the mean, standard deviation, minimum and maximum values of each variable, at each site, from the 1st of November of the previous year to the date of sampling. We made this choice in order to account for winter storms (typical of NW France between November and March; (Leckebusch et al. 2006; Poppeschi et al. 2021) that could have an influence on the sampled communities (e.g., Harris et al. 2011; Corte et al. 2017). We did not consider the summer and autumn conditions in the year prior to sampling as they were considered too distant in time to be relevant predictors of the observed communities (Lessin et al. 2019).

All variables were quantitative and continuous, except for the semi-quantitative fishing pressure coded 'No', 'Low, 'High' according to the type of fishing practiced in each habitat.

The details of the protocols, numerical model products and techniques used to extract and calculate each of the variables can be found in Appendix 1.

TABLE 1: List of the abiotic explanatory datasets and their variables before selection, their abbreviations, how they were acquired, for which habitat, and examples of studies where these variables have been shown as potential drivers of macrofaunal β diversity. *For each variable of the hydrology & hydrodynamics and meteorology datasets, the mean, standard deviation, minimum and maximum values from the November 1st of the previous year to the date of sampling were taken. Number of inhabitants and land use surfaces were estimated at the buffer and/or watershed scale (see Appendix 1). IBAR = intertidal bare habitat, IBIO = intertidal biogenic habitat, SBAR = subtidal bare habitat, SBIO = subtidal biogenic habitat.

Acquisition	Data	Variables	Abbreviation	Habitat	Potential drivers of Macrofauna β diversity
Spatiotemporal data					
In situ	Sediments (grain-size distribution and organic matter content)	mean (µm) median (µm) trask or sorting index kurtosis (µm) gravels (%) sand (%) mud (%) organic matter (%)	mean.grain D50 So kurtosis gravels sand Mud OM	●●▲▲	Ellingsen 2002; Ysebaert and Herman 2002; Dauvin et al. 2004; Blanchet et al. 2005; Dutertre et al. 2013; Veiga et al. 2017
	Zostera marina morphological and structural traits	density (*shoot.m*$^{-2}$) leaf biomass (*g.m*$^{-2}$) root biomass (*g.m*$^{-2}$) mean sheath height (*mm*) mean leaf length (*mm*) leaf width (*mm*) number of leaveas per shoot broken leaves (%)	density leaf.biom root.biom sheath.height leaf.length leaf.width leaves/shoot broken	●	Boström and Bonsdorff 2000; Hovel et al. 2002; Bouma et al. 2009
Numeric	Hydrology & Hydrodynamics*	bottom temperature (°*C*) salinity (*psu*) current velocity (*m.s*$^{-1}$)	bottomT sal current	●●▲▲	Snelgrove 1998; Gray 2002; Lercari and Defeo 2003, 2006; Dutertre et al. 2013; Couce et al. 2020
	Meteorology*	air temperature (°*C*) wind velocity (*m.s*$^{-1}$) total rainfall (*mm*) minimum air temperature (°*C*) maximum air temperature (°*C*) daily range temperature (°*C*)	T wind rain minT maxT drangeT	●●	Rees, 1977; Boström and Bonsdorff 2000; Cardoso et al. 2008; Grilo et al. 2011
Spatial data					
Numeric	Fetch	fetch (*km*)	fetch	●●▲▲	Rees, 1977; Hovel et al. 2002; Boström et al. 2006
	Depth	depth (*m*)	depth	▲▲	Snelgrove 1998; Ellingsen 2002; Dauvin et al. 2004; Dutertre et al. 2013
	Population	number of inhabitants (log)	hab	●●▲▲	Lerberg 2000; Lotze et al. 2006
	Land use	artificial surfaces (*km*^{2}) agricultural areas (*km*^{2})	artif agri	●●▲▲	Lerberg et al. 2000; Cloern et al. 2016
Expert	Fishing	recreational fishing professional fishing dredging	RF (No/Low/High) PF (No/Low/High) DR (No/Low/High)	●● ●▲ ▲	Currie and Patry 1996; Thrush et al. 1998; Hily et al. 2008; Sciberras et al. 2018

Environment
Proxy anthropogenic pressures
IBAR
IBIO
SBAR
SBIO

2.2.3. Environmental variable selection

First, within each dataset (corresponding to the "spatiotemporal" data of Table 1), collinear variables were removed using Variance Inflation Factors (VIF) (Legendre and Legendre 2012) with a threshold of 10. Then, of the remaining variables, some were grouped as environmental (green color in Table 1) and variable selection within this group was performed for each habitat separately. For that purpose, redundancy analyses (RDA) (Rao 1964; Legendre and Legendre 2012) were performed, with the response matrix being the community matrix of Hellinger-transformed taxa abundances in a given habitat, and the explanatory matrix including all environmental variables remaining after VIF analysis for a given group of predictor. The Hellinger distance coefficient is equivalent to the Euclidean distance computed on the square root of species relative abundances. It does not give an excessive weight to rare species and has the advantage of fulfilling the metric and Euclidean properties (Legendre and Gallagher 2001; Legendre and De Cáceres 2013). Full models were tested for significance using 999 permutations of the community data. As they were all significant, we proceeded with forward selection of the environmental variables based on adjusted R^2 (Blanchet et al. 2008). Subsequent analyses were based on models including either the selected set of environmental variables and the proxies of anthropogenic pressures (together called "abiotic variables) or these abiotic variables coupled with data modeling spatial and temporal patterns (Table 2).

TABLE 2: Selected variables in each habitat for the analyses. Z.m = *Zostera marina*, Sp.Linear = Spatial linear trend, Sp. = Spatial, Tp. = Temporal, s.d. = standard deviation, min = minimum, max = maximum, IBAR = intertidal bare habitat, IBIO = intertidal biogenic habitat, SBAR = subtidal bare habitat, SBIO = subtidal biogenic habitat

Habitat	Sediments	Hydrology & Hydrodynamics	Meteorology	*Z.m* traits	Anthropogenic	Sp. Linear	Sp. dbMEMs	Tp. dbMEMs
IBAR	OM kurtosis So mean.grain mud	fetch s.d. current min current s.d. sal max sal min bottomT mean bottomT	s.d. wind min wind s.d. maxT max maxT mean maxT max T		hab agri artif RF PF	spatial linear trend	MEMs 1 to 2	MEMs 1 to 6
IBIO	OM kurtosis So D50 mud	fetch s.d. current min current s.d. sal max sal min bottomT	s.d. wind max wind max maxT mean maxT mean minT	leaf.width density	hab agri artif RF	spatial linear trend	MEMs 1 to 2	MEMs 1 to 6
SBAR	OM kurtosis mud	depth fetch s.d. current min current s.d. sal max sal max bottomT min bottomT			hab agri artif PF	spatial linear trend	MEMs 1 to 2	MEMs 1 to 6
SBIO	OM kurtosis mean.grain D50 mud	depth fetch s.d. current min current s.d. sal max sal max bottomT min bottomT			hab agri artif DR	spatial linear trend	MEMs 1 to 2	MEMs 1 to 6

Environment | Proxy anthropogenic pressures | Space | Time

2.3. Data analyses

RDA was conducted in each habitat separately, between the community matrix of Hellinger-transformed taxa abundances (response matrix) and the matrices of selected abiotic variables (i.e., environmental variables + proxies of anthropogenic pressures as explanatory matrix). In hierarchical partitioning, the individual contribution of a predictor is defined as its unique contribution to the total model plus its average shared contributions with the other predictors (Lai et al. 2022). As we were not able to assess the individual contribution of each abiotic variable by hierarchical partitioning as calculation speed is currently a limitation with the R package "rdacca.hp" (Lai et al. 2022), we estimated the importance of each abiotic variables in each habitat by conjointly looking at the proportion of variance explained (adjusted R^2) by each variable in simple (without the other variables as condition) and partial (with the other variables as condition) RDAs. We also plotted the average of residuals at each site and year combination to try to identify years and/or sites where models based on abiotic variables either failed to explained the observed β diversity or, on the contrary, performed rather well.

Additionally, we conducted variation partitioning and hierarchical partitioning based on RDA analyses (Lai et al. 2022) with all variables of Table 2, to calculate the unique, shared and individual contributions of each matrix of predictors (i.e., environmental matrix, proxy of anthropogenic pressures matrix, spatial linear trend, spatial dbMEMs, temporal dbMEMs) to the explained variation of communities within each habitat. We were able to compute the individual contribution in this case as the number of individual contributions was reduced to the number of matrices (i.e., 5).

All analyses were conducted with the R programming language version 4.1.2 (R Core Team 2021) and packages, "adespatial" (Dray et al. 2021), "vegan" (Oksanen et al. 2022) and "rdacca.hp" (Lai et al. 2022). Outputs from the "rdacca.hp" package were plotted using the "UpSetVP" package (Liu 2022).

3. Results

Simple RDAs between the community matrix and the matrix of abiotic variables (i.e., environmental variables + proxies of anthropogenic pressures) were all significant ($p < 0.001$) and respectively explained: 49.4% of total variation (adjusted R^2) in IBAR, 61.6% in IBIO, 56.0% in SBAR and 53.8% in SBIO. Based on model predictions, sites appeared to differ along environmental gradients within each habitat and spatial heterogeneity seemed to be higher than the temporal one, especially for IBAR, IBIO and SBAR (Figure 2). The main spatial patterns highlighted by the RDA, and the identity of the predicted underlying drivers, differed across habitats, although some commonalities appeared such as the important predicted role of sediment properties and of the degree of exposure of the sites, as well as the non-negligible role of anthropogenic pressures (Figure 2). The main community gradient predicted in IBIO distinguished sheltered muddy sites (on the left of the RDA) from sites exposed to high wind and current velocities resulting in well-sorted sediment (on the right). Proxies of anthropogenic pressures (in particular the type of land use and the number of inhabitants) drove the variation along the second axis of the RDA for that habitat, although the number of inhabitants seemed to be an important predictor in each habitat. Although the predicted spatial patterns were markedly different in IBAR, an important role of site exposure and sediment properties was also visible (the two axes distinguishing the muddiest site at the bottom, from sites with well-sorted sediment on the top right and sites with coarse sediments on the top left, Figure 2). However, a higher role of anthropogenic proxies, in particular fishery-related variables, was reported as a major discriminant of IBAR communities along the first RDA axis. In SBIO, sedimentary conditions discriminated one site (Trevignon (29), which also present a singular community, see Chapter I) from the others, whereas depth and proxies of anthropogenic pressures (i.e., number of inhabitants, land use) explained the community difference between the three sites of Baie de Saint-Brieuc (6), Rade de Brest – Rozegat (22) and Camaret (24), and the other beds of Molene (19) or Belle-ile (33). Overall, RDA failed to explain spatial differences amongst the remaining SBIO sites (high convex hull overlaps), but rather explained temporal community differences within these sites (e.g., temporal dynamics within Morlaix (13) and Meaban (35) predicted from changes in current velocities and sediment properties). On the contrary, sites in SBAR were more dispersed and bathymetry, percentage of mud, current velocity, fetch as well as fishing pressure (low professional fishing) played an important role in their dispersion along the two axes. While spatial patterns were better predicted than in SBIO, it appeared from these first two RDA axes that temporal variation remained an important

component of the explained variance in SBAR, contrary to the two intertidal habitats. Finally, these RDA allowed to identify some species that appeared related to sites characterized by specific abiotic conditions (e.g., *Apseudopsis latreillii* related to Sainte-Marguerite (16), Gavres (30), Callot (15) and Arcouest (8) in IBAR also characterized by a high mean of grain-size distribution and high recreational fishing).

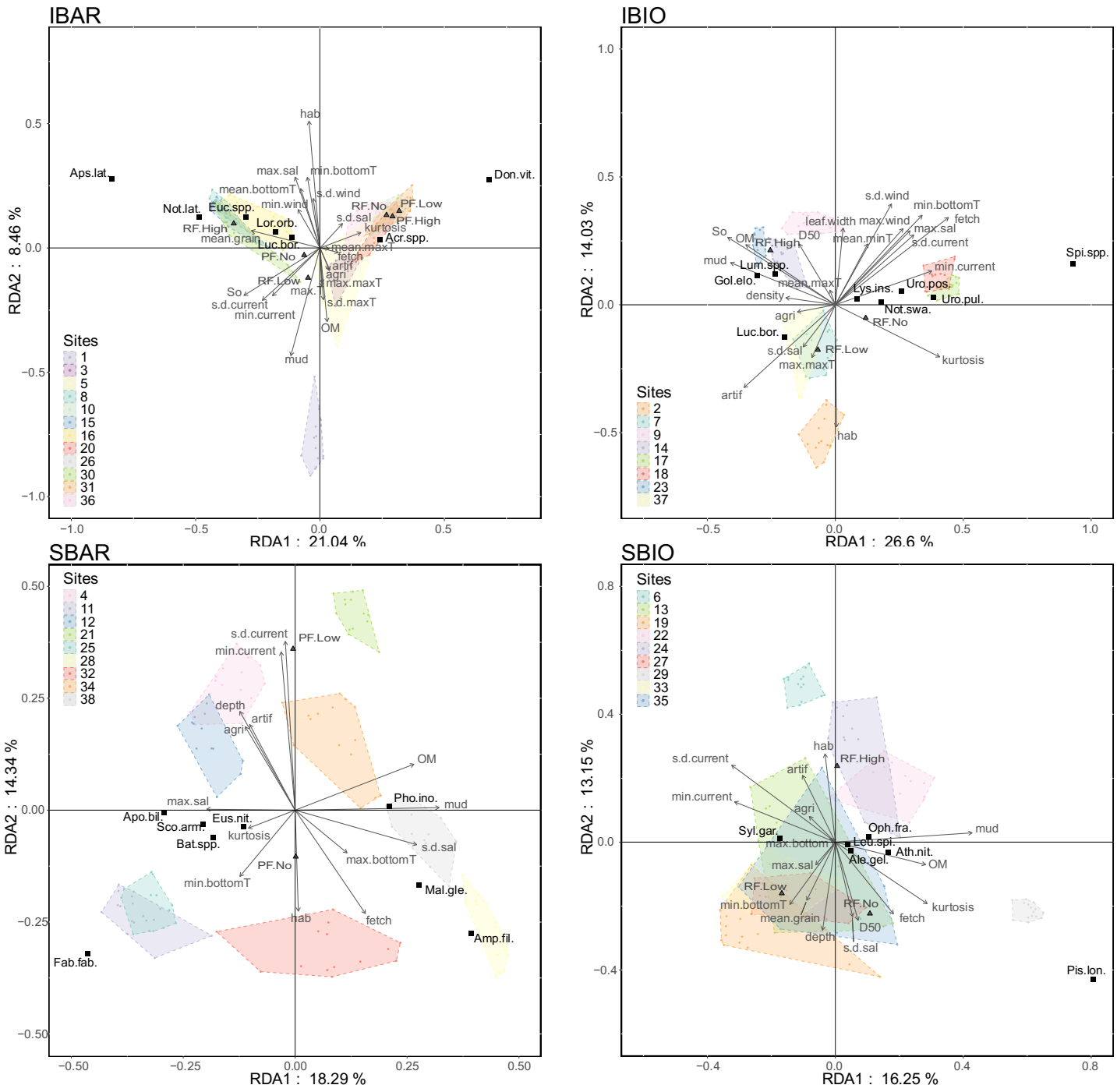


FIGURE 2: RDA triplots (scaling 2 – weighted average), for each habitat (IBAR = intertidal bare habitat, IBIO = intertidal biogenic habitat, SBAR = subtidal bare habitat, SBIO = subtidal biogenic habitat), only the first two canonical axes are represented. The percentages represent the proportion of total variance explained by each axis. Arrows represent the abiotic variables. Triangular points are the centroids of each level of the categorical variables (i.e., fishing pressure). Squares represent a subset of taxa whose variances along these two axes represent more than 30% in IBAR, 40% in IBIO, 40% in SBAR and 30% in SBIO of their total variances (assessed with the function "goodness" of the "vegan" package). Points represent the fitted observations (i.e., one site at one year), all observations from a single site are grouped within a convex hull. Full description of abiotic variable abbreviations can be found in Table 1. Species abbreviations: Aps.lat. = *Apseudopsis latreillii*, Not.lat. = *Notomastus latericeus*, Euc.spp. = *Euclymene spp.,* Lor.orb. = *Loripes orbiculatus*, Luc.bor. = *Lucinoma borealis*, Acr.spp. = *Acronida spp*., Don.vit. = *Donax vittatus*, Lum.spp. = *Lumbrineris spp*., Gol.elo. = *Golfingia (Golfingia) elongata*, Lys.ins. = *Lysianassa insperata*, Not.swa. = *Nototropsis swammerdamei*, Uro.pos. = *Urothoe poseidonis*, Uro.pul. = *Urothoe pulchella*, Spi.spp. = *Spio spp*., Fab.fab. = *Fabulina fabula*, Apo.bill. = *Aponuphis bilineata*, Sco.arm. = *Scoloplos (Scoloplos) armiger*, Bat.spp. = *Bathyporeia spp*., Eus.nit. = *Euspira nitida*, Mal.gle. = *Maldane glebifex*, Pho.ino. = *Pholoe inornata*, Amp.fil. = *Amphiura filiformis*, Syl.gar. = *Syllis garciai*, Leu.spi. = *Leucothoe spinicarpa*, Ale.gel. = *Alentia gelatinosa*, Oph.fra. = *Ophiothrix fragilis*, Ath.nit. = *Athanas nitescens*, Pis.lon = *Pisidia longicornis*.

To assess the importance of each abiotic predictor in explaining the variation of the communities in each habitat, we looked at the adjusted R^2 of each predictor in simple and partial RDAs (Figure 3). In simple RDAs, the predictors with the highest importance in the four habitats were all related to fishing pressure while variables related to hydrodynamics (fetch in IBIO) and sediment properties (i.e., sorting index and percentage of mud in the other habitats) often ranked second or third (Figure 3). The highest percentage of variation explained by a single variable was greater than 15% in IBAR, IBIO and SBIO but lower than 10% in SBAR. Moreover, the explained variation was relatively equivalent between the different predictors in SBAR and IBIO, whereas predictors importance was highly uneven in IBAR and SBIO. In partial RDAs, explained variation of each predictor decreased in comparison to the simple RDAs, except for artificial surfaces and agricultural areas in IBAR. The predictor with the highest importance in simple RDAs remained the same in all habitats except for IBIO where the number of inhabitants became the most important predictor after partialling out the variation explained by all other predictors. In SBAR, proxies of anthropogenic pressures showed increased effect compared to the other abiotic variables. This increased estimated effect of proxies of anthropogenic pressures in partial RDA compared to simple RDA, indicated that they explained a unique and different share of variation compared to the other variables, a feature that is consistent across habitats. Interestingly, some predictors became significant in partial RDA while they were not in simple RDA (e.g., mean of maximum air temperatures in IBAR and maximum bottom temperature in SBIO).

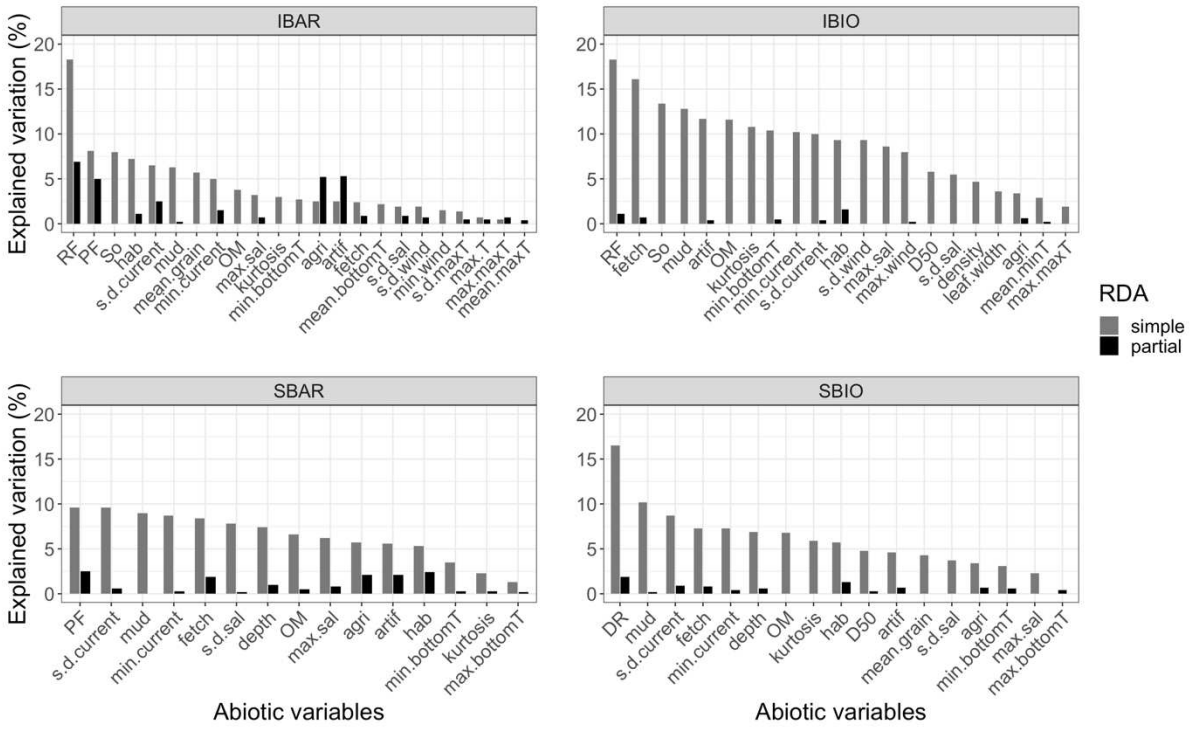


FIGURE 3: Explained variation (adjusted R^2) of each abiotic variable separately, either in simple RDA (without all other variables as conditions) or in partial RDA (with all other variables as conditions), within each habitat (IBAR = intertidal bare habitat, IBIO = intertidal biogenic habitat, SBAR = subtidal bare habitat, SBIO = subtidal biogenic habitat). Only significant abiotic variables from simple or partial RDA models are presented ($p < 0.05$).

Mean of the residuals per year and habitat of the simple RDAs with all selected abiotic predictors are represented in Figure 4. The higher the mean of the residuals, the more the models failed to explain the observed community β diversity. The highest yearly residual means were in IBAR whereas the lowest were in SBIO, meaning the model provided better predictions of yearly β diversity in SBIO. IBAR also showed the highest temporal variability in the residual values. Indeed, the model seemed be less effective at explaining β diversity during the first 4 years of monitoring (2005-2008). On the contrary, the efficiency of the model to explain β diversity appeared stable over time in SBIO. Model efficiency seemed to be equivalent between IBIO and SBAR even though it seemed to fluctuate more over time in SBAR.

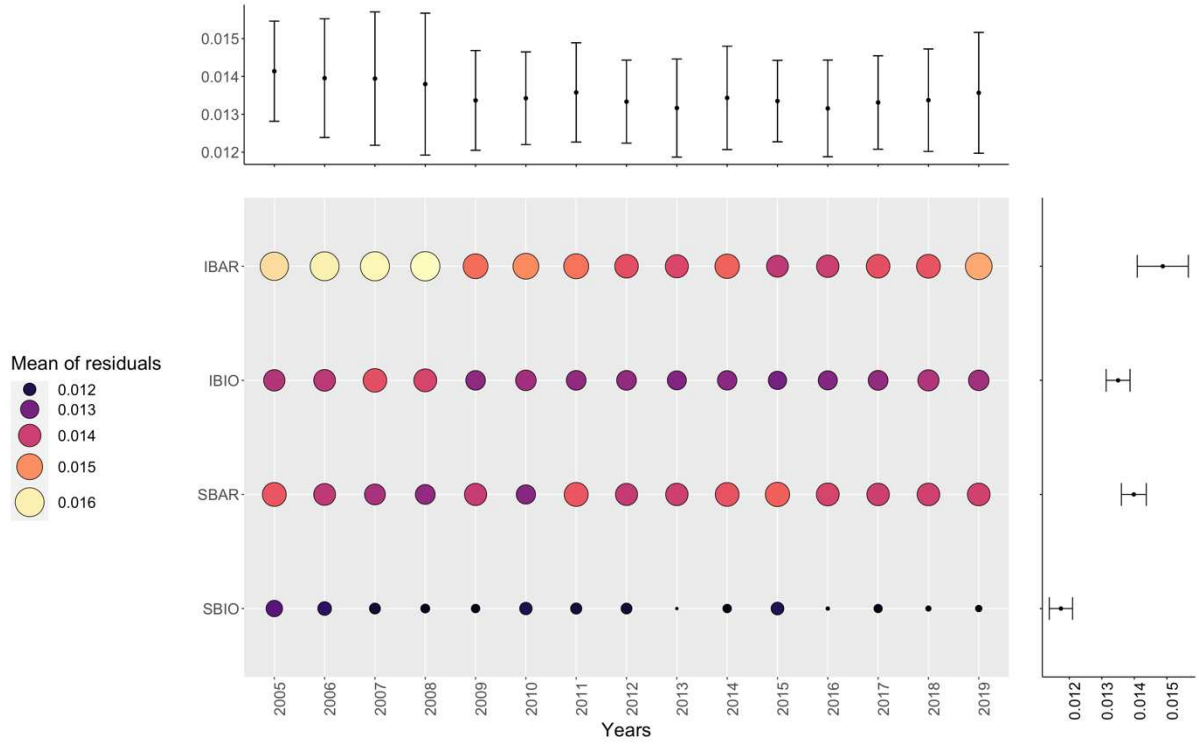


FIGURE 4: RDA models residual means for each year and habitat combination (IBAR = intertidal bare habitat, IBIO = intertidal biogenic habitat, SBAR = subtidal bare habitat, SBIO = subtidal biogenic habitat). Marginal plots represent marginal mean (point) +/- marginal standard deviation (whiskers).

When adding spatial and temporal predictors (i.e., spatial linear trend, spatial dbMEMs, and temporal dbMEMs) as explanatory variables in the models (on top of the variables describing environmental conditions and anthropogenic pressures), explanatory power reached more than 50% (adjusted R^2) in each habitat (from 53.4% in IBAR to 64% in IBIO; Figure 5). In hierarchical partitioning, each group of explanatory variables had different individual contributions to the global models: anthropogenic pressure proxy matrix and environmental matrix had higher individual contributions in each habitat, followed by the multi-scale spatial structures (spatial dbMEMs), the linear spatial trend and the temporal structure variables (temporal dbMEMs). The latter was not significant in simple RDA, contrary to the fraction explained by spatial dbMEMs, suggesting that temporal dynamics are not significantly structured in time and that they are of minor extent compared to the spatial variation of communities (Appendix 4). Overall, most of the spatial and temporal structure in the variation and dynamics of the communities was well described by the environmental and anthropogenic predictors, as indicated by the very low individual contribution of spatial and temporal dbMEMs (< 2.5% for both). Nonetheless, the partial RDAs indicated that there were still significant spatial and temporal structures unexplained by these variables (Appendix 4). Notably, the fraction explained by temporal dbMEMs became significant in partial RDA (Appendix 4) and explained a higher proportion of variance than the unique fraction explained by the spatial predictors (Figure 5), suggesting that the environmental and anthropogenic variables mostly captured spatial signals. This was illustrated by the amount of explained variation cumulatively represented by the fractions shared by the spatial predictors with either the environmental variables, the proxies of anthropogenic pressures, or both (Figure 5). There were however important differences between bare and biogenic habitats in how these different shared fractions contributed to the total explained variation, meaning that the spatial signals captured by the anthropogenic and environmental variables differed between these two habitat types. Finally, a high proportion of community variation was explained by the shared fraction between the anthropogenic and environmental variables (i.e., abiotic matrix) alone, representing the effects of these variables that are not spatially or temporally structured. The latter is higher in biogenic habitats compared to bare ones. However, the fraction unique to anthropogenic variables and the one unique to environmental ones show the opposite pattern, being higher in bare habitats compared to biogenic ones. Hence, the amount of variation explained by anthropogenic and environmental variables that is not spatially or temporally structured seems fairly equivalent across habitats.

Habitat	Total explained variation (%)	Significance
IBAR	53.2	***
IBIO	64.0	***
SBAR	59.5	***
SBIO	56.4	***

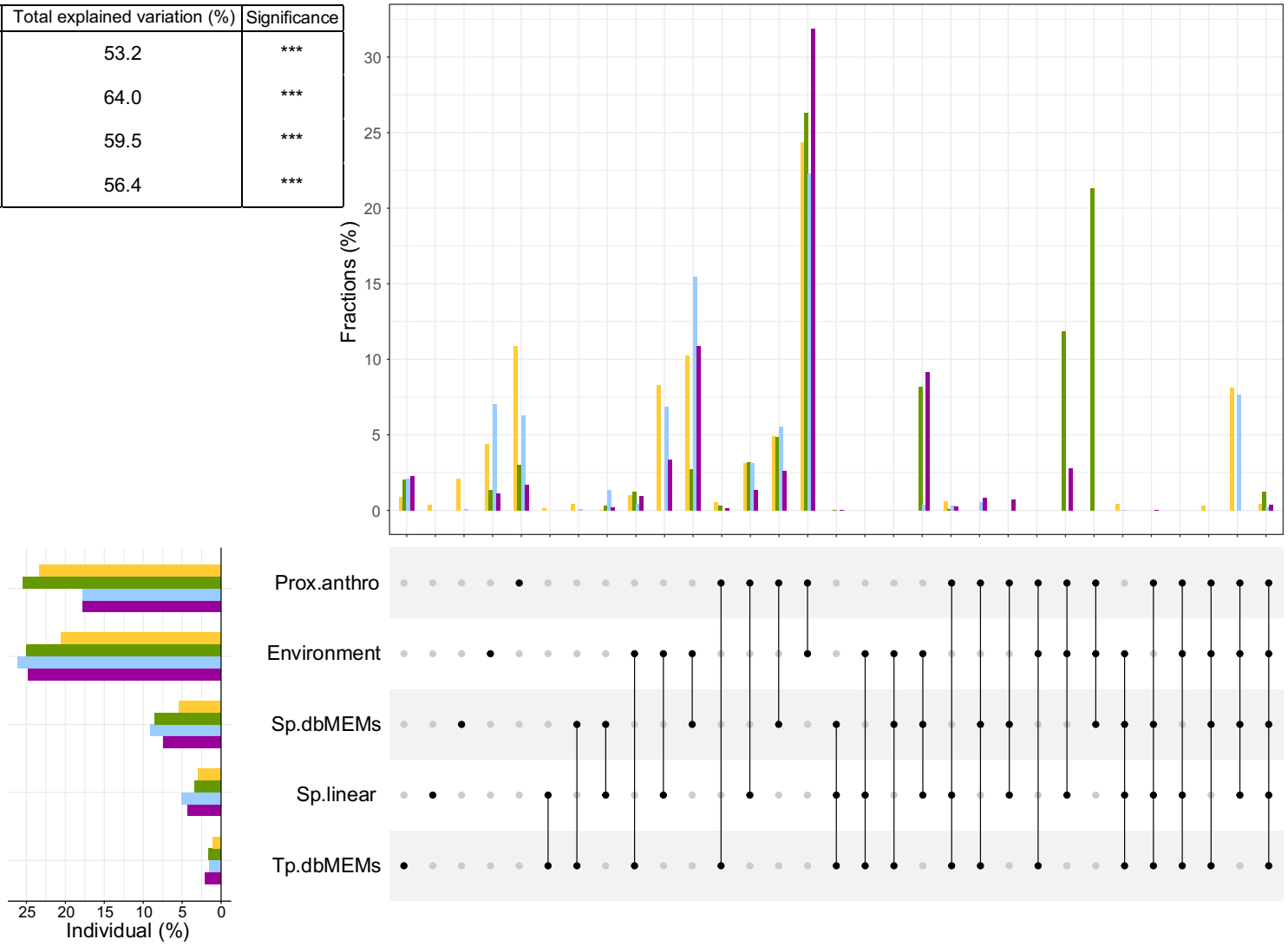


FIGURE 5: Variation and hierarchical partitioning between the community matrix and each explanatory matrix within each habitat (IBAR = intertidal bare habitat, IBIO = intertidal biogenic habitat, SBAR = subtidal bare habitat, SBIO = subtidal biogenic habitat). The top left table gives the total explained variation and significance of the global RDA models in each habitat (*** = $p < 0.001$). The barplot on the bottom left shows the individual contribution of each explanatory matrix assessed by hierarchical partitioning. The plot on top represents the percentage of variation (adjusted R^2) explained by the different matrices in variation partitioning (fractions < 0 are not represented). The lower panel indicates the matrices taken into account as explanatory (black dots) or conditional (grey dots).

4. Discussion

4.1. Efficiency of abiotic variables in explaining spatial and temporal β diversity

As already demonstrated in marine ecosystems (Soininen 2014), hierarchical and variation partitioning showed that abiotic variables explained the highest proportion of β diversity, with low amount of community variation that is structured in space and time but not related to abiotic changes. The RDA models with the selected abiotic variables explained from 49.4% to 61.6% of the β diversity in the four habitats. In the same study area, Dutertre et al. (2013) showed that environmental variables explained 51% of the β diversity of subtidal soft sediments while Quillien et al. (2015) obtained models explaining from 15% to 72% of community variations in intertidal sandy beaches. Likewise, in intertidal seagrasses communities, environmental variables explained 9% to 76% of β diversity in northern New Zealand (using Canonical Correspondence Analysis - CCA; Turner et al. 1999), and up to 25.6% in the northern Baltic Sea (using RDA; Boström et al. 2006). In Northeast Brazil, CCA between environmental variables and benthic invertebrate community explained 30% of the total variance (Costa et al. 2021). All reported values are adjusted R^2 except for CCA for which it does not exist. These studies did not use the exact same set of environmental variables and did not incorporate proxies of anthropogenic pressures, thus the proportions of explained variations are not fully comparable but give an idea of the variety of results obtained in the same habitats and in different areas. Moreover, CCA preserves the χ^2 distance that gives a high weight to rare species. Still, while this variability may bear some methodological imprints, it may also be representative of meaningful variation in the ecological processes governing benthic communities across different habitats (Boyé et al. 2019), across different locations (Watt and Scrosati 2013) and across different scales (Turner et al. 1999; Chase et al. 2018). We discuss below some of the ecological factors that can explain these variations and try to delineate the main drivers of community changes in benthic ecosystems.

4.2. Role of natural and anthropogenic factors

Nearly all studies that explored the main sources of community variation in marine ecosystems before, including the meta-analyses from Cottenie (2005) and Soininen (2014) only took into account environmental variables and did not include proxies of anthropogenic pressures. Here, hierarchical partitioning showed that environmental variables had the highest individual importance in explaining community β diversity. In particular, hydrodynamics and grain-size distribution variables played an important role in communities β diversity. Sediment

characteristics are a determining factor that control the presence and abundance of soft-bottom fauna as each species can tolerate a specific sediment particle range (Snelgrove and Butman 1994) and hydrodynamics can alter these sedimentary environments, thus these variables have often been demonstrated to be important drivers of macrofauna β diversity (Gray 2002; Hily et al. 2008; Dutertre et al. 2013; Veiga et al. 2017; Couce et al. 2020).

Nonetheless, in terms of explanatory power, environmental variables were followed by proxies of anthropogenic pressures. In his thesis, Boyé (2018) conducted similar analyses on the same habitats, using a dataset partially overlapping with the one used here, but without incorporating proxies of anthropogenic pressures, and his models showed lower percentage of explained variance compared to ours (40% to 60% for his global models *versus* 53% to 64% in ours). This highlights the importance of understanding and accounting for the spatial and temporal distribution of anthropogenic pressures (e.g., Burrows et al. 2014; Halpern et al. 2015) to explain and accurately predict the current distribution of benthic species and communities., especially for ecosystems under such high anthropogenic pressures (Korpinen et al. 2021).

The individual importance of proxies of anthropogenic pressures was higher in the intertidal zone. These pressures were surely better characterized for intertidal habitats since we used land data and we estimated the values for the subtidal sites from the values of the closest intertidal ones (see Appendix 1). Moreover, it is also very likely that the effect of anthropogenic pressures would be more mitigated in the subtidal zone (Bacouillard et al. 2020). Among the proxies of anthropogenic pressures, fishing pressures explained a high proportion of variance in simple RDAs. However, part of that explained variance could also be explained by other variables in IBIO, SBAR and SBIO, as shown by the reduced amount of variance it explained in the partial RDAs. Thus, some factors may confound the perceived effect of fishing pressures: as fishing depends on the species present in the communities and because the sites were dominated by different taxa, the amount of variation explained by the fishing variables could be linked to the fact that they reflect the spatial variation of the different sites' communities. For instance, professional fishing is associated with sites dominated by *Donax spp.* in IBAR (Figure 2). Alternatively, specific environmental conditions could be favorable or detrimental to fishing activities or the targeted taxa: for example, *Donax vittatus* is characteristic of wave exposed sandy bottoms (Allen and Moore 1987). Yet, fishing can have a direct impact on the fauna (e.g., by increasing mortality of certain species, favoring other species by reducing predation etc.) and also indirect ones by modifying habitat characteristics (e.g., sediment resuspension, habitat destruction etc.) (Hall-Spencer and Moore 2000; Hily et al. 2008; Sciberras et al. 2018). These effects may overlap/correlate and/or combined with natural

stressors (Bowler et al. 2020; Stockbridge et al. 2020), which could explain their shared fraction of explained variance.

Overall, the environmental variables and proxies of anthropogenic pressures seemed, in variation partitioning, to be highly correlated and they also appeared to be spatially structured. This spatial structure can be explained by the fact that proxies of anthropogenic pressures do not present temporal variation (Table 1; Appendix 1) and that, at the scale of the study area, the spatial variation of environmental variables can be more important than the temporal variations (e.g., see Appendices of Chapter I). Moreover, as developed above for fishing pressure, this may indicate that human activities are located where particular types of environments are more favorable to human activities, or that environment and anthropogenic pressures might have a combined effect on macrofauna communities. Interestingly however, in IBAR the high proportion of variance explained by recreational fishing (RF) or professional fishing (PF) explained some aspects of community variation that were not explained by other variables (high R^2 in partial RDAs). Other proxies of anthropogenic pressures (artificial surfaces, agricultural areas and number and inhabitants) also stood out as important in partial RDAs, in the bare habitats especially. These proxies, that can characterize pollution, eutrophication or human use of the different sites, have therefore distinct signatures on the community variation across this region. Watersheds with urban and industrial development have already been demonstrated to alter hydrodynamics processes, to have an impact on the levels of chemical contaminants and to increase the severity and frequency of hypoxia episodes in tidal creeks where macrobenthic species were characterized by a low richness and abundances (Lerberg et al. 2000).

4.3. Role of biogenic habitats

While total explained variation was similar in all habitats, abiotic variables explained higher proportions of variance in IBIO (61.6%) than in IBAR (49.4%). This was unexpected and contradicts our hypotheses that biogenic habitats could mitigate the effect of environmental conditions (e.g., Peterson et al. 2004; Maxwell et al. 2017). However, results were consistent with this hypothesis in the subtidal zone with 56% of β diversity explained by abiotic variables in SBAR *versus* 53.8% in SBIO. Biogenic habitats mostly mitigate the effect of extreme events but not of average spatial variation *per se* (Jurgens and Gaylord 2018; Jurgens et al. 2022). The highly dynamic nature of intertidal habitats is only partially characterized by our environmental variables that summarize average variation of climatological conditions (but not extreme events or annual/seasonal variability). By mitigating extreme events, IBIO may lead to more

predictable communities given our dataset, while in IBAR, different timing of disturbances across sites may blur the relationship with our set of abiotic variables. Indeed, less disturbed communities are more likely to show signs of deterministic niche processes than communities frequently disturbed by extreme events, which are more prone to appear as stochastic or neutral (Bracewell et al. 2017).

Moreover, in IBIO we also used biotic environmental explanatory variables that described the morphology of the foundation species (i.e., shoot density and leaf widths of *Zostera marina*). These variables have been shown to influence the density and diversity of benthic macrofauna in seagrass meadows (Boström and Bonsdorff 2000; Hovel et al. 2002; Bouma et al. 2009a). This suggests that taking into account habitat complexity variables might improve the quality of the model and better describe macrobenthic community variation, except if these variables are collinear with abiotic ones. Habitat complexity of maerl beds monitored in Brittany is currently being investigated and quantified (Jardim et al. 2022) and we hope to verify this hypothesis in future work, especially in long-term series, as rhodolith morphologies can affect macrofauna community structure as well (Berlandi et al. 2012; Solano-Barquero et al. 2022).

Usually, the spatial linear trend and the spatial dbMEMs are not collinear as they should model different spatial structures (Legendre and Legendre 2012). However, we decided to characterize the linear trend as a distance from the northern to the southern site along the coast in the different habitats and this spatial structure was often capture by one dbMEM especially in the biogenic habitats (Appendices 2 and 3). Along the coasts of Brittany, different water bodies follow one another and have different physico-chemical properties (Morice et al. 2020). This environmental gradient might influence the presence of different morphological types of the two biogenic habitats (Boyé et al. 2021; Jardim et al. 2022) and by cascading effects, the community that live in. The shared fraction between abiotic and habitat complexity variables therefore represents both indirect effect of environmental conditions, mediated by changes in foundation species, and potential interaction between abiotic variables and foundation species (e.g, Watt and Scrosati, 2013). However, these direct and indirect effects remain largely unexplored and are hard to disentangle (Miller et al. 2018). More studies are needed to clarify the intricate mechanisms linking the environmental conditions, to biogenic habitats and to their associated fauna, which are currently lumped together in the shared fraction of our variation partitioning.

4.4. Potential drivers of unexplained community variation

Residual fraction of community variation can be due to environmental or more likely biotic factors not included in the analysis, historical events or random variation (Legendre and Legendre 2012). Space and time had no important individual effect compared to the environment and proxies of anthropogenic pressures. Time had the lowest individual importance, still in variation partitioning the unique fraction of time was significant (Appendix 4). This fraction can be interpreted as neutral drift in the communities, which means variation in species demography caused by random reproduction and survival of individuals due to species interactions (e.g, competition, predator-prey interactions, etc.) (Legendre and Gauthier 2014). However, in our study the spatial structure clearly dwarfed temporal variations.

Most of the spatial variation of communities was capture by our set of abiotic variables according to the explained variance attributed to the shared fractions of abiotic and spatial variables. Yet, only two positive dbMEMs were generated to model positive spatial correlations. This was surely due to the fact that the sites within each habitat are quite far from each other, thus the threshold used to generate the dbMEMs was high (Legendre and Gauthier 2014). Therefore, the spatial dbMEMs only achieved to model large scaled spatial structures, and fine scale structures (which represent spatial correlation produced by neutral biotic processes such as ecological drift or random dispersal), were missed and could not be modeled in the spatial fraction (Borcard et al. 2018).

Analyzing the residuals of RDA models with only abiotic variables allowed to evaluate to what extent simple RDAs failed to explain the community variation, on average for each year and habitat. In IBAR, the model was less successful in characterizing β diversity during the first four years of the monitoring (2005-2008), especially in 2008 which seems to show the highest values of residuals. Interestingly, in March 2008 a high energy storm hit the French Atlantic coast and the western part of the English Channel which resulted in morphological changes and transport of intertidal bare sediment in the region (Fichaut and Suanez 2011). Such extreme modifications of beach morphodynamics are known to have deep impacts on macrofaunal communities (Harris et al. 2011). This supports the hypothesis that our models did not adequately capture the effects of extreme events on the communities. Although we tried to take into account the variability of the temporally varying environmental variables by computing the minimum, maximum and standard deviation of their values during the months preceding the sampling dates, we may not have properly characterized extreme events of short duration that could have impacted the communities. Moreover, drivers of macrobenthos dynamics acting at larger spatial scales such as the North Atlantic Oscillation (NAO) or the Atlantic

Multidecadal Oscillation (AMO) were not taken into account in our models and might have improved our capacity to model the temporal variability of the communities (Drinkwater et al. 2003; Nye et al. 2014). Even though the residual values were slightly higher during the first four years of the time series in IBIO, they did not show a variability as observed in IBAR. In the subtidal zone, residuals were also lower in SBIO compared to SBAR. Again, this supports the hypothesis that biogenic habitats may mitigate the effect of environmental variables, especially in extreme physical environments as the intertidal zone (Crain and Bertness 2006).

5. Conclusion and perspectives

This study was based on a new method coupling hierarchical partitioning and variation partitioning and using more than four explanatory fractions mixing environment, proxies of anthropogenic pressures, space and time, used for the first time on benthic macrofauna. It took into account proxies of anthropogenic pressures acquired with an original method and which have demonstrated their efficiency in the analyses, suggesting the importance to characterize and integrate these variables in studies on the drivers of benthic macrofauna β diversity.

As already demonstrated in marine systems, abiotic variables explained a more important proportion of benthic macrofauna β diversity than space and time, even within a given habitat. However, proxies of anthropogenic pressures are rarely included in the explanatory variables, as well as space and time conjointly. The individual effect of anthropogenic pressure proxies was at least equivalent to the environment fraction in the intertidal. Fishing pressure had a very strong explanatory power in beaches (IBAR), more than in the other three habitats. In addition, biogenic habitats seemed to mitigate the effect of the environment, more so in exposed areas as the intertidal zone. This study suggested that taking into account variables describing habitat physical complexity (such as morphological and structural traits of *Zostera marina* here) could better explain patterns of β diversity and thus account for the indirect effect of the environment on β diversity *via* variations in habitat structure.

Fully disentangling the joint effects of space, environment, and anthropogenic activities would require experimental analyses or direct measurement of pressures. This study shows that intertidal habitats, and in particular sandy beaches, are sensitive to anthropogenic pressures, which could be taken into account in conservation measures. Evaluating and comparing the importance of different anthropogenic pressures between habitats could allow us to evaluate the sensitivity of each one and to take balanced management measures according to the stakes of each habitat (diversity and functionality). The proxies of anthropogenic pressures that were

used here varied only spatially and not temporally, quantifying them over time would allow a better understanding of their interactions with environmental pressures and their synchrony or asynchrony.

Appendices

Appendix 1: The protocols, numerical model products and techniques used to extract and calculate each of the explanatory variables are detailed below.

- Distance between sites

Distances among sites were calculated as the shortest paths along the coast using the *gdistance* R package (Etten 2017). This calculation relied on a transition layer that was built on a 100 m resolution raster constructed from polygon layer made available by OpenStreetMap (http://openstreetmapdata.com/data/land-polygons). Land polygons were modified to correct for invalid polygons using the *rgeos* R package (Bivand et al. 2021).

- Grain-size distribution

In each habitat, an additional sediment core was collected at each point for grain size distribution and organic matter content assessment. Sediment samples were dried in an oven (48h at 60°C), weighed, rinsed on a 63 µm sieve, dried (48 h at 60°C) and weighed again, then passed through sieve columns. This protocol allowed to separate the sediment into 15 fractions (<63 µm, 63-80, 80-100, 100-125, 125-160, 160-200, 200-315, 315-500, 500-800, 800-1250, 1250-2000, 2000-3150, 3150-5000, 5000-10000 and >10000 µm) whose masses were measured. Since the protocols have evolved during the time series (fractions were not the same as those described above in SBAR before 2015 and in IBAR and IBIO in 2004 and 2005), we decided to merge some fractions in order to homogenize the data as much as possible to allow a comparison between habitats. As a result, the following fractions were used for the calculation of granulometric indices: < 63 µm, 63-125, 125-500, 500-2000, > 2000 µm.

These data were used to calculate the following summary indices using the "G2Sd" R package (Fournier et al. 2014):

- Mean of the grain-size distribution (logarithmic Folk and Ward method, µm scale)
- Median of the grain-size distribution (logarithmic Folk and Ward method, µm scale)
- Trask or Sorting index defined as $\frac{D25}{D75}$ with D25 the 25th percentile and D75 the 75th percentile of the grain-size distribution
- Kurtosis of the grain-size distribution (logarithmic Folk and Ward method, µm scale).

Lastly, fractions were grouped into gravels (> 2 mm), sand (63 µm to 2 mm) and mud (< 63 µm) (Fournier et al. 2014).

Finally, the percentage of organic matter was estimated by mass loss after combustion at 450°C for 5 hours.

Values at the site level were estimated by averaging data from the three points within each site.

Overall, 8% of observations contained missing values in the intertidal habitats in total and 10% in the subtidal habitats in total. Missing values were imputed using k-Nearest neighbor imputation with the median value of the 5 closest neighbors based on Gower distance computed on the matrix containing: the remaining sedimentary variables (i.e., grain-size distribution data), hydrodynamics data (current velocity, fetch and depth, the latter only for the subtidal habitats), as well as two variables containing the identity of site and year of the samples. This imputation procedure was performed for the two tidal zones separately. This procedure was done using the *kNN* function of the "VIM" R package (Kowarik and Templ 2016).

- *Zostera marina* morphological and structural traits

In IBIO, at each of the 3 points, all *Zostera marina* shoots in two 0.05 m^2 quadrats (except in 2016 and 2017 where two 0.1 m^2 quadrats were used, without visible impacts on the time series) were collected to measure densities (shoot.m^{-2}), leaves (precisely leaves and sheaths) and roots (rhizomes) biomasses (g.m^{-2}), and describe each shoot's morphology with measures of sheath height (mm), leaves length (mm) and width (mm), as well as the number of leaves per shoot and broken leaves.

Sheath height was measured from the first node to the separation mark of the leaves. The length of each leaf was measured from the first node to the apex. The number of broken leaves was counted and expressed as a percentage of the total number of leaves found in each quadrat. One leaf of median length was used to estimate the leaf width for each shoot. Leaves and roots biomasses were estimated as dry weight after 48 hours desiccation at 60°C for each quadrat. The detailed protocol of the biometric measurements can be found in Auby et al. (2018).

Total *Zostera marina* leaves and roots biomasses and densities were scaled up and expressed per square meter for the two quadrats. Data were estimated at the point level by averaging the data from the two quadrats. Values were estimated at the site level by averaging the data from the three points within each site.

Overall, between 2 and 4 values were missing depending on the variable. They were imputed by k-Nearest neighbor imputation using the median value of the 5 closest neighbors based on Gower distance. This imputation procedure was performed using the matrix containing the identity of the site and year of the samples along with the remaining biometric

data. This procedure was done using the *kNN* function of the "VIM" R package (Kowarik and Templ 2016)

- Hydrology

Daily mean bottom temperature (°C), current velocity ($m.s^{-1}$) and salinity (psu) were extracted and computed from the ocean physic Multi-Year product IBI_REANALYSIS_PHYS_005_002 (Sotillo et al. 2015), downloaded from the E.U. Copernicus Marine Service platform (https://marine.copernicus.eu/) in September 2020 (note that products are regularly updated, see product improvements pages http://marine.copernicus.eu/services-portfolio/product-improvements). This product is defined on a standard grid at 1/12° (~ 6-9 km), 50 vertical levels for mean daily and monthly values and only surface levels for hourly values.

Data were extracted and averaged in a buffer of radius equivalent to the resolution of the model around each point. For points where no model cell intersected the buffer, the radius of the buffer was changed to a radius equivalent to the resolution of the model plus the minimum distance of the point to the closest model cell.

Bottom temperature (°C) is the daily mean seafloor potential temperature (only defined on one layer). Salinity (psu) was computed from the daily mean salinity averaged on all the vertical levels of the model (i.e., over the entire water column). Current velocity ($m.s^{-1}$) was extracted from the hourly (with the same spatial resolution) in order to properly account for tidal currents. However, those were only available. for the surface layer. Thus, current velocity was computed using the hourly eastward (uo) and northward (vo) velocities at the surface level: hourly current velocities were obtained using the formula $\sqrt{uo^2 + vo^2}$, then daily mean current velocity was obtained by averaging hourly current velocities of the day considered.

Data values were estimated at the site level by averaging the data from the points at each site.

- Meteorology

For the intertidal habitats, daily mean air temperature (°C) and wind velocity ($m.s^{-1}$), daily total rainfall (mm), minimum daily air temperature (°C), maximum daily air temperature (°C), and daily air temperature range (°C) were extracted and computed from the SIM2 model of Météo-France (Le Moigne et al. 2020). This product is defined at an 8 km grid resolution.

Data were extracted and averaged in a buffer of radius equivalent to the resolution of the model around each point. For points where no model cell intersected the buffer, the radius of

the buffer was changed to a radius equivalent to the resolution of the model plus the minimum distance of the point to the closest model cell.

Daily air temperature range (°C) was computed by subtracting the minimum daily air temperature to the maximum daily air temperature.

Values were estimated at the site level by averaging the data from the three points within each site.

- Fetch

Fetch was calculated using land polygon data made available by OpenStreetMap (http://openstreetmapdata.com/data/land-polygons) and an archive of the "fetchR" R package (because it is no longer available on CRAN) downloaded at https://cran.r-project.org/src/contrib/Archive/fetchR/fetchR_2.1-1.tar.gz. Land polygons were modified to correct for invalid polygons using the "rgeos" R package (Bivand et al. 2021). The average wind fetch, referred to as 'fetch', was calculated in kilometers as the average length of nine radiating fetch segments (one every 10 degrees) with a maximum distance for any fetch segment set to 300 km. Values were estimated at the site level by averaging the values from the three points within each site.

- Depth

For the subtidal habitats, bathymetric data were retrieved from the EMODnet Digital Terrain Model (DTM) with a grid resolution of 1/16 * 1/16 arc minutes (circa 115 * 115 meters) (EMODnet Bathymetry Consortium 2018). Data were extracted and averaged in a buffer of radius equivalent to the resolution of the model around each point. Values were estimated at the site level by averaging the values from the three points within each site.

- Population

For the intertidal habitats, the number of inhabitants in buffers of 2 km radius around each point were estimated using a shapefile layer of the administrative division of French communes made available by OpenStreetmap at https://www.data.gouv.fr/fr/datasets/decoupage-administratif-communal-francais-issu-d-openstreetmap/, merged with population density (inhabitants/km^2) of these communes retrieved from the Insee (Institut national de la statistique et des études économiques) censuses of 2007, 2012 and 2017 downloaded from l'Observatoire des territoires (https://www.observatoire-des-territoires.gouv.fr/). The radius value of 2 km was set arbitrarily and chosen to take into account the effect of the local population without

overestimating this value for islands for example, where larger buffers could have intercepted communes from the opposite land. Data were downloaded in September 2020 and the 2020 communes' nomenclature was used. Because the number of inhabitants changed very little between the 3 selected years, the choice was made to keep only the average of the number of inhabitants of these three years to characterize the points.

Values were estimated at the site level by averaging the data from the three points within each site and they were then log transformed to make the data distribution more symmetrical. Values for subtidal sites were inferred to be the same as those from the nearest intertidal site.

- Land use

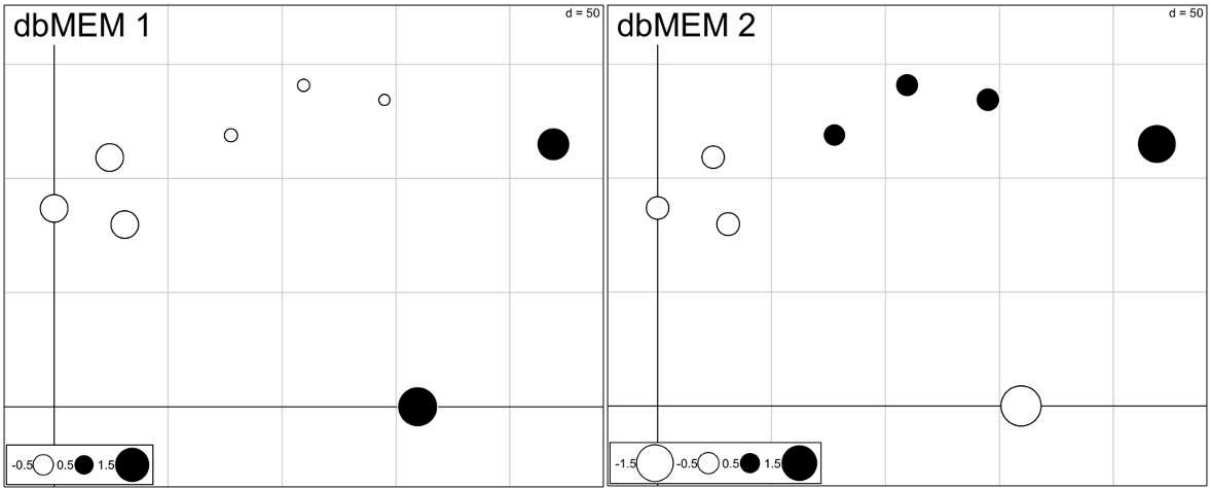
For the intertidal habitats, we computed the surfaces (km^2) covered by artificial surfaces and agricultural areas in 10 km radius buffers around points and in watersheds in the vicinity of points. This 10 km radius value was set arbitrarily and chosen so that buffers can intercept adjacent watersheds. Land use data came from the CORINE Land Cover (CLC) database available at https://www.statistiques.developpement-durable.gouv.fr/corine-land-cover-0. The shapefiles were downloaded in September 2020, the CLC database was available for the years 1990, 2000, 2006 and 2012. We used the 2006 and 2012 data as they are those covered by our time series. We focused on the artificial surfaces and agricultural areas according to the CLC level 1 nomenclature. We downloaded a shapefile layer of Brittany divided into watersheds available at https://www.data.gouv.fr/fr/datasets/bassins-versants-de-bretagne/. Finally, we used raster files from the BD ALTI® DTM which is a gridded digital terrain model that describes the shape and normal altitude of the ground surface. We used the 75 m resolution grid. Files were made available by the Institut national de l'information géographique et forestière (IGN-F) (http://www.ign.fr/).

The assumption was that watersheds with the lowest elevation points falling within the 10 km buffers around the points could discharge near them. We calculated the surface (km^2) covered by artificial surfaces and agricultural areas in the buffers and if the lowest elevation point of a watershed was falling within the buffer, the surfaces covered by artificial surfaces and agricultural areas in the watershed were added. Since the computed surfaces were relatively stable between 2006 and 2012, the choice was made to keep only the average of the values between these two years to characterize the points. Values for subtidal sites were inferred to be the same as those from the nearest intertidal site.

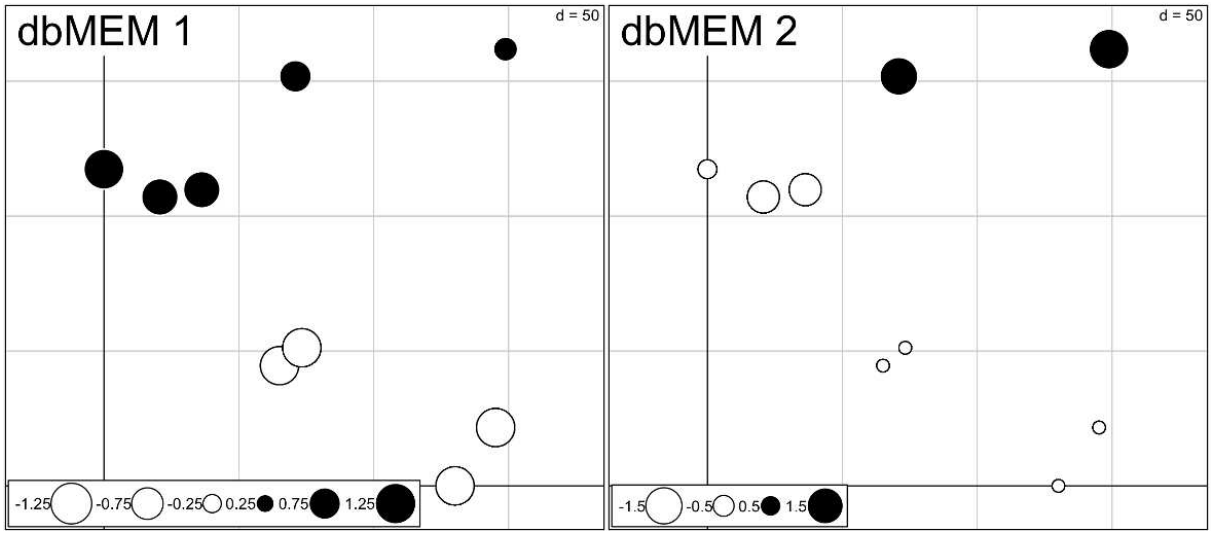
- Fishing pressure

Fishing pressure was characterized by expert opinion for each site in a semi-quantitative way ('No', 'Low', 'High') according to the intensity of fishing carried out in each of the habitats (recreational and professional fishing in IBAR, recreational fishing in IBIO, professional fishing in SBAR and dredging in SBIO).

All numerical analyses were conducted with the R programming language version 4.1.2 (R Core Team 2021). Spatial analyses were conducted with the R packages "raster" (Hijmans et al. 2022), "sf" (Pebesma 2018), "sp" (Pebesma and Bivand 2005; Bivand et al. 2013), "maptools" (Bivand et al. 2022) or on the QGIS3.14 software (QGIS Development Team 2022).



Appendix 2: Distance-based Moran's Eigen Vector Maps (dbMEM) in the intertidal biogenic habitat (IBIO) representing positive spatial correlation. Black circles correspond to positive values in each eigenvector while white circles correspond to negative values. The position of the circles represents their spatial coordinates along the coasts of Brittany while their size is proportional to the absolute value of their position along each eigenvector.



Appendix 3: Distance-based Moran's Eigen Vector Maps (dbMEM) in the subtidal biogenic habitat (SBIO) representing positive spatial correlation. Black circles correspond to positive values in each eigenvector while white circles correspond to negative values. The position of the circles represents their spatial coordinates along the coasts of Brittany while their size is proportional to the absolute value of their position along each eigenvector.

Appendix 4: Adjusted R^2 and p-value of the simple RDA (without all other variables as conditions) or partial RDA (with all other variables as conditions) models for each fraction within each habitat (IBAR = intertidal bare habitat, IBIO = intertidal biogenic habitat, SBAR = subtidal bare habitat, SBIO = subtidal biogenic habitat). "Space" represents the spatial dbMEMs and the spatial linear trend taken together.

Habitat	Simple RDA				Partial RDA			
	Time	Space	Environment	Prox.anthro	Time	Space	Environment	Prox.anthro
IBAR	R^2 = 0.003 p = 0.298	R^2 = 0.129 p = 0.001	R^2 = 0.331 p = 0.001	R^2 = 0.338 p = 0.001	R^2 = 0.009 p = 0.001	R^2 = 0.025 p = 0.001	R^2 = 0.044 p = 0.001	R^2 = 0.109 p = 0.001
IBIO	R^2 = 0.000 p = 0.500	R^2 = 0.317 p = 0.001	R^2 = 0.530 p = 0.001	R^2 = 0.488 p = 0.001	R^2 = 0.020 p = 0.001	R^2 = 0.003 p = 0.001	R^2 = 0.013 p = 0.001	R^2 = 0.030 p = 0.001
SBAR	R^2 = 0.000 p = 0.513	R^2 = 0.228 p = 0.001	R^2 = 0.435 p = 0.001	R^2 = 0.271 p = 0.001	R^2 = 0.021 p = 0.001	R^2 = 0.014 p = 0.001	R^2 = 0.070 p = 0.001	R^2 = 0.063 p = 0.001
SBIO	R^2 = 0.007 p = 0.167	R^2 = 0.200 p = 0.001	R^2 = 0.462 p = 0.001	R^2 = 0.296 p = 0.001	R^2 = 0.023 p = 0.001	R^2 = 0.002 p = 0.042	R^2 = 0.001 p = 0.001	R^2 = 0.017 p = 0.001

Chapter III

Résumé en français

Ce chapitre, dont le contenu a fait l'objet d'une note acceptée dans la revue Marine Ecology Progress Series, est une étude méthodologique intermédiaire visant à évaluer si un sous-ensemble de la communauté de macrofaune benthique pourrait suffire pour évaluer la dynamique de l'ensemble de la communauté dans chacun des habitats (i.e., substitution taxonomique). Elle vise également à tester si la CTA est un outil efficace pour évaluer ce type de questionnement dans le cadre des séries à long-terme. L'efficacité de la substitution a été peu testée dans les études de surveillance à long-terme. La surveillance à long-terme des systèmes marins est coûteuse, prend du temps et nécessite une expertise fine pour identifier les taxons présents. La substitution taxonomique apparait comme une aide pour surmonter ces problèmes et refléter avec précision les caractéristiques des communautés. Nous avons testé ici l'efficacité de sous-ensembles de taxons (Polychètes, Crustacés et Mollusques) pour résumer la dynamique de l'ensemble de la communauté de macrofaune benthique, sur le long-terme, dans les quatre différents habitats côtiers étudiés. Ici, nous avons utilisé 13 années (2007-2019) de données issues du suivi de la macrofaune benthique acquises dans le cadre du REBENT, couvrant un total de 32 sites dans les quatre habitats. Nous avons utilisé la CTA afin de comparer, grâce à une méthode de corrélation multidimensionnelle, les géométries des trajectoires. Cela a permis de tester les similitudes entre la dynamique globale de la communauté, la dynamique des sous-ensembles de taxons et la dynamique des taxons restants (i.e., toute la communauté amputée du sous-ensemble étudié) dans chacun des habitats. Les résultats ont montré que le sous-ensemble des Polychètes reflétait le mieux la diversité spatiale des différents sites. Au niveau de la dynamique temporelle, les différences entre les sous-ensembles étaient moins marquées mais les polychètes apparaissaient toutefois comme le meilleur sous-ensemble apte à traduire la dynamique temporelle de la communauté globale, avec une efficacité supérieure dans les habitats biogéniques par rapport aux habitats nus.

Taxonomic surrogates for long-term macrobenthic community monitoring: an application with Community Trajectory Analysis

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Abstract

Biodiversity monitoring, essential to detect impacts of natural and anthropogenic changes on marine ecosystems is costly, time-consuming, and requires high taxonomic expertise. Taxonomic surrogacy might be a solution to overcome these problems and accurately reflect species-level community patterns, but its efficiency has mainly been assessed as taxonomic sufficiency and rarely from long-term monitoring data. Here, the efficiency of subset-taxa (i.e., Polychaeta, Crustacea, and Mollusca) for summarizing long-term community dynamics was tested in different coastal habitats. The dataset came from a yearly long-term macrobenthic monitoring program (2007-2019) in Western France, in two biogenic and two bare habitats. Community Trajectory Analysis (CTA), a statistical approach allowing for quantitative measures and comparisons of temporal trajectories, was used to test for similitudes between overall community, subset-taxa, and non-subset-taxa dynamics. Polychaeta best reflected the spatial diversity of the different sites as well as the temporal dynamics of the non-Polychaeta species, with more efficiency in biogenic compared to bare habitats. Our study confirmed that subset-taxa may reflect long-term benthic habitat dynamics and that CTA is an effective tool to test their efficiency.

1. Introduction

With current anthropogenically-driven changes, long-term biodiversity monitoring becomes essential to detect changes in ecosystem structure and functioning (Dornelas et al. 2013). Biodiversity is mostly monitored through species-level morphological identification of organisms, a costly time-consuming task requiring high taxonomic expertise (Olsgard and Somerfield 2000; Wodarska-Kowalczuk and Kedra 2007). Biodiversity surrogates can help overcome these difficulties: more readily estimated, they might strongly correlate with species richness and reflect species-level community patterns consistently (Olsgard and Somerfield 2000). Different types of surrogates exist: a higher taxon as a surrogate for a lower taxonomic level one (higher-taxa), a taxon for another of the same taxonomic level (cross-taxa) and a taxon for the entire target community (subset-taxa) (Mellin et al. 2011).

For soft-bottom macrofauna, commonly used to assess anthropogenic impacts or environmental changes in coastal marine ecosystems, the relevance of taxonomic surrogacy to address changes in community composition and structure has already been evaluated, frequently over gradients of pollution or disturbances (Olsgard and Somerfield 2000; Kokesh et al. 2022). However, most studies analysed the efficiency of higher-taxa rather than other surrogates (Bevilacqua et al. 2012), and scarcely in the context of long-term monitoring (but see Pitacco et al. 2019). The few studies focusing on long-term series relied on methods not explicitly designed for temporal dynamics (e.g., Kokesh et al. 2022). The most investigated subset-taxa were Polychaeta, Crustacea, Mollusca and Echinodermata, generally the most diverse and abundant taxonomic groups in soft-bottom communities. Polychaeta were frequently found to be the most reliable subset-taxa (Olsgard et al. 2003; Kokesh et al. 2022). However, for long-term monitoring, little attention has been given to the assumption that surrogates of taxonomic diversity are constant over time (Magierowski and Johnson 2006), a statement that needs to be quantitatively assessed. Finally, the efficiency of subset-taxa may be habitat-dependent and vary with type and magnitude of disturbances (Wodarska-Kowalczuk and Kedra 2007; Mellin et al. 2011).

While many methods have been developed to describe long-term evolution of marine communities, Community Trajectory Analysis (CTA) is a recently developed multivariate method specifically tailored to study temporal community dynamics (De Cáceres et al. 2019). From a classical ordination of a species abundance matrix, it performs a geometric analysis of temporal trajectories in all dimensions to characterize and compare temporal patterns in community dynamics.

Using CTA and 13-year monitoring of benthic macrofauna at 32 sites along Brittany's coasts (France), we investigated whether long-term dynamics of soft-bottom communities could be summarized by the subset-taxa method and which subset-taxa among Polychaeta, Crustacea and Mollusca was the most efficient. Subset-taxa temporal trajectories were compared to those of overall and non-subset taxa communities (i.e., whole community minus subset-taxa). We addressed these questions with four soft-bottom habitats exposed to different environmental constraints: two associated with foundation species, i.e., eelgrass and maerl beds, and two bare sedimentary habitats. Focusing on spatial and temporal changes in α and β taxonomic diversities, we hypothesized that: 1) surrogate performance for community dynamics is taxa-dependent and 2) the subset-taxa method efficiency is habitat-dependent.

2. Materials & Methods

2.1. Sampling

Macrobenthic species abundances from 32 sites were recorded yearly from 2007 to 2019 in four habitats along 500 km of the coast of Brittany (France): intertidal eelgrass meadows (8 sites), intertidal sandy beaches (9 sites), subtidal maerl beds (7 sites) and subtidal soft sediments (8 sites), respectively referred to as intertidal biogenic (IBIO), intertidal bare (IBAR), subtidal biogenic (SBIO) and subtidal bare (SBAR) habitats. Nine to ten replicates were collected at each site (intertidal: 0.03 m^2 core, subtidal: 0.1 m^2 Smith-McIntyre grab; Appendix 1). Specimens were identified to the lowest possible taxonomic level (mostly species) and taxonomic homogenization was performed to ensure consistent taxonomic resolution over time and space (Appendix 1).

2.2. Data analysis

The relationships between the number of Subset-Only (i.e., number of species in the subset) and Non-Subset species (i.e., the remaining species) was assessed with Ordinary Least Squares regressions and tested using 999 permutations (Legendre and Legendre 2012).

We used Hellinger distances to analyse β-diversity between sites and years for: (i) overall, (ii) Non-Subset and (iii) Subset-Only community in the 4 habitats. Observations were represented with Principal Coordinates Analysis (PCoA) and consecutive observations of a given site were linked by a segment; all segments of a site constitute its temporal trajectory. CTA (De Cáceres et al. 2019) was then performed on all dimensions. Resemblance between trajectory pairs were assessed with symmetrized directed segment path dissimilarity (D_{SDSP}) (De Cáceres et al. 2019) using their geometry (shape, size, direction, position). Because trajectory position might be influenced by site-specific factors, we centred trajectories prior to D_{SDSP} calculation to focus on compositional dynamics rather than spatial variation.

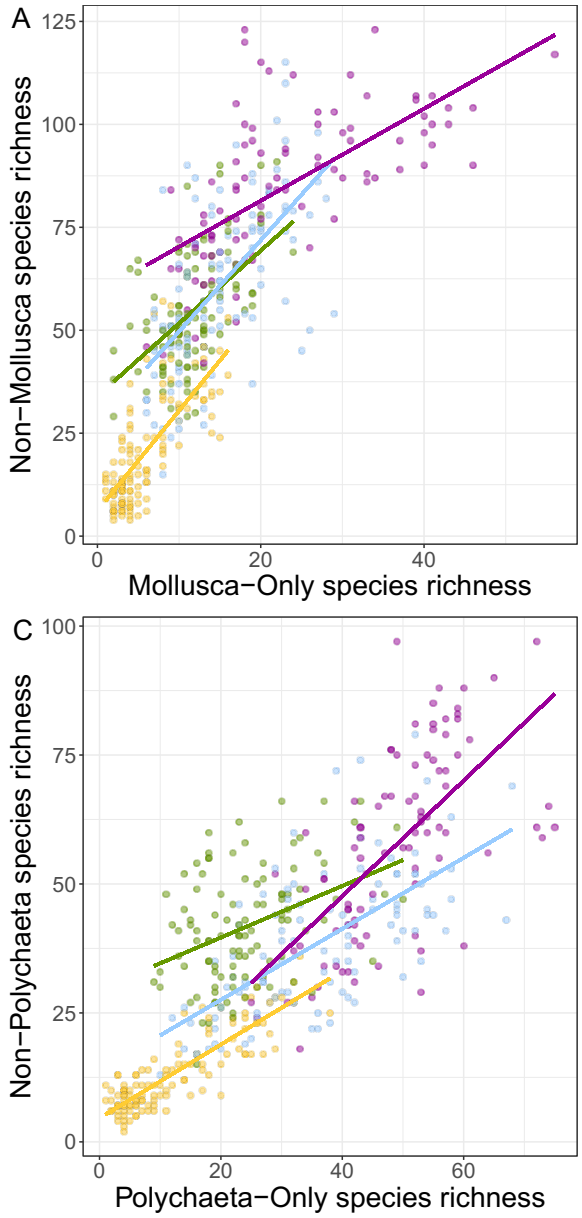
Co-inertia analysis seeks common structures between datasets, and the RV coefficient, a multivariate generalization of squared Pearson correlation, measures the closeness of two separate ordinations (Legendre and Legendre 2012). It ranges from 0 to 1 and was tested with 999 permutations. We tested the co-structure between Non-Subset and Subset-Only datasets as the whole community and Subset-Only datasets are not independent. RVs were computed for three different ordinations: PCoA representing Hellinger distances between observations (raw trajectories), PCoA representing centred trajectories, and PCoA representing dissimilarity of site dynamics (D_{SDSP}). The first configuration takes into account spatial differences in

community composition, the second smooths these differences to focus on temporal dynamics and the last explicitly compares similarities between community dynamics using a CTA metric. All dimensions of PCoAs were considered to compute RV coefficients.

All analysis were conducted with the R programming language version 4.2.2 (R Core Team, 2022) and packages ‘ecotraj’ (De Cáceres et al. 2019; Sturbois et al. 2021c) and ‘ade4’ (Thioulouse et al. 2018).

3. Results

Results revealed significant positive linear relationships between the number of Non-Subset and Subset-Only species in all habitats except for Crustacea in IBIO (Figure 1), with the highest R^2 between Non-Polychaeta and Polychaeta-Only in IBAR and the lowest for Non-Polychaeta and Polychaeta-Only in IBIO. Crustacea were absent from several IBAR samples.



D

	Subsets	IBAR	IBIO	SBAR	SBIO
Linear regression	Mollusca	R^2 = 0.53 ***	R^2 = 0.28 ***	R^2 = 0.40 ***	R^2 = 0.41 ***
	Crustacea	R^2 = 0.43 ***	R^2 = 0.01	R^2 = 0.40 ***	R^2 = 0.32 ***
	Polychaeta	R^2 = 0.74 ***	R^2 = 0.15 ***	R^2 = 0.43 ***	R^2 = 0.42 ***
Species richness	Overall community	332	493	514	648
	Mollusca	71	93	119	151
	Crustacea	109	184	160	178
	Polychaeta	124	156	185	250
Species richness (%)	Mollusca	21%	19%	23%	23%
	Crustacea	32%	37%	31%	27%
	Polychaeta	37%	32%	36%	39%
Total abundance	Overall community	47 365	128 424	129 007	237 463
	Mollusca	6 812	10 557	27 841	25 057
	Crustacea	23 510	45 482	19 994	147 663
	Polychaeta	16 175	67 795	70 880	56 939
Total abundance (%)	Mollusca	14%	8%	22%	11%
	Crustacea	49%	35%	15 %	62%
	Polychaeta	34%	52 %	55%	24%

FIGURE 1: Linear regressions between number of Non-Subset and Subset-Only species (Mollusca (A), Crustacea (B), Polychaeta (C)) in intertidal bare (IBAR), intertidal biogenic (IBIO), subtidal bare (SBAR) and subtidal biogenic (SBIO) habitats. One point represents the number of species in one observation (i.e., one site-year combination), solid regression lines are only represented when significant. R^2, model significance, species richness and total abundance are given in (D). Significance code: blank = $p > 0.05$, *** = $p < 0.001$.

Figure 2 represents two-dimensional community trajectories of IBIO as an example. Total variance of the first two PCoA axes ranged from 41% (Non-Polychaeta) to 52% (Polychaeta-Only). Visually considering overall community trajectories, sites clearly occupied different positions in the biplot, reflecting site-specific composition and structure. Site trajectory positions were more similar between overall community and Polychaeta-Only compared to Mollusca-Only or Crustacea-Only. Moreover, Non-Polychaeta trajectory positions diverged more from those of the overall community than either Non-Mollusca or Non-Crustacea. Polychaeta might perform better when representing spatial β-diversity patterns than Crustacea or Mollusca and might drive the overall community dynamics. Such considerations were mainly true for every studied habitat (Appendices 2-4).

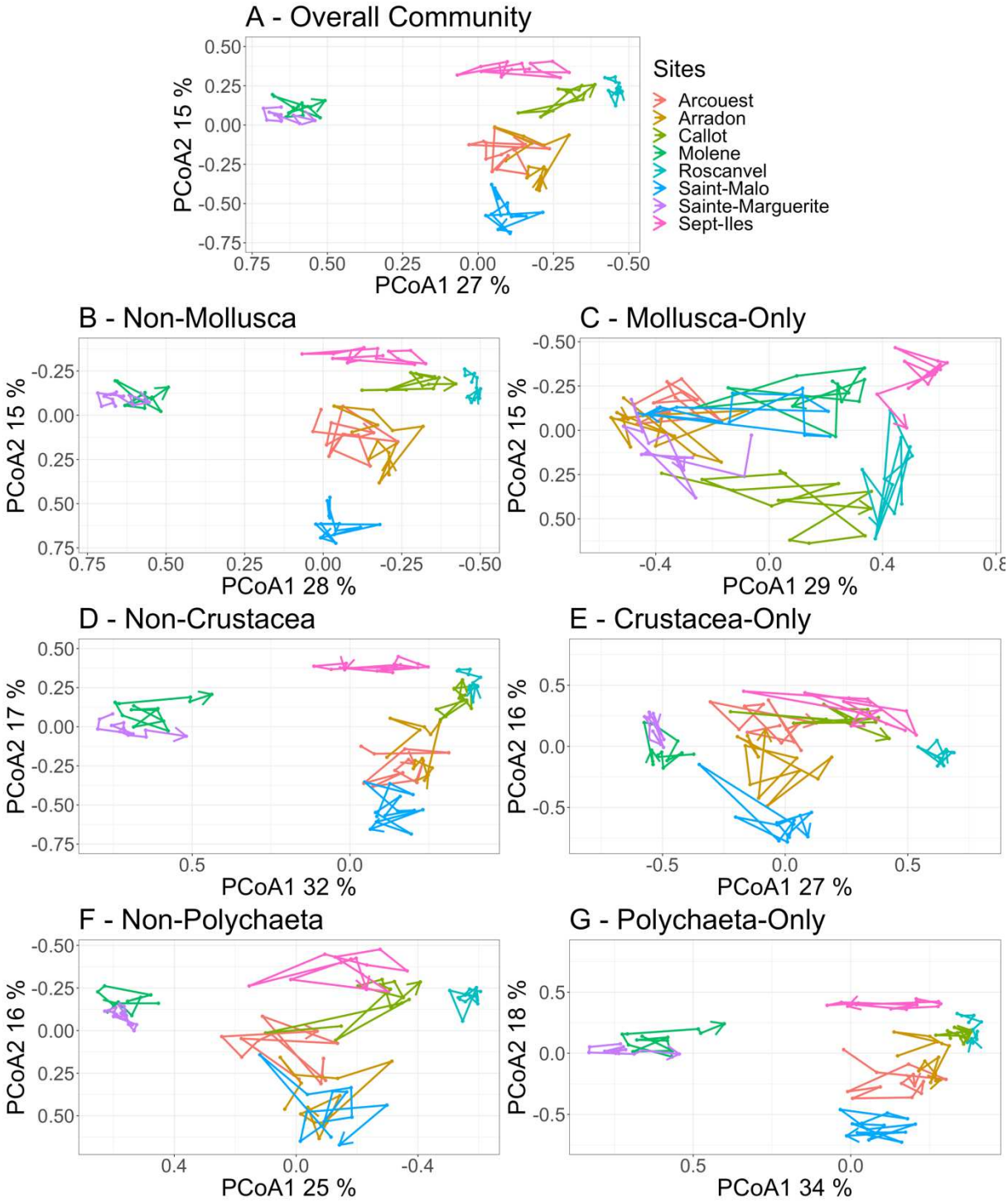
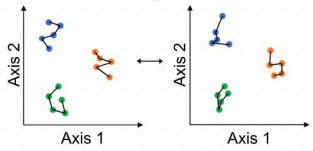
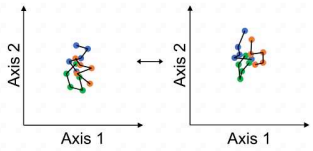
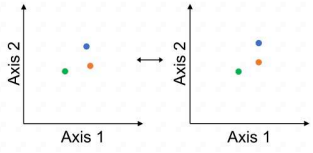


FIGURE 2: Two-dimensional (PCoA) representation of community trajectories (2007-2019) of the overall community (A), Non-Subset (B, D, F) and Subset-Only (C, E, G) in the intertidal biogenic habitat. One point represents the community state of a site in a given year (one observation). Site specific consecutive community states are linked by segments which taken together depicts the site trajectory. Arrows represent final community state of a trajectory.

Raw trajectories RVs were all significant (Table 1). Highest values were found between Non-Polychaeta and Polychaeta-Only in all habitats, supporting the idea that Polychaeta were better surrogates for studying β-diversity between sites and years. After trajectory centring, RV coefficients all strongly decreased but remained significant. Interestingly, ordinations of centred trajectories were still the closest for Polychaeta. Most RV coefficients on PCoAs based on D_{SDSP} were not significant. In this configuration, significant RVs mean that two sites with similar dynamics in the Subset-Only dataset have similar dynamics in the Non-Subset dataset. This was stronger for Polychaeta in biogenic habitats. Indeed, comparing Non-Polychaeta and Polychaeta-Only datasets, RVs were significant in IBIO and SBIO. On the contrary, for Non-Mollusca and Mollusca-Only datasets, RVs were never significant, while Non-Crustacea and Crustacea-Only datasets showed significant RV only in SBIO.

TABLE 1: RV coefficients between configuration of points in two ordinations (here always between the ordination of the Non-Subset dataset under consideration, i.e., Mollusca, Crustacea and Polychaeta, and the Subset-Only ordination) in intertidal bare (IBAR), intertidal biogenic (IBIO), subtidal bare (SBAR) and subtidal biogenic (SBIO) habitats. Ordinations are PCoAs representing different point configurations: "Raw trajectories" (consecutive observations in a PCoA based on their Hellinger distances and linked by segments), "Centered trajectories" (previous ordination after centring trajectories), and "D_{SDSP}" (PCoA of centred trajectories using D_{SDSP}, here a point represents one site trajectory). Significance code: blank = $p > 0.05$, * = $p < 0.05$, *** = $p < 0.001$. Schemes represent two axes' ordinations as in figure 2 but RV coefficients were computed on all dimensions.

Configuration	Subsets	IBAR	IBIO	SBAR	SBIO
Raw trajectories 	Mollusca	RV = 0.67 ***	RV = 0.51 ***	RV = 0.77 ***	RV = 0.68 ***
	Crustacea	RV = 0.67 ***	RV = 0.74 ***	RV = 0.44 ***	RV = 0.71 ***
	Polychaeta	RV = 0.77 ***	RV = 0.81 ***	RV = 0.80 ****	RV = 0.75 ***
Centered trajectories 	Mollusca	RV = 0.22 *	RV = 0.29 ***	RV = 0.43 ***	RV = 0.42 ***
	Crustacea	RV = 0.23 ***	RV = 0.40 ***	RV = 0.44 ***	RV = 0.42 ***
	Polychaeta	RV = 0.26 ***	RV = 0.42 ***	RV = 0.47 ***	RV = 0.48 ***
D_{SDSP} 	Mollusca	RV = 0.73	RV = 0.94	RV = 0.95	RV = 0.93
	Crustacea	RV = 0.90	RV = 0.96	RV = 0.94	RV = 0.93 *
	Polychaeta	RV = 0.89	RV = 0.97 *	RV = 0.96	RV = 0.96 *

4. Discussion

Our study covers a diversity of habitats and years to generalize results, alleviating difficulties or biases potentially associated to meta-analyses conducted from datasets with highly contrasting environments and sampling strategies. Similarly to previous local studies, our results showed Polychaeta better translated both community spatial differences and temporal dynamics compared to Crustacea or Mollusca (e.g., Olsgard and Somerfield 2000; Wodarska-Kowalczuk and Kedra 2007; Kokesh et al. 2022). But in contrast with most studies on temporal dynamics which used non-metric multidimensional scaling (nMDS), sometimes combined with Mantel tests (Gladstone et al. 2020), a method that has been subject to criticisms (Legendre et al. 2015), we here assessed the effectiveness of taxonomic surrogacy with a method explicitly designed to quantitatively evaluate temporal dynamics.

Polychaeta efficiency could scarcely be linked to their numerical dominance or richness, as they were sometimes surpassed by Crustacea in both (Figure 1D). However, Polychaeta do harbour a high diversity of biological traits (Olsgard et al. 2003), with a very wide range of feeding, motility, reproduction modes and life spans (Giangrande 1997; Jumars et al. 2015). They also include species sensitive and tolerant to disturbances (Olsgard et al. 2003; del Pilar Ruso et al., 2009). Thus, we hypothesize Polychaeta mimicked the range of functional guilds encountered in the whole community, hence the dynamics of a majority of Non-Polychaeta taxa. Their high functional diversity would also allow to deal with various environmental conditions and/or habitats (Jumars et al. 2015), which is convenient for studies involving environmental gradient or different habitats.

Although Polychaeta performed better, their efficiency as subset-taxa was habitat-dependent. Such discrepancies have already been shown (Magierowski and Johnson 2006; Wodarska-Kowalczuk and Kedra 2007; Mellin et al. 2011), emphasizing the need to choose surrogates according to target habitat or community. As such, Polychaeta were the best predictors of α-diversity in all habitats except IBIO where Crustacea performed better. Nevertheless, they were still the best predictor of spatial β-diversity and community dynamics in IBIO. Indeed, positive correlations between site dynamics' dissimilarities of Polychaeta-Only and Non-Polychaeta were found in both biogenic habitats (IBIO and SBIO). Maerl beds (SBIO) high complexity may enhance niche partitioning leading to high species diversity and functional redundancy in this habitat, that evenly harbours all modalities of Polychaeta traits in each site (Boyé et al. 2019). In this habitat, the high functional diversity of Polychaeta may allow for a good representation of the dynamics of other taxa with similar ecological functions.

However, this might not hold for IBIO where Polychaeta were less numerous and displayed specialized traits (Boyé et al. 2019), unlikely to mimic the overall community. An alternative hypothesis could be that biogenic habitats enhance stability (Toumi et al. 2023), allowing for the maintenance of the same dynamic for Polychaeta-Only and Non-Polychaeta.

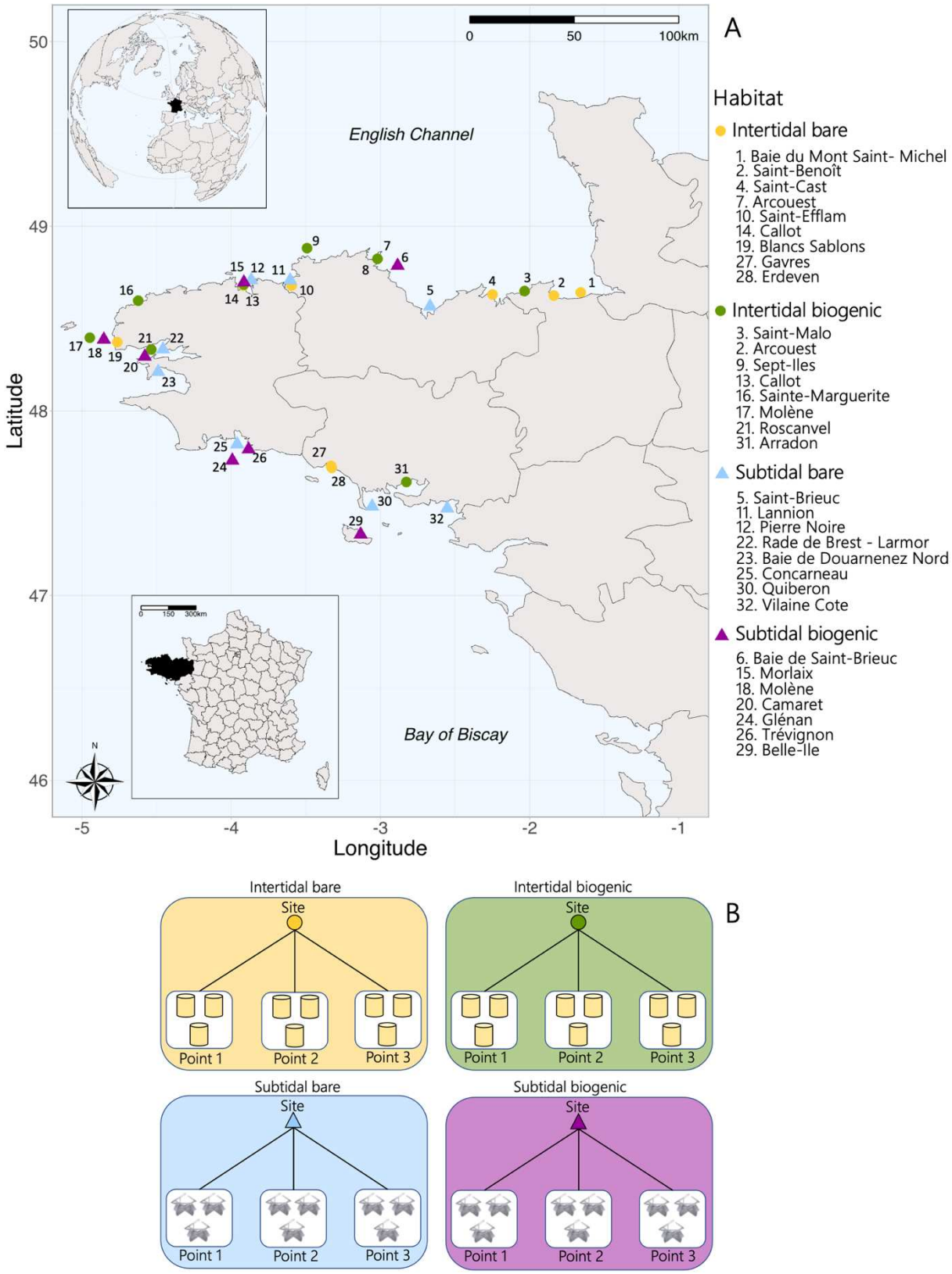
We expect more fluctuant dynamics in bare habitats, especially the more exposed IBAR (Toumi et al. 2023). Bare habitats also harbour less species diversity for a given tidal zone and Polychaeta in IBAR have site-specific biological traits (Boyé et al. 2019). Less numerous taxa showing various responses to frequent stress may explain the reduced efficiency in bare habitats. Higher variability of bare environments could lead to greater stochasticity in community dynamics, hindering establishing a link between surrogates and community dynamics.

Although correlations between site dynamics' dissimilarities were only significant in biogenic habitats for Polychaeta, we cannot exclude their efficiency in bare habitats: considering raw or centred configurations, RVs were always significant and maximised for Polychaeta. These configurations reflect taxonomic temporal dynamics, thus we posit that they were translated in bare habitats and Polychaeta were the best subset to do so.

Significant RV values were highest for raw configurations, reinforcing the suitability of Polychaeta as spatial β-diversity surrogates. Centred configurations revealed that β-diversity was more spatial than temporal. RV values were highest but non-significant with D_{SDSP}, but in this instance power is reduced as sample size is the number of sites (maximum 9 in this study).

CTA appears as a suitable tool to quantitatively compare dynamics between community subsets. Polychaeta were the best subset-taxa for long-term dynamics of soft-bottom macrobenthic diversity. Their efficiency was demonstrated in all habitats, especially biogenic ones. Prior to initiating a monitoring program based on a community subset, we recommend to test the efficiency of taxonomic surrogacy on a time series of the entire community if available, or to refer to surrogacy studies on the same kind of environment beforehand.

Appendices

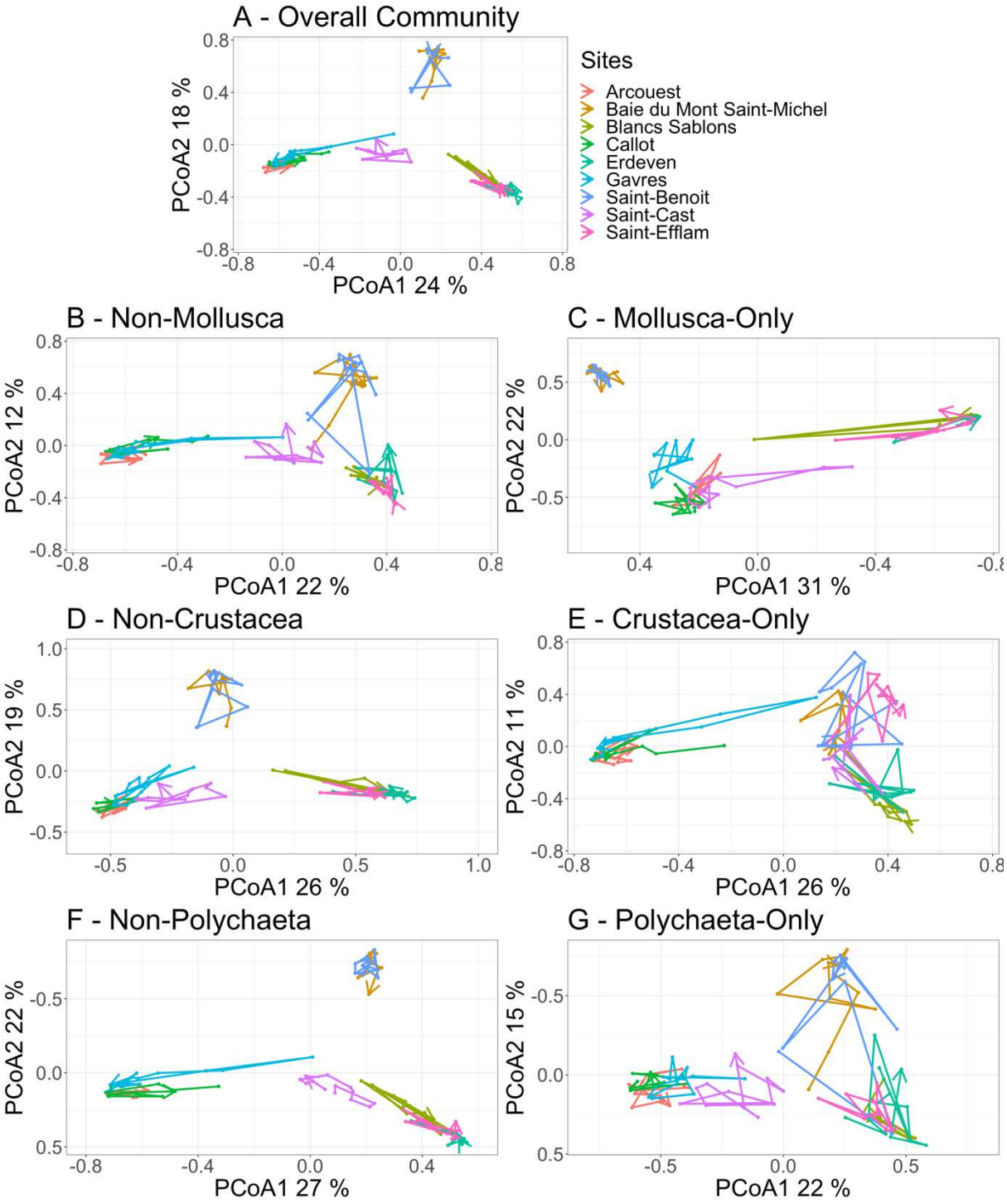


Appendix 1: A) Map of the monitored sites in the four distinct habitats along the coast of Brittany (France). B) Sampling method in each habitat: Benthic macrofauna communities (organisms > 1mm) have been monitored yearly since 2003 along coasts of Brittany (France) within the REBENT program

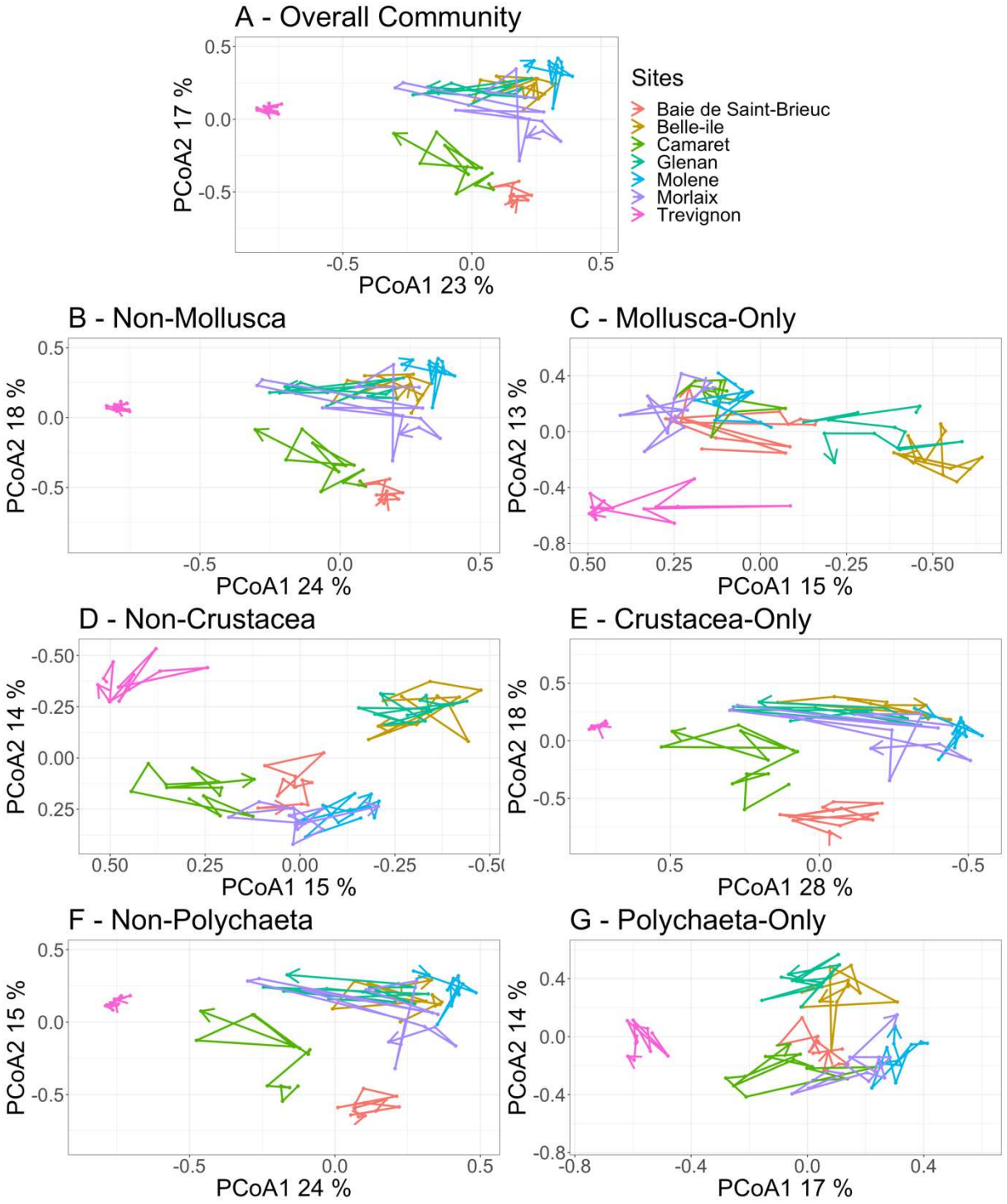
(https://rebent.ifremer.fr). We focused on four habitats: intertidal eelgrass meadows (only *Zostera marina* beds are monitored within the REBENT), intertidal sandy beaches, subtidal maerl beds (principally *Lithothamnion corallioides* and *Phymatolithon calcareum*) and subtidal soft sediments (respectively referred to as intertidal bare habitat (IBAR), intertidal biogenic habitat (IBIO), subtidal bare habitat (SBAR) and subtidal biogenic habitat (SBIO) in the text).

At each site three faunal samples were taken at each of three fixed sampling points distributed 200 m apart (0.03 m^2 cores in the intertidal and 0.1 m^2 Smith-McIntyre grabs in the subtidal; see Boyé et al., 2019), except for Pierre Noire (12) where up to 10 grabs were taken at the sampling site. Sampling was performed between the end of February and the beginning of May, before the recruitment of most species in the region. In the laboratory, specimens were sorted, counted and identified to the lowest possible taxonomic level (usually species). Since the acquisition and identification of specimens were not carried out by the same people over the years of the monitoring program, we proceeded to a taxonomic homogenization: for each recorded taxon, names were checked thanks to the World Register of Marine Species to ensure a consistent taxonomic resolution and their distribution in time and space was scrutinized by experts in benthic taxonomy. Degradation to higher taxonomic levels was undertaken for doubtful identifications, safeguarding against major misidentification, differences in identification among operators, or changes in time in given taxonomic groups due to updates in the taxonomic literatures. Particular care was taken for rare species and decision on their taxonomic degradation was made according to the robustness of the criteria discriminating the species, the level of expertise needed to discern them, and the likelihood of their presence in the studied area given their known distribution range. We favoured the possibility of underestimating the true diversity over that of keeping potential artificial patterns (see Boyé et al., 2017).

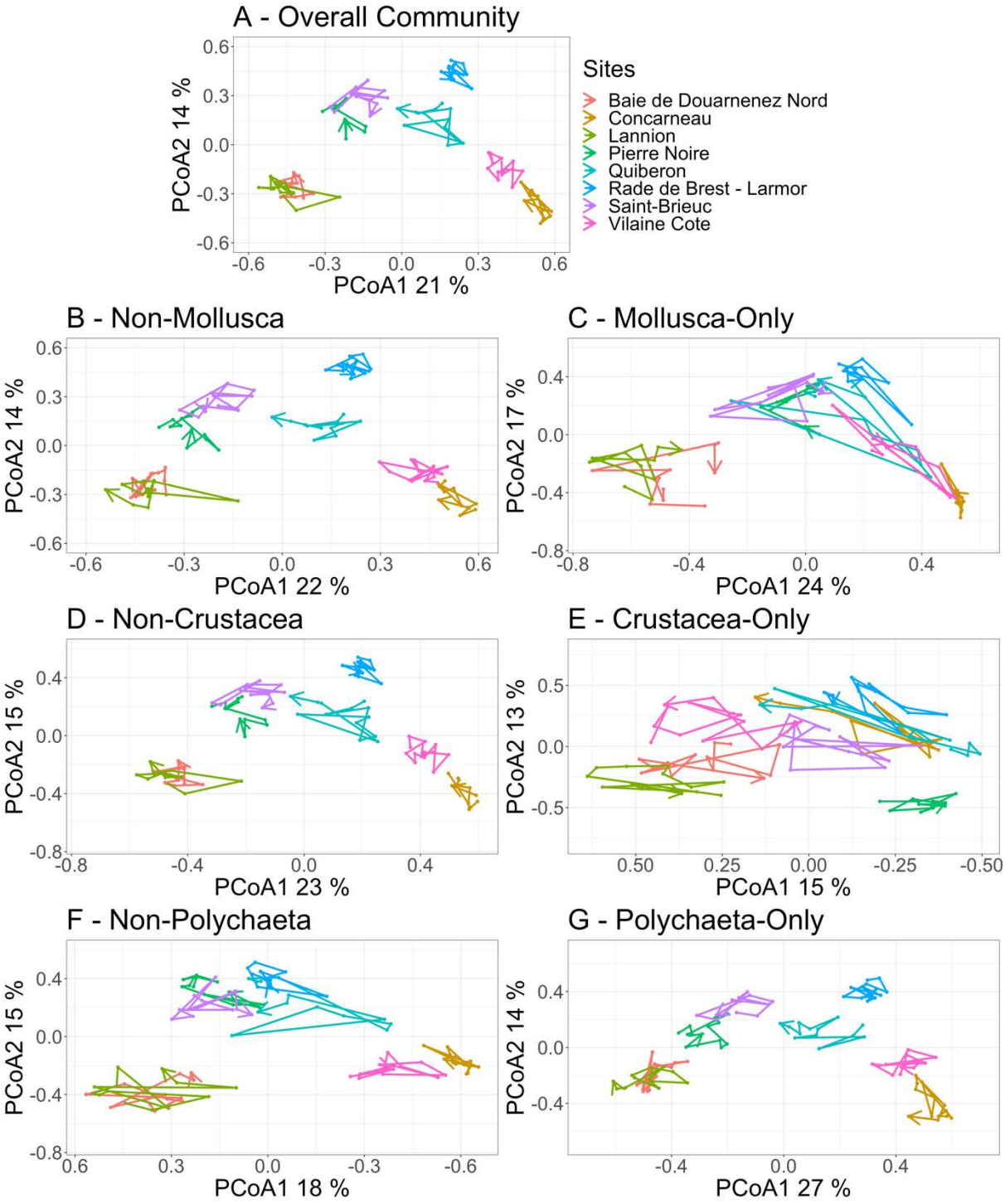
In order to minimize the prevalence – and potential effect – of missing data as much as possible, we only selected sites with complete time series and with at least 3 core or grab samples in any particular year. Samples were pooled to estimate abundances at the site level. In the end, this led to a selection of 32 sites monitored (9 in IBAR, 8 in IBIO, 8 in SBAR and 7 in SBIO) from 2007 to 2019 while keeping a spatial resolution covering the coasts of Brittany and encompassing most of the environmental settings found in this region.



Appendix 2: Two-dimensional (PCoA) representation of community trajectories (2007-2019) of the overall community (A), Non-Subset (B, D, F) and Subset-Only (C, E, G) in the intertidal bare habitat (IBAR). One point represents the community state of a site in a given year (one observation). Site specific consecutive community states are linked by segments which taken together depicts the site trajectory. Arrows represent final community state of a trajectory.

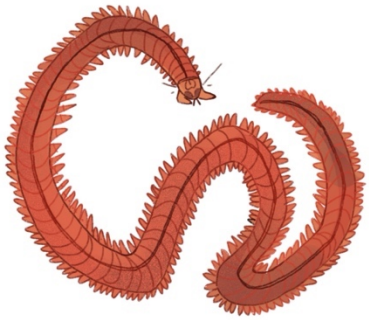


Appendix 3: Two-dimensional (PCoA) representation of community trajectories (2007-2019) of the overall community (A), Non-Subset (B, D, F) and Subset-Only (C, E, G) in the subtidal biogenic habitat (SBIO). One point represents the community state of a site in a given year (one observation). Site specific consecutive community states are linked by segments which taken together depicts the site trajectory. Arrows represent final community state of a trajectory.



Appendix 4: Two-dimensional (PCoA) representation of community trajectories (2007-2019) of the overall community (A), Non-Subset (B, D, F) and Subset-Only (C, E, G) in the subtidal bare habitat (SBAR). One point represents the community state of a site in a given year (one observation). Site specific consecutive community states are linked by segments which taken together depicts the site trajectory. Arrows represent final community state of a trajectory.

Chapter IV



Résumé en français

Après nous être concentrés principalement sur la facette taxonomique de la diversité dans les précédents chapitres, le présent chapitre aborde les dynamiques spatiotemporelles de la macrofaune benthique des quatre habitats côtiers d'un point de vue fonctionnel. Beaucoup d'études menées en écologie se concentrent principalement sur la diversité taxonomique des communautés, alors que la diversité fonctionnelle peut apporter un éclairage nouveau sur la dynamique de la biodiversité dans l'espace et le temps. En postulant que les Polychètes, en plus de traduire efficacement les dynamiques de l'ensemble de la communauté de macrofaune benthique au niveau taxonomique, sont capables de représenter des proxys efficaces de la dynamique fonctionnelle de l'ensemble de la communauté, nous avons ici étudié les variations spatiotemporelles de la diveristé β fonctionnelle en nous focalisant sur cet assemblage. Nous avons également identifié les principaux facteurs environnementaux et anthropiques contrôlant la diversité β fonctionnelle dans chaque zone tidale. Pour ce faire, nous avons utilisé 15 années (2005-2019) de données issues du suivi de la macrofaune benthique effectué dans le cadre du REBENT, couvrant un total de 38 sites dans les quatre habitats. Ces données ont été combinées avec une matrice de 11 traits fonctionnels comprenant un total de 45 modalités, des données environnementales et des proxys de pressions anthropiques. Nous avons utilisé des indices de diversité α fonctionnelle et la décomposition de la diversité β fonctionnelle pour décrire et comparer les structures fonctionnelles des habitats. Les relations entre les traits et les facteurs abiotiques (i.e., variables environnementales et proxys de pressions anthropiques) ont été estimées à l'aide de RDA et de partitionnement hiérarchique de la variation. Les résultats ont révélé une utilisation différente de l'espace fonctionnel propre à chaque habitat. Ainsi, l'habitat intertidal nu présentait une faible richesse fonctionnelle associée à une forte équitabilité tandis que l'habitat intertidal biogénique présentait une plus forte richesse fonctionnelle dont les espèces dominantes supportaient des traits spécialisés par rapport au pool fonctionnel régional. Dans le subtidal, l'habitat biogénique montrait une plus forte richesse et redondance fonctionnelle par rapport à l'habitat nu. Un gradient de diversité β fonctionnelle a été observé de la zone intertidale à la zone subtidale et des habitats nus vers les habitats biogéniques. Dans tous les cas, la majeure partie de la diversité β fonctionnelle trouvait son origine dans les différences de richesse fonctionnelle entre les sites plutôt qu'entre les années. En effet, les patrons fonctionnels des habitats étaient stables dans le temps. Nous avons fait l'hypothèse que les différents mécanismes fonctionnels propres à chacun des habitats participent à la stabilité observée à l'échelle régionale. Au sein d'un même étagement, les habitats biogéniques et nus abritaient des traits fonctionnels distincts. Il apparaît que la diversité β fonctionnelle était

principalement déterminée par les caractéristiques des sédiments étroitement liées au type d'habitat considéré mais surtout aux variables anthropiques dans la zone intertidale. En effet, dans cette zone les proxys de pressions anthropiques, tels que la densité de population, l'occupation du sol dans les alentours des sites et les pressions de pêche, expliquaient la plus grande proportion de diversité β fonctionnelle, ce qui met une nouvelle fois en avant la nécessité de mieux caractériser ces pressions mais aussi de protéger différentes facettes de la diversité.

Spatiotemporal patterns of functional α and β diversity and their underlying drivers in biogenic and bare habitats

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Abstract

Understanding the patterns of biodiversity, their underlying drivers and identifying general rules that elucidate the functioning of ecosystems is a key challenge in ecology, especially in the current context of increasing changes in ecosystems. Historically, ecologists have mainly focused on the taxonomic diversity of communities but functional diversity may bring novel insight into the maintenance of biodiversity over space and time. Here, we described and compared the spatiotemporal patterns and variation in Polychaeta functional traits distributions and diversity between four habitats: two biogenic habitats in the intertidal and subtidal zones and two bare sedimentary habitats in the same tidal zones. We also identified the main environmental and anthropogenic factors controlling functional β diversity in each tidal zone. To do so, we used data collected over 15 years (2005-2019) in the REBENT benthic coastal invertebrates monitoring program, covering a total of 38 sites in these four habitats, at a regional scale in the North-East Atlantic. These data were combined with a matrix of 11 functional traits divided in a total of 45 modalities, environmental data and proxies of anthropogenic pressures. We used α functional indices and decomposition of functional β diversity to describe and compare habitats' functional structures. Traits-abiotic drivers' relationships were estimated with redundancy analyses and hierarchical partitioning. Results revealed a habitat-dependent use of the functional space. Moreover, a gradient of functional β diversity was observed from the intertidal to the subtidal zone and from bare to biogenic habitats. Most of functional β diversity was due to functional richness differences between sites rather than between years. Within a tidal zone, biogenic and bare habitats harbored distinct functional traits and functional β diversity was mainly driven by sediment characteristics and closely linked habitat type or anthropogenic variables in the intertidal zone.

1. Introduction

In the current context of global erosion of biological diversity (Naeem et al. 2012; Thomas 2013) due to increasing climatic changes and anthropogenic threats on ecosystems, understanding the patterns of biodiversity, their underlying drivers and identifying general rules that elucidate the functioning of ecosystems is a key challenge in ecology (Loreau 2010) to improve our ability to predict ecosystem changes. It is also of high priority in order to set up effective management strategies or adjusting conservation policies (Micheli and Halpern 2005; Cadotte et al. 2011). Ecologists have often used taxonomic α and β diversity to describe biodiversity patterns and investigate the underlying mechanisms, however this may not be sufficient to fully understand the mechanisms structuring communities and for predicting ecosystem processes (Villéger et al. 2008; Mouillot et al. 2011). Indeed, functional approaches, relying on functional traits – any morphological, physiological or phenological feature that impacts fitness via its effects on growth, reproduction and survival (Violle et al. 2007) – may provide complementary information on the ecological functions performed by organisms and novel insight into the origin and maintenance of biodiversity over space and time (Edie et al. 2018).

Functional traits do not constitute direct measures of ecosystem processes but are efficient proxies of ecological functions, thus allowing to apprehend ecosystem functioning (Cadotte et al. 2011; Cadotte 2017). To this objective, many indices of functional diversity, which can be defined as the number, type and distribution of functions performed by organisms within an ecosystem (Díaz and Cabido 2001), have been developed and used at different spatial scales (e.g., α, β) (Villéger et al. 2008, 2013; Carmona et al. 2016; Mammola 2019). In addition to spatial patterns, functional traits, also considered as Essential Biodiversity Variables (Pereira et al. 2013), can be used in biomonitoring context to evaluate the temporal variation of functional diversity and how organisms respond to ecosystem changes independently of taxonomic structure or total richness (Martini et al. 2021). Examining community changes from a trait-based perspective allows identifying characteristics linking species with similar environmental responses and better assessing how environmental changes could affect community and ecosystem structure (Mouillot et al. 2013b). Not only could abiotic variations determine taxonomic but also functional community dynamics (McLean et al. 2019a). Indeed, as functional diversity might enhance resilience to changes in communities, especially if several species support similar functional traits, assessing functional redundancy of communities can give clues about communities' response to potential environmental changes or disturbances

(Fonseca and Ganade 2001; McLean et al. 2019a). Several examples showed that there were incongruences in spatiotemporal dynamics between the taxonomic and functional structure of communities. For example, despite long-term compositional changes in communities, their functional structure could be sustained (Clare et al. 2015; Sturbois et al. 2021a), potentially through traits distribution and redundancy in communities.

Marine benthic ecosystems play a major role in coastal functioning (Snelgrove et al. 2014) and deliver valuable ecosystem services. Particularly, biogenic habitats harbor taxonomically and functionally diverse communities and contribute directly or indirectly to a major part of ecosystem functions provided by marine coastal areas (Barbier et al. 2011). However, coastal ecosystems are facing severe natural and anthropogenic pressures and biogenic habitats are threatened by the homogenization of benthic landscapes and habitat loss (Airoldi and Beck 2007). Biogenic habitats can dampen the effect of environmental constraints on communities (Jurgens and Gaylord 2018), thus functional diversity might be expected to be higher in such habitats compared to bare ones. Yet, despite marked differences in taxonomic diversity between biogenic and bare habitats, functional diversity patterns can appear more complex and depend on the scale of observation. For example, bare sediment sites can harbor less species richness and abundances than seagrass beds but they can be as functionally diverse at the habitat scale (Boyé et al. 2019; Kindeberg et al. 2022). Hence, better understanding how traits are dispersed and distributed within different habitat types and how their abundances are influenced by environmental gradients or anthropogenic variables would allow to better apprehend the ecological processes occurring in these habitats including their potential response to perturbations.

Benthic macrofauna is often used in monitoring programs of coastal marine ecosystems as indicator of changes, since most macrobenthic species are non-migratory (thus exposed to the local physical environment), show various life spans and exhibit different tolerances to environmental stresses (Dauer 1993). Moreover, they play important roles in marine ecosystems such as nutrient cycling, bioturbation and secondary production (Snelgrove 1998). Especially, Polychaeta is a phylogenetically diverse class exhibiting a large range of functional traits, having a critical role in ecosystems functioning through bioturbation for example (Queirós et al. 2013) and including species both sensitive and tolerant to strong environmental changes (Olsgard et al. 2003). Moreover, they might mimic the spatiotemporal dynamics of overall macrofaunal communities as suggested in Chapter III and we also expect them to be good functional surrogates of overall macrofaunal communities

Here we investigated the temporal α and β functional diversity of four distinct soft-bottom habitats exposed to different abiotic constraints using functional traits of Polychaeta species monitored during 15 years (2005-2019) in 38 sites distributed along 500 km of Brittany coasts (France). The set of habitats included two biogenic habitats associated with foundation species (i.e., seagrass and maerl beds) respectively in the intertidal and the subtidal zones, and two bare sedimentary habitats also in these two different zones. Building on the study of Boyé et al. (2019) that encompassed 3 years of this monitoring, we aimed to further our understanding of the links between the functional structure of the selected habitats and the environmental or anthropogenic pressure variability. More specifically we focused on identifying the origins of within-habitat functional β diversity such as functional richness differences or functional replacement, the functional redundancy of the habitats and the traits modalities contributing the most to the functional β diversity between habitat types. Therefore, our objectives were to i) describe and compare the spatiotemporal patterns and variation in functional traits distributions and diversity between the four habitats, ii) to identify the most structuring traits-environment relationships in each habitat.

2. Material and Methods

2.1. Macrofauna sampling

Benthic communities have been monitored yearly since 2003 along the coasts of Brittany (France) within the REBENT program (http://www.rebent.org). We focused on four habitats: intertidal seagrass beds (formed by *Zostera marina*), intertidal sandy beaches, subtidal maerl (or rhodolith) beds (principally formed by *Lithothamnion corallioides* and *Phymatolithon calcareum*) and subtidal soft sediments. These four habitats are respectively referred to as intertidal bare habitat (IBAR), intertidal biogenic habitat (IBIO), subtidal bare habitat (SBAR) and subtidal biogenic habitat (SBIO) from this point forward.

At each site three faunal samples were taken at each of three fixed sampling points distributed 200 m apart (using 0.03 m^2 cores in the intertidal and 0.1 m^2 Smith-McIntyre grabs in the subtidal; see Boyé et al. 2019), except for the Pierre Noire site where 10 grabs were taken at each visit. For all four habitats, an additional (core or grab accordingly) is taken at each point and used to estimate grain size distribution and organic matter content at the time of the faunal sampling. Sampling was performed between the end of February and the beginning of May, before the recruitment of most species in the region (Dauvin et al. 2007; Boyé et al. 2019). In the laboratory, specimens were sorted, counted and identified to the lowest possible taxonomic level (usually species). Since the acquisition and identification of specimens were not systematically carried out by the same people over the years, we proceeded with taxonomic homogenization: each recorded taxon was scrutinized by experts in benthic taxonomy and their names were checked thanks to the World Register of Marine Species (WoRMS Editorial Board 2021) to ensure for taxonomic resolution consistency.

To minimize the impact of missing data on the analyses, we selected sites that both had at least 3 core or grab samples in any particular year and less than 4 sampled years missing (out of 15). Samples were pooled to estimate abundances at the site level. This led to a selection of 38 sites monitored from 2005 to 2019 while keeping a spatial resolution covering the coasts of Brittany and encompassing most of the environmental settings found in this region (Boyé et al. 2017, 2019). Of these 38 sites, 12 were in IBAR, 8 in IBIO, 9 in SBAR and 9 in SBIO (Figure 1). Hereafter, the term “observation” refers to a sampling occasion at a given site in a given year (here the study encompassed a total of 550 observations).

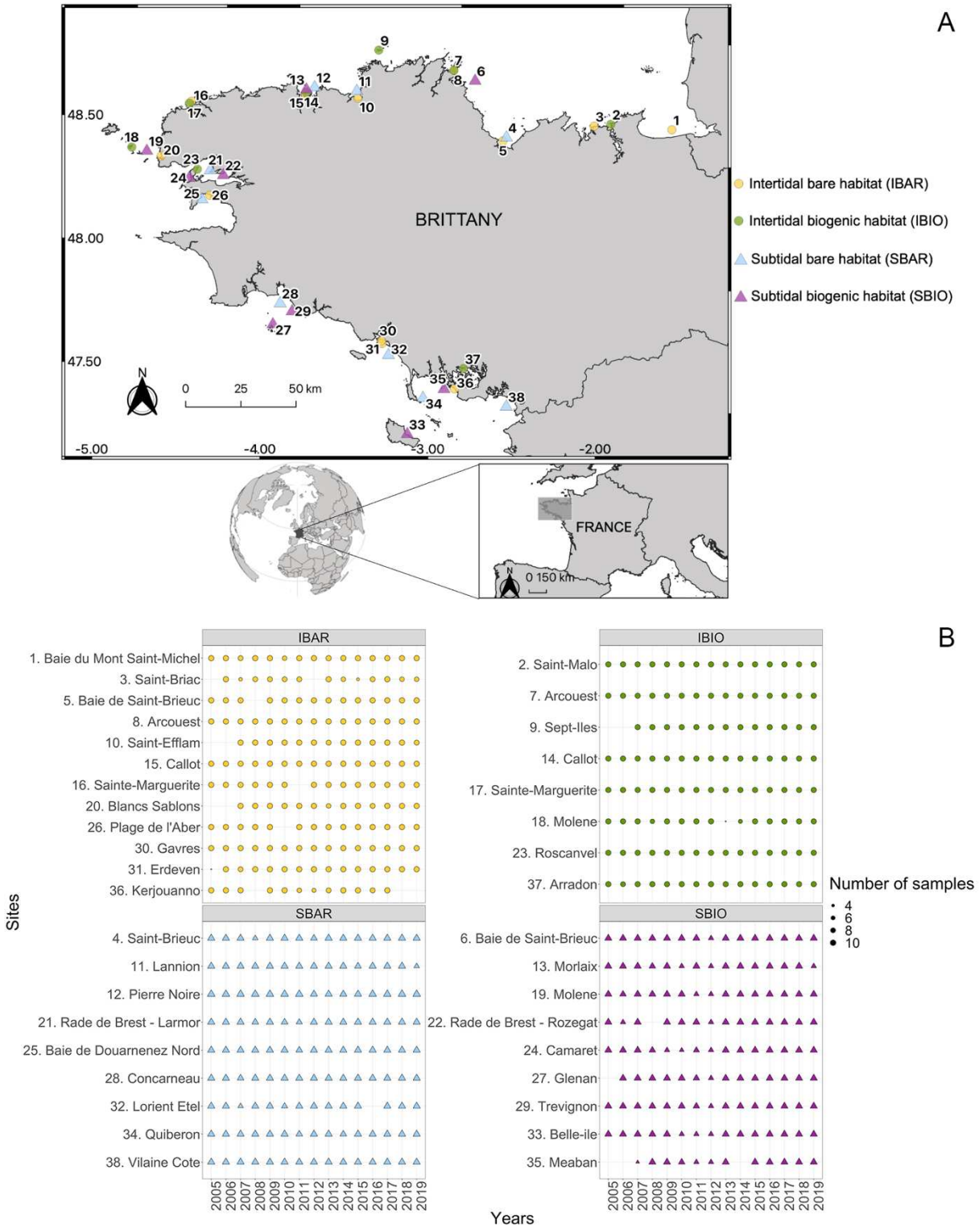


FIGURE 1: A) Map of the sites in the four monitored habitats along the coast of Brittany (France), (sources: OpenStreetMap, European Environment Agency). B) Data availability for each site in each habitat from 2005 to 2019. The size of the points is proportional to the number of samples (cores in the intertidal and grabs in the subtidal) that were aggregated to estimates taxon abundances at the site level.

2.2. Traits collection

The traits and modalities used were the same as in the study conducted by Boyé et al. (2019): 11 traits divided in a total of 45 modalities detailed in Table 1. We coded traits for the taxa not present in this previous study, resulting in a complete matrix of coded traits for 312 Polychaeta taxa. We also tried to fill in the missing data especially concerning the "life span" trait which had been removed from the previous study because of the lack of information collected on this trait. Species were scored for each trait modality based on their affinity using a fuzzy coding approach that allowed to capture the influence of intraspecific and ontogenic variability (Chevenet et al. 1994). The coding procedure is detailed in Appendix 1.

Trait data were collected from publicly available databases (e.g., Polytraits; Faulwetter et al. 2014, WoRMS; WoRMS Editorial Board 2021), reviews on reproductive and feeding ecology of Polychaeta (Fauchald and Jumars 1979; Giangrande 1997; Dorresteijn and Westheide 1999; Rouse and Pleijel 2006; Jumars et al. 2015) and on bioturbation potential (Queirós et al. 2013), primary literature on specific species or genera, or from expert knowledge. Information was collected at the lowest possible taxonomic level and inferred when missing from data available from other species in the genus, or in the most extreme cases, in the same family (feeding-related and mobility traits only and for families showing low variability for these traits). For the traits “life span”, “reproduction frequency”, “development mode” and “sexual differentiation”, data were missing for 21%, 9%, 5% and 1% of the species respectively. These traits were imputed following the same method as in Boyé et al. (2019): missing values were imputed using nearest neighbor imputation relying on Gower dissimilarity that accommodates missing data. Missing traits were imputed based on the median value of the functionally closest species for which the trait was known as well as those falling within a threshold dissimilarity of 0.01 times the dissimilarity between this closest species and the species to be inferred.

The fuzzy coded species-by-trait matrix was then transformed into a “proportion matrix” where trait category scores are converted into a relative expression of trait modalities so that the sum of the trait category scores for an individual trait and a given taxon equals one to standardize the description of species attributes (Martini et al. 2021). The observation-by-trait matrix containing the total abundances of each modality within the assemblages was then obtained using the matrix product of the observation-by-species matrix containing the abundances of the Polychaeta taxa in the assemblages, with the proportion matrix. In this matrix, the sum of each trait for an observation is the total abundance of the species found in the assemblage.

TABLE 1: List of traits and modalities with their abbreviations used in this study and their associated functions and ecological processes (according to Beauchard et al. 2017; Boyé et al. 2019).

Traits	Modalities	Abbreviations	Functions and ecological processes
Maximum size (mm)	<2 2–5 5-10 10-50 50-100 100-200 >200	Size_inf2 Size_2-5 Size_5-10 Size_10-50 Size_50-100 Size_100-200 Size_sup200	Sensitivity (small) or resistance (large) to predation, thermal resistance, fecundity increase, metabolic oxygen consumption rate
Feeding method	Subsurface deposit feeder Surface deposit feeder Active suspension feeder Passive suspension feeder Grazer Predator Scavenger Parasitic	SSDF SDF ASF PSF Grazer Pred Scav Parasitic	Food acquisition, growth requirements, demographic control (predation), nutrient cycling
Food size	Microphagous Macrophagous	Microphagous Macrophagous	Food acquisition, growth requirements, nutrient cycling
Adult preferred substrate position	Infaunal Epibenthic	Infaunal Epibenthic	Biogeochemical requirements, niche creation, refuge, nursery, below sediment oxygenation
Living habit	Tube dweller Burrower Crawler Swimmer Attached	Tube_dweller Burrower Crawler Swimmer Attached	Foraging mode, ability to escape predation, migratory requirements, dispersal
Daily adult movement capacity (m)	None <10 10-100 100-1000	Mob_0 Mob_inf10 Mob_10-100 Mob_100-1000	Ability to escape predation, migratory requirements, dispersal
Bioturbation	None Surficial modifiers Biodiffusors Upward conveyors Downward conveyors Regenerators	Bioturb_N Bioturb_S Bioturb_B Bioturb_UC Bioturb_DC Bioturb_R	Food acquisition, impact on biogeochemistry, organic matter re-distribution, habitat provision
Sexual differentiation	Hermaphrodite Gonochoric	Hermaphrodite Gonochoric	Reproductive success, recolonization, dispersal
Development mode	Asexual Direct Indirect-planktotrophic Indirect-lecithotrophic	Dev_asex Dev_direct Dev_plankto Dev_lecitho	Demographic resilience, juvenile dispersal, dispersal potential
Reproduction frequency	Iteroparous Semelparous	Iteroparous Semelparous	Reproductive success, recolonization, dispersal
Life span	Short (<2 years) Medium (2-5 years) Long (>5 years)	Short_life_span Medium_life_span Long_life_span	Reproductive success, recolonization, dispersal

2.3. Estimation of within-habitat α and β functional diversities

The estimation of α and β diversity indices was based on the construction of a trait space based on a subset of Principal Coordinates Analysis (PCoA) axes (Villéger et al. 2008). PCoA was performed on Euclidean distances computed on the proportion matrix. To compare our results with the ones obtained by (Boyé et al. 2019), we first aimed to create a functional space with the same dimensions, i.e., keeping 5 PCoA axes after removing observations with less than 5 species (which led to 505 observations, see Appendix 2). However, to compute β diversity indices, we used the "beta.hull" function from the "BAT" R package (Mammola and Cardoso 2020) which could not handle more than 3 PCoA axes for constructing convex hulls. Thus, we kept 3 PCoA axes which resulted in a reduced-space representing 50% of the original variance (quality of the representation measured with R^2-like ratio as described in Legendre and Legendre 2012).

The following indices were computed to characterize the functional structure of the four monitored habitats:

- Functional Richness (FRic) corresponds to the convex hull volume occupied by the species of an assemblage in the multidimensional trait space and representing amount of functional space filled by a community (Villéger et al. 2008; Mouillot et al. 2013b),
- Functional Evenness (FEve) corresponds to the regularity of the species abundance distribution along the minimum spanning tree that links the species in the multidimensional space (Villéger et al. 2008; Mouillot et al. 2013b),
- Functional Divergence (FDiv) corresponds to the proportion of total abundances supported by species with the most extreme trait values (Villéger et al. 2008; Mouillot et al. 2013b),
- Functional dispersion (FDis) corresponds to the mean distance of individual species to the centroid of all species in the multidimensional trait space, taking into account the species relative abundances (Laliberté and Legendre 2010),
- Functional Redundancy (FRed) quantifies the degree to which species in a community share similar ecological characteristics, i.e., whether ecological roles are supported by few or many species and individuals. It is computed as follow: $FRed = 1 - U$ where U is the Uniqueness: $U = \frac{1-D}{1-Q}$, with D corresponding to the Simpson diversity and Q the Rao's quadratic diversity (Pavoine and Ricotta 2019).

  FRic, FEve, FDiv and FDis were computed with the "FD" R package (Laliberté et al. 2014), FRed was computed with the "adiv" R package (Pavoine 2020).

Functional β diversity was decomposed into β_{total}, $\beta_{replacement}$ and $\beta_{richness}$ components, with $\beta_{total} = \beta_{replacement} + \beta_{richness}$, following the framework of (Figure 2; Mammola and Cardoso 2020). Before computing this functional β diversity decomposition with the "BAT" R package, we constructed convex hulls with this same package, using the same procedure as for the "FD" R package. We verified that the "BAT" package gave the same results as the "FD" package concerning α diversity indices to ensure consistency between the result.

All habitats were taken together in the analyses to compute the indices above in order to ensure a consistent comparison of these indices between habitats as they were computed in the same multidimensional space.

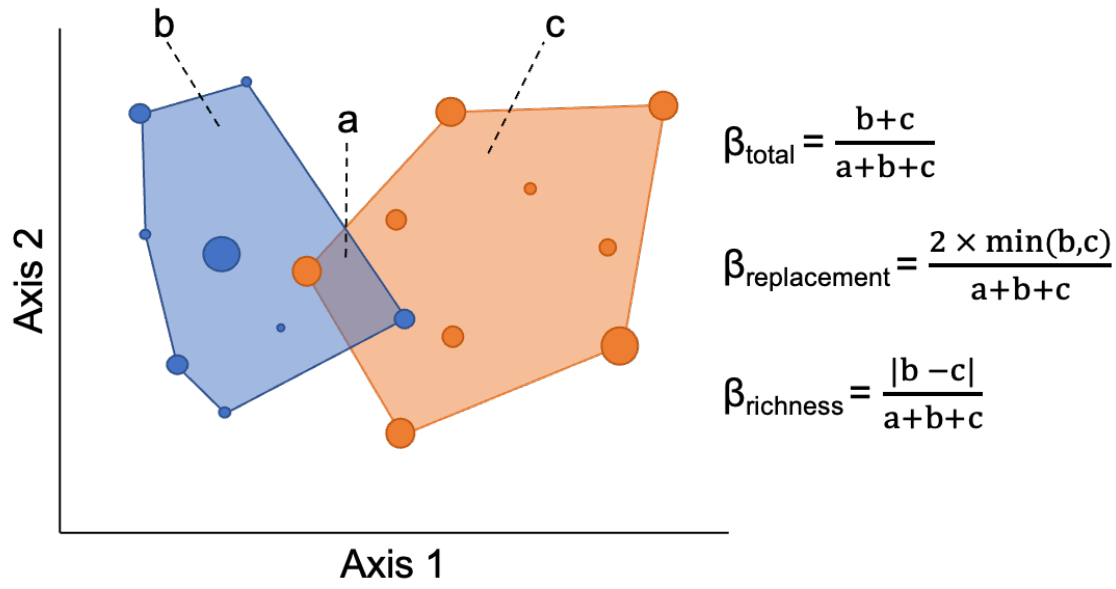


FIGURE 2: Formulas and schematic representation of the measure of functional β diversity and its components using the $\beta_{total} = \beta_{replacement} + \beta_{richnes}$ decomposition, between two convex hull volumes occupied by two communities (blue and orange) in the functional space (here represented by two traits). Volumes b and c represent the unique portion of volume occupied by the blue and orange communities respectively and volume a represent the intersection (i.e., similarity) between these two volumes. The figure is taken and modified from Mammola (2019) and Mammola and Cardoso (2020).

2.4. Abiotic drivers of between-habitat functional β diversity

To assess the influence of the abiotic drivers on the functional β diversity, we took all the observations available (550) and we separated the analyses between the intertidal and the subtidal zones in order to assess the influence of the habitat type (bare or biogenic) on the functional β diversity within each tidal level. We performed Redundancy Analyses (RDA; Rao 1964) within each tidal level, using the Hellinger-transformed observation-by-trait matrix as the response matrix and the matrix of abiotic variables as the explanatory matrix.

The list of the abiotic variables used can be found in Table 1 of Chapter II. For the intertidal zone we removed the biometry dataset as it only concerns IBIO and not IBAR. In the intertidal, professional fishing was coded as "PF_NO" in IBIO as no professional fishing take place in this habitat. In the subtidal, professional fishing and dredging were merged as one "Fishing" pressure. We used the same procedure of variable selection as detailed in Chapter II, section 2.2.3. (VIF and forward selection), except that the selection was conducted at the scale of the tidal zone and not at the scale of the habitat. Selected abiotic variables used in RDAs are listed in Table 2. RDA analyses were conducted with the "vegan" R package (Oksanen et al. 2022).

Additionally, we conducted a hierarchical partitioning (Lai et al. 2022) in order to assess the individual contribution of each abiotic dataset containing the selected variables (Table 2) and the type of habitat (bare or biogenic) to the explained variation of communities within each tidal zone. The individual contribution of a predictor is defined as its unique contribution to the total model plus its average shared contributions with the other predictors (Lai et al. 2022). Hierarchical partitioning analyses were conducted with the "rdacca.hp" R package (Lai et al. 2022).

All analyses were conducted with the R programming language version 4.2.2 (R Core Team 2022).

TABLE 2: Selected abiotic variables used in the Redundancy Analyses in the two tidal zones. Selected variables were then grouped in the following categories: sediment characteristics (named "Sediment" in the analyses), hydrology, hydrodynamics, meteorology, depth and proxies of anthropogenic pressures (named "Prox.anthro" in the analyses) for hierarchical partitioning. Variables description and methods of acquisition can be found in Chapter II, Table 1 and Chapter II, Appendix 1.

Tidal zone	Sediment	Hydrology	Hydrodynamics	Meteorology	Depth	Prox.anthro
Intertidal	mud D50 MO So	mean T s.d. T s.d. sal max sal	s.d. current fetch	mean maxT s.d. wind		hab artif agri RF PF
Subtidal	mud D50 MO So kurtosis mean.grain	s.d. sal max sal min T	min current s.d. current fetch		depth	hab artif agri Fishing

3. Results

3.1. Functional α diversity

A gradient of functional richness can be observed from the intertidal to the subtidal zone and from bare to biogenic habitats within a same tidal zone, with IBAR having the lowest FRic values and SBIO the highest (Figure 3A). Thus, a wider diversity of functions was represented in this former habitat. Differences in the distribution patterns of FRIC values between habitats are also notable, indeed, these values seemed to be more evenly distributed between sites and years in biogenic habitats than in bare habitats. The differences between habitats were less notable concerning FEve values although they might be slightly higher in bare habitats (Figure 3C, 3D) indicating that the functional traits of these habitats were supported by species with somewhat less variable abundances than in biogenic habitats. For FDiv, the values seemed to be somewhat higher in the intertidal compared to the subtidal habitats (Figure 3E, 3F). Especially, IBIO seemed to be the habitat where the dominant species were those supporting the least common traits compared to the regional trait pool. FDis values were higher in the subtidal but with similar patterns between bare and biogenic habitats of the same tidal level, even though SBIO showed the highest values (Figure 3G, 3H). SBIO was therefore the habitat with a majority of functionally different species compared to the regional trait pool. Finally, functional redundancy seemed to follow the same gradient as functional richness but with much more similarity between bare and biogenic habitats in the intertidal (Figure 3I, 3J). In SBIO, the different functional traits were supported by a higher proportion of species and individuals. The differences between the functional structure of the four habitats were relatively conserved during the 15 years of monitoring, although intertidal habitats showed a greater spatial heterogeneity in the functional indices computed (Figure 3B, 3D, 3F, 3H, 3J). Moreover, the trends of the FRic index for the two subtidal habitats followed the same temporal pattern (Figure 3B).

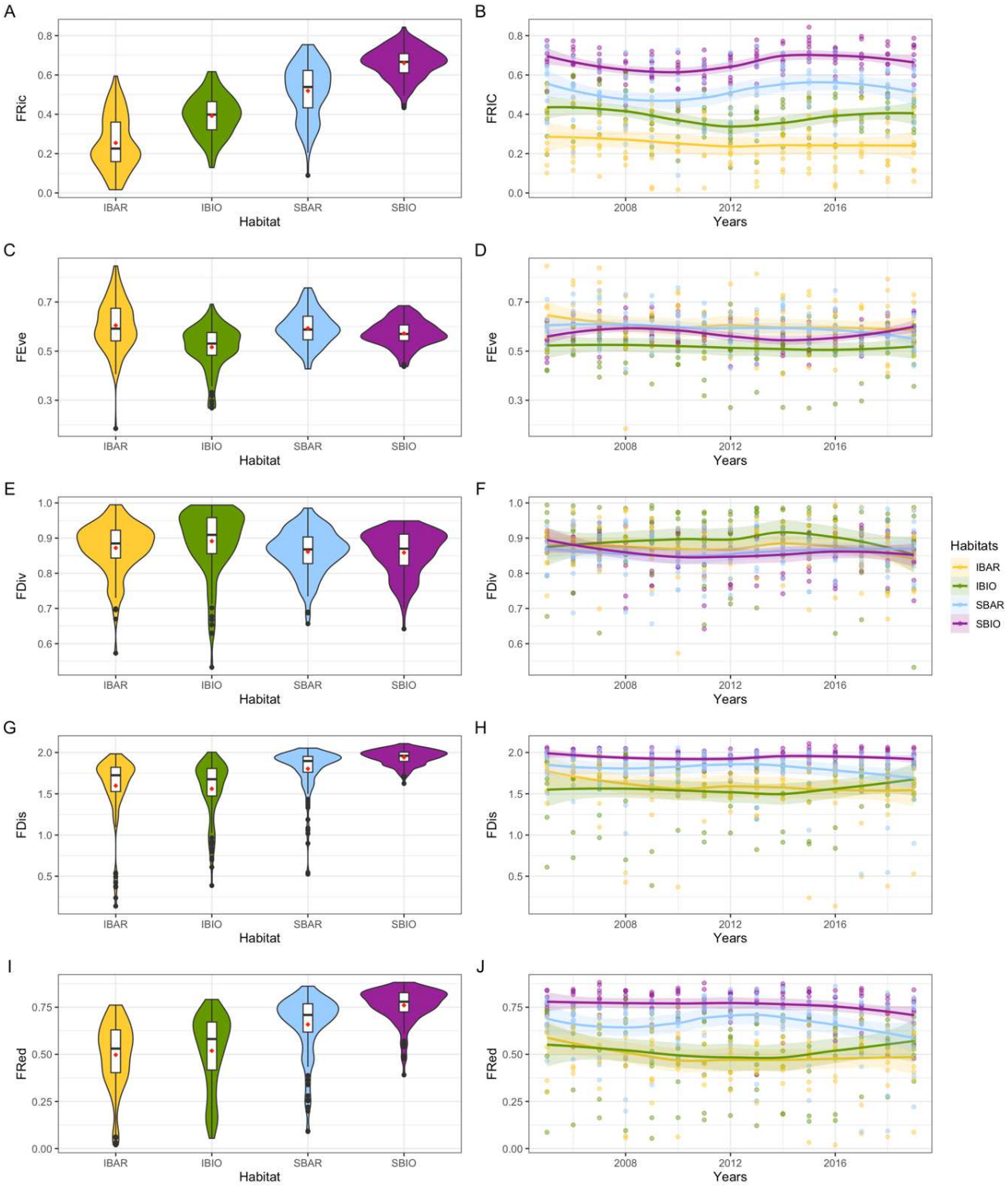


FIGURE 3: Comparison of functional α diversity indices between habitats: functional richness (FRic, A and B), functional evenness (FEve, C and D), functional divergence (FDiv, E and F), functional dispersion (FDis, G and H) and functional redundancy (Fred, I and J). Violin and box plots on the left represent the indices distribution within each habitat, i.e., taking into account all within-habitat observations, red diamond indicates the mean of the distribution. Right panels represent the temporal variation of functional indices, one point represents the index value of a site in a given year, lines represent the habitat-wise trend of each habitat and was obtained through a loess (local polynomial regression fitting). The envelopes surrounding these average trends represent their 95% confidence interval. IBAR = intertidal biogenic habitat, IBIO = intertidal biogenic habitat, SBAR = subtidal bare habitat, SBIO = subtidal biogenic habitat.

3.2. Within-habitat β diversity

Triangle plots representing within-habitat functional β diversity decomposition into functional richness difference and functional replacement are shown in Figure 4. In all pairwise comparison, IBAR presented the highest functional dissimilarity between sites or years, mostly driven by functional richness differences even if some observations seemed to have highest functional richness difference values than other. On the contrary, SBIO harbored the highest spatiotemporal stability with the highest similarity between years or sites. The four habitats presented almost the same proportion of functional replacement between observations and the dissimilarities seemed driven mostly by functional richness differences. Within-site analyses inform on the temporal variation within sites of the habitat considered, whereas within-year analyses inform on the spatial variation within a habitat. In within-site analyses, the similarity between observations increased in the four habitats whereas it remained approximately the same as the general pattern in within-year analyses, meaning that within-site β diversity was mostly driven by the spatial differences between sites than the temporal variation within a site, and especially by functional richness differences between sites.

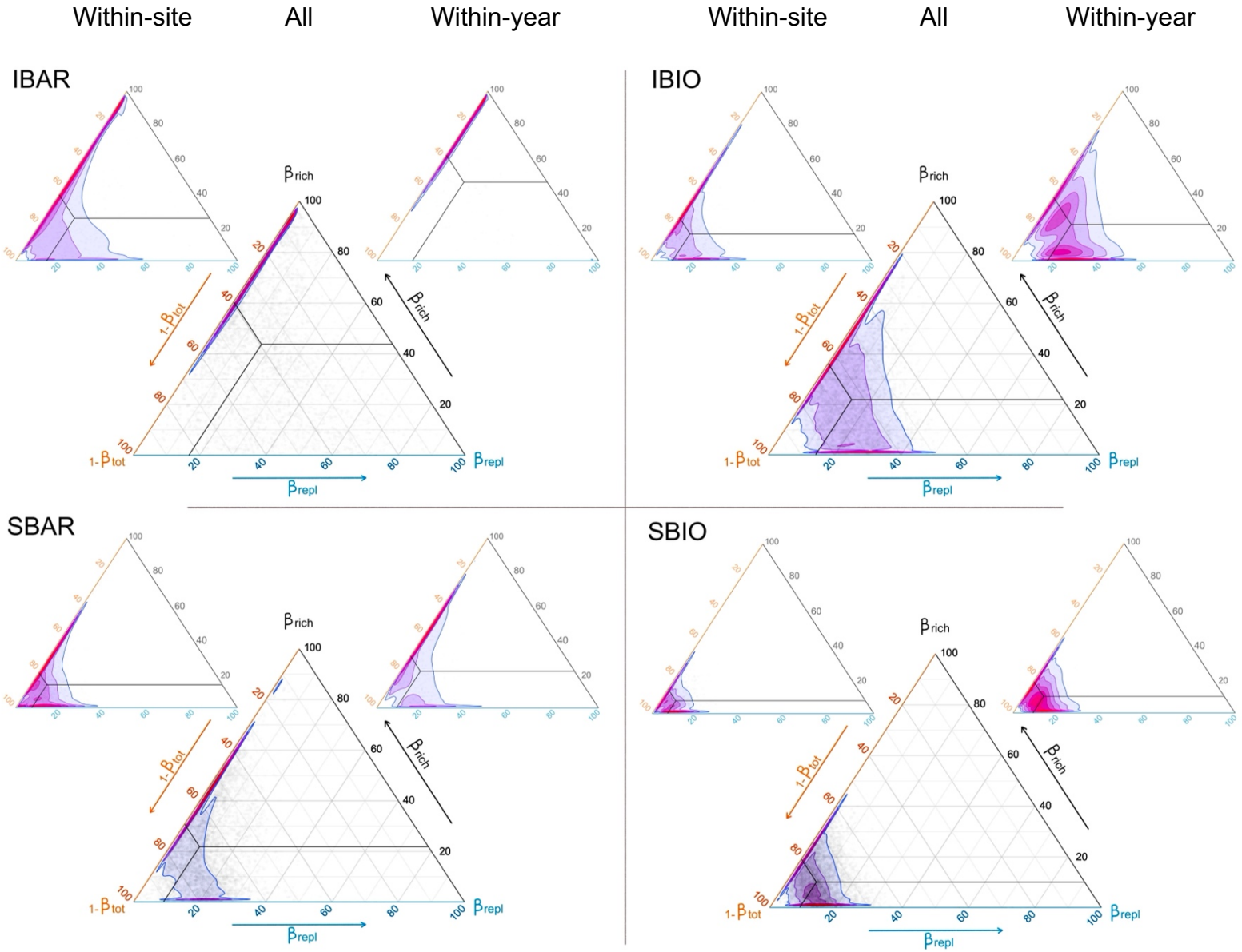


FIGURE 4: Triangular plots illustrating the spatial and temporal variation of the functional β diversity within each habitat: functional similarity ($1 - \beta_{tot}$) is decomposed into functional replacement ($\beta_{replacement}$) and functional richness difference ($\beta_{richness}$). In each panel, larger triangles represent all pairwise comparisons (i.e., comparisons between all sites and years within a habitat), left triangles represent within-site comparisons (i.e., representing the temporal variation only) and right triangles the within-year comparisons (i.e., representing the spatial variation only). Points in large triangles represent one observation; the density of points was also estimated by two-dimensional kernel with high densities in red and low densities in blue. The line represents the mean on each axis. IBAR = intertidal biogenic habitat, IBIO = intertidal biogenic habitat, SBAR = subtidal bare habitat, SBIO = subtidal biogenic habitat.

3.3. Between-habitat functional β diversity and drivers

RDA models explained 44.4% of variance in the intertidal zone and 49.9% in the subtidal zone (adjusted R^2), both were significant ($p < 0.001$) (Figure 5 and 6). The first two axes represented 33.54% of the total variance in the intertidal and 31.89% in the subtidal. Within the two tidal levels, the main driver of variability on the first axis was the type of habitat (bare or biogenic). In the intertidal (Figure 5), the first axis separated sites on the left where there was a high variability in current velocity and a high mean bottom temperature *versus* low variability in current velocity and low mean bottom temperature on the right. Sites at the top were more exposed to hydrodynamics condition (high fetch) than sites at the bottom (muddy sites). IBAR seemed more characterized by highly mobile, microphagous, and biodiffusers Polychaeta while IBIO seemed characterized by downward and upward conveyors and Polychaeta with a lecithotrophic development. In the subtidal (Figure 6), the first axis of the RDA plot separated coarse grains on the left and finer grains on the right and the second axis muddy sites at the bottom and sites exposed to higher salinity values at the top. SBAR was characterized by semelparous, surficial modifiers Polychaeta while SBIO was characterized by iteroparous and epibenthic Polychaeta.

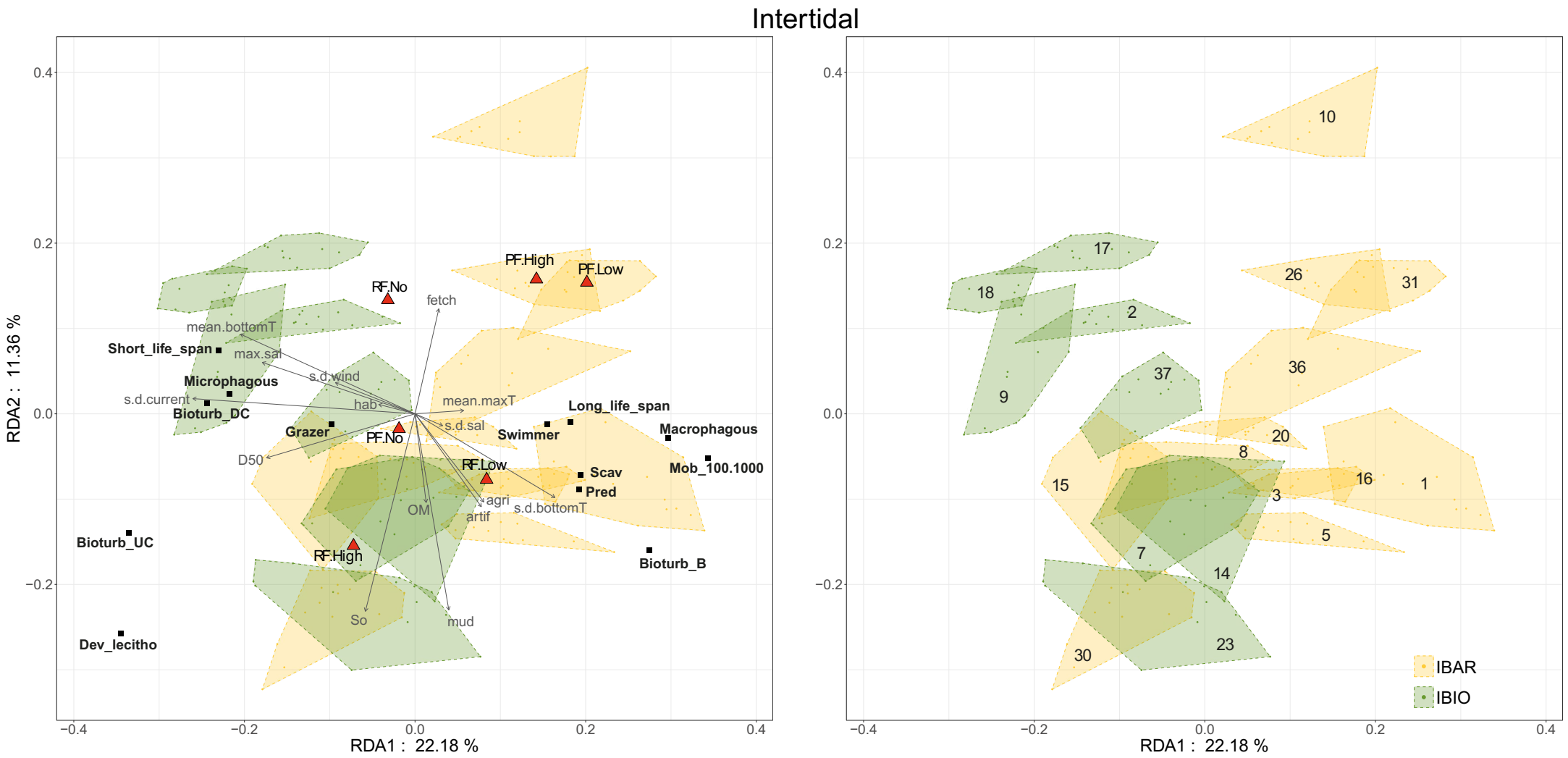


FIGURE 5: RDA triplots (scaling 2 – linear combinations) for the intertidal zone, only the first two canonical axes are represented. The percentages represent the proportion of total variance explained by each axis. Solid arrows represent the abiotic variables. Red triangles are the centroids of each level of the categorical variables (i.e., fishing pressures). Squares represent a subset of trait modalities whose variances along these two axes represent more than 25% of their total variances along these two axes (assessed with the "goodness" function of the "vegan" package). Points represent the fitted observations, all observations from a single site are grouped within a convex hull. Numbers in the right panel are sites. Full description of abbreviations can be found in Chapter II, Table 1. IBAR = intertidal bare habitat, IBIO = intertidal biogenic habitat.

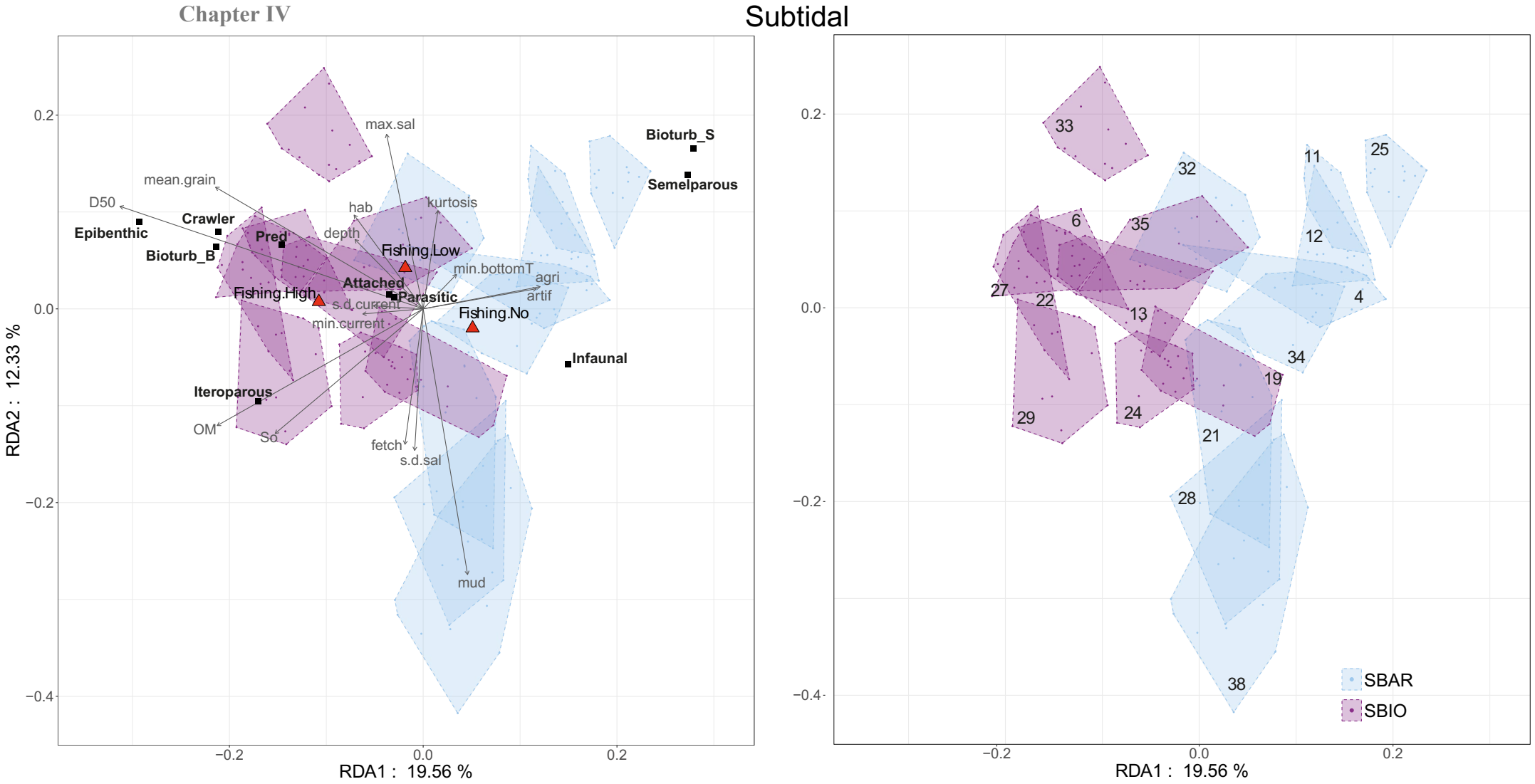


FIGURE 6: RDA triplots (scaling 2 – linear combinations) for the subtidal zone, only the first two canonical axes are represented. The percentages represent the proportion of total variance explained by each axis. Solid arrows represent the abiotic variables. Red triangles are the centroids of each level of the categorical variables (i.e., fishing pressures). Squares represent a subset of trait modalities whose variances along these two axes represent more than 25% of their total variances along these two axes (assessed with the "goodness" function of the "vegan" package). Points represent the fitted observations, all observations from a single site are grouped within a convex hull. Numbers in the right panel are sites. Full description of abbreviations can be found in Chapter II, Table 1. SBAR = subtidal bare habitat, SBIO =subtidal biogenic habitat.

When considering habitat type (bare or biogenic) as an explanatory factor in hierarchical partitioning, models explained 46.9% and 52.7% of variance in the intertidal and subtidal zone respectively (Figure 7). Proxies of anthropogenic pressures had the highest individual importance in the intertidal zone followed by sediment characteristics, habitat type and hydrodynamics variables which had approximately the same individual importance. In the subtidal zone, sediment characteristics and proxies of anthropogenic pressures had the highest individual importance with approximately the same values, followed by the type of habitat in third position.

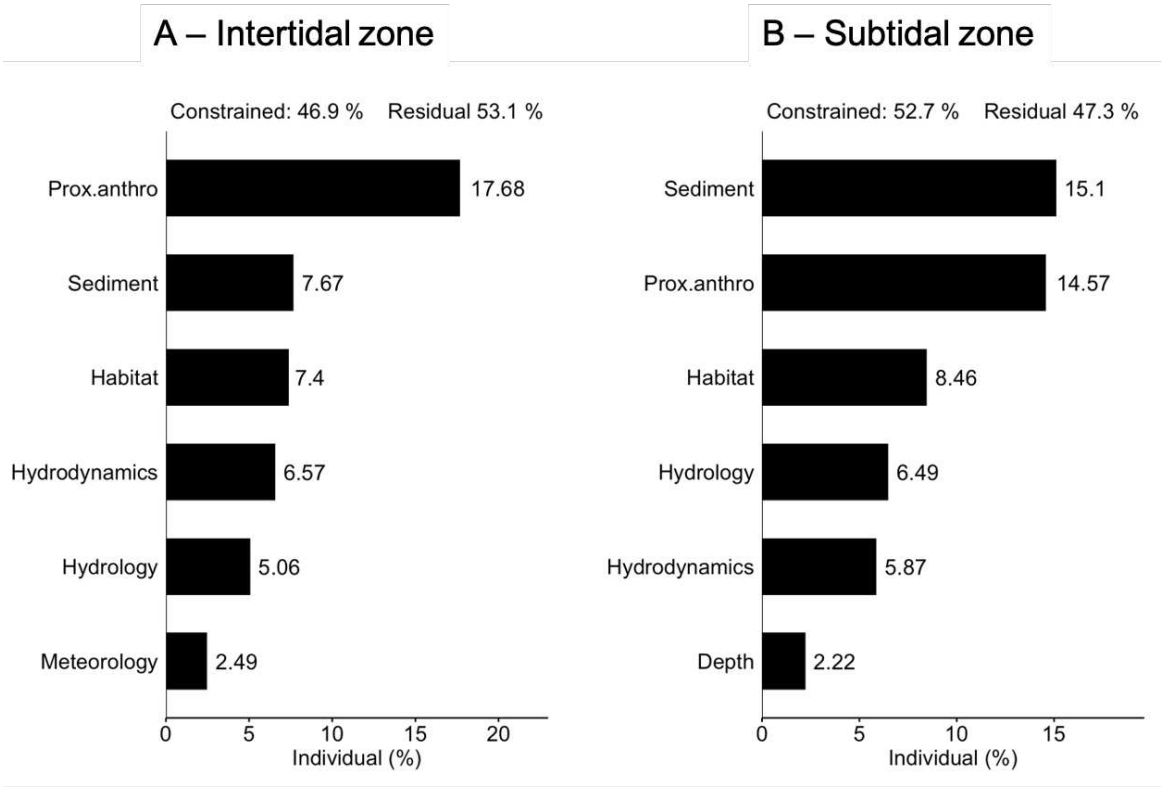


FIGURE 7: Individual contribution of each category of selected abiotic variables assessed by hierarchical partitioning in the intertidal zone (A) and the subtidal zone (B). "Constrained" indicates the total explained variation (adjusted R^2) and "Residual" the variation unexplained by the RDAs computed before hierarchical partitioning.

4. Discussion

4.1. Functional α and β diversity patterns

Biogenic habitats have been shown to enhance functional richness compared to bare habitats (Henseler et al. 2019; Boyé et al. 2019; Stelzer et al. 2021). With higher structural complexity biogenic habitats may increase niches availability (e.g., via the three-dimensional structure of maerl beds or the root-rhizome system of *Zostera* meadows) and availability of food and shelter, as well as buffer the effect of environmental conditions, thus allowing the settlement of diverse taxa supporting different ecological functions (Boström et al., 2006; Boström and Bonsdorff, 1997; Stelzer et al., 2021).

Functional richness was more homogeneously distributed in biogenic habitats, indicating higher spatial and temporal variations in the functional composition of bare habitats. Considering the temporal stability of FRic in all habitats and the importance of functional richness differences in site-to-site (i.e., within-year) comparisons in bare habitats, it appeared that some bare habitats supported wider functional spaces than others. One hypothesis might be that habitat structures of biogenic habitats buffered the effect of the environmental gradient on communities (Peterson et al. 2004; Bulleri et al. 2018) allowing to maintain a more constant functional pool within these habitats at the regional scale. Moreover, it has been demonstrated that seagrass beds in sheltered localities can support very similar suites of macrobenthic taxa with similar traits even in different oceans, suggesting that seagrasses can provide a standard suite of niches independently of their locality (Barnes and Hendy 2015). On the contrary, intertidal bare sediments showed higher between-site variability, potentially because sites exposed to hydrodynamics conditions had their communities more often reset (Defeo and McLachlan 2005; Boyé et al. 2019) than those in more sheltered areas (*cf.* Chapter I).

In contrast to FRic, functional evenness was higher in bare habitats, especially in the intertidal zone: each ecological role was supported by similar species richness and abundance (Villéger et al. 2008). This pattern was already demonstrated in the study of Boyé et al. (2019) and Stelzer et al. (2021) observed the same between maerl beds and the underlying bare sediment in Brazil. As discussed in Chapter I and argued by Boyé et al. (2019), the numerous transient species in IBIO, with low abundances and occurrences, might support a combination of unique traits different from dominant taxa. It might be the same for the rare species in SBIO even though FEve differences between SBIO and SBAR were much less pronounced.

High evenness might increase community resistance (McLean et al. 2019a) which might explain the relative preservation of the functional structure over time in bare habitats in our

study. Functional redundancy is another factor that may provide a buffer against the effect of species losses on trait diversity and help to maintain the functional structure of the communities (Micheli and Halpern 2005; McLean et al. 2019a). Here, SBIO was the habitat with the highest functional redundancy: this habitat harbored a high diversity of functional traits, with species with relatively unique traits compared to the functional regional pool (high FDis). These traits were represented by a high proportion of species and/or individual, which might enhance the recovery and resilience potential of this habitat. Indeed, some species could take on critical functional roles if other failed in case of a disturbance. In the best-case scenario, if common species share combinations of functional traits with rare species, ecosystem functioning might be maintained despite the loss of rare species which can be often the first to disappear (Ellingsen et al. 2007; Mouillot et al. 2013a).

Yet, further analyses might be needed to assert this in SBIO. When comparing the two biogenic habitats, the functional space of IBIO was organized differently from SBIO since both functional evenness and redundancy were low. Moreover, in IBIO, dominant species supported specialized functional traits at the edge of the functional space (high FDiv). Indeed, species in IBIO might be more adapted to a microphagous feeding mode as seagrass canopies may favor the accumulation of organic material (Hu et al., 2022). As demonstrated by Boyé et al. (2019), species in IBIO shared similar characteristics fairly different from all other species from the regional pool. As evenness is low in this habitat, if dominant species are sensitive to disturbances or support vulnerable traits, then communities could be highly impacted in case of disturbance. However, it is important to note that the choice and number of traits could have important impacts on trait diversity patterns and redundancy, for example if communities have high redundancy along one trait axis but little along another (in our study only three axes were taken) (Micheli and Halpern 2005; Violle et al. 2007; McLean et al. 2019a).

As stated above, functional β diversity within habitats was mostly driven by spatial functional richness differences whereas functional replacement was low in all habitats: although there were differences in the volume occupied in trait space between observations, overall, the same pool of traits was maintained in IBAR, SBAR and SBIO. In IBAR, observations were the most dissimilar and it was rather due to spatial than temporal variability. On the contrary, functional similarity was high in SBIO both in space and time. This is in line with the study of Boyé et al. (2019) that showed that most functions of the regional pool were found in each SBIO site while bare sediments only harbored this diversity of traits at the regional scale thanks to their high within-habitat β diversity. Moreover, Brittany harbors a mosaic of benthic habitats (Gallon et al. 2017), which might enhance facilitation and promote multi-functionality at the

regional scale (Alsterberg et al. 2017). Even though the functional structure of the four habitats seemed generally preserved during the 15 years, it is worth noting that some within-site comparisons in IBAR still presented a high dissimilarity driven by functional richness differences between two (not necessarily consecutive) years. As stated above, sandy beaches are highly variable environments and the effect of extreme events and sediment modification in more exposed localities might have led to more variation in community and functional structure over time (*cf.* Chapter I).

4.2. Environmental drivers of functional β diversity

RDA models between trait composition and environmental variables and proxies for anthropogenic pressures allowed to identify the drivers of functional β diversity between biogenic and bare habitats in the intertidal and subtidal zones. These analyses clearly showed marked differences between biogenic and bare habitats within a tidal zone, although habitat type ranked third in hierarchical partitioning within the two tidal zones.

In the intertidal, proxies of anthropogenic pressures ranked first while they explained approximately the same proportion of variance as the sediment characteristics in the subtidal zone. Anthropogenic pressure proxies were clearly related to habitat type in this case as there is no professional fishing in IBIO and no high level of fishing pressure was recorded in SBAR. Yet, when removing these pressures from RDAs (Appendix 3) the global structure did not change. As discussed in Chapter II, fishing pressures could also be linked to favorable environmental conditions, thus the collinearity between fishing pressures and habitat type or environmental conditions can blur their real effect on the functional structure of the communities (Frid 2000; Jac et al. 2022). However, the high effect of the proxies of anthropogenic pressures could not be totally excluded, especially in the intertidal where communities are exposed to both terrestrial and marine constraints and frequent stresses more rarely encountered in the subtidal (Moran 1999; Helmuth et al. 2006). Indeed, some changes in species distribution in communities exposed to stressors can be linked to their functional traits such as body-size, motility or life-span (Bremner et al. 2003; Queirós et al. 2013). For example, trawling or dredging can promote predators or scavengers (Ramsay et al. 1998; Dannheim et al. 2014) and motile organisms (Hall-Spencer et al. 1999) while sewage pollution can enhance deposit-feeders (Poore and Kudenov 1978). Thus, the alteration of marine communities can disrupt the ecological functions that species assemblages perform (Micheli and Halpern 2005) and potentially impairs ecosystem services (Cadotte et al. 2011).

Sediment characteristics had the highest individual importance in the subtidal zone and the second highest importance in the intertidal zone. Therefore, the different sediment characteristics found between biogenic and bare habitats in the two different tidal zones could explain the presence of different species that support different ecological traits in our study. Indeed, sediment characteristics are a determining factor that control the presence of the soft-bottom fauna as each species can tolerate a specific sediment particle range (Snelgrove and Butman 1994) while hydrodynamics can alter sedimentary environments such as in highly exposed sandy beaches. Moreover, sediment characteristics are factors that can depend on the type of habitat considered as seagrass beds enhance sediment stability and cover fine sediment (Boström and Bonsdorff 1997; Duarte 2002) and maerl beds can change the sedimentary habitat for macrofauna (e.g., through high content of dead fragments) (Foster 2001; Stelzer et al. 2021).

Some authors discussed that biogenic habitats themselves could better explain the taxonomic and functional composition of invertebrate assemblages by promoting and diversifying primary production, thus trophic inputs (Grall et al. 2006; Berlandi et al. 2012; Henseler et al. 2019; Stelzer et al. 2021; Kindeberg et al. 2022). Although we incorporated the indirect effect of habitats (by indicating the type of habitat considered), we did not consider habitat structure effects in this study (e.g., biometry variables as in Chapter II) in order to compare biogenic and bare habitats with the same set of explanatory variables within each tidal zone. Further analyses may be needed to assess their effect on the macrofaunal communities studied.

Additionally, RDAs showed that some IBAR sites were less distinct from IBIO sites than other IBAR sites, potentially because of a similar functional structure to IBIO sites. Indeed, these sites were located close to a seagrass bed, possibly allowing larval exchanges and migration between the two habitats (Boyé et al. 2019) and a potentially higher functional diversity in these IBAR sites due to the edge effect of seagrass beds (Hu et al. 2022). It is also possible that these nearby sites were subject to the same local environment allowing close functional patterns.

The distribution of modalities modeled by the RDAs also demonstrated opposing ecological processes between the habitats. In the intertidal zone, seagrass structures might favor the capture and accumulations of detritus and other organic particles (Hu et al. 2022) which can explain why microphagous species (i.e., suspension feeders, deposit feeders) were mostly associated with this habitat while macrophagous (i.e., scavengers, predator or carnivores) were mostly associated with IBAR. Moreover, the models predicted a predominance of highly mobile Polychaeta in IBAR. Motility of Polychaeta could be related to their feeding modes (Jumars et

al. 2015), indeed an active motility is essential in order to capture preys but also to escape predators (Gibson et al. 2001). Another hypothesis could be that highly mobile species are favored in environment where the sediment is often reorganized or resuspended by high wave energy, allowing them to quickly find shelter on the bottom (Quillien 2016).

The presence of short-lived species in IBIO and long-lived ones in IBAR was quite unexpected as long living species are more often found in stable and less disturbed conditions (Ghodrati Shojaei et al. 2015) as encountered in IBIO. However, Breine et al. (2018) found that, in the Southern North Sea, coarse sands were dominated by free-living, scavengers, predators and biodiffuser species (as in IBAR), while fine sands were dominated by suspension and deposit feeders with short life span (as in IBIO). In the subtidal zone, maerl beds were associated with epibenthic iteroparous and biodiffuser taxa and bare sediments with infaunal semelparous taxa. The complex tridimensional structure of maerl beds creates a wide variety of microhabitats enhancing the presence the presence of taxa living above the substrate (Berlandi et al. 2012), in particular of taxa of rocky affinity that could not live in soft bottoms (Foster 2001). Moreover, coarser sediments might enhance the presence of biodiffusers (Breine et al. 2018). Again, it highlighted the significant effect of sediment characteristics on the functional structure of the macrofauna. Current knowledge on polychaeta reproduction and development mode as well as the links between certain modalities and the environment does not allow to draw robust hypothesis between traits modality and the habitat conditions. Yet, we can expect that functional modalities requiring a higher environmental stability might be found in habitats with milder environmental conditions (e.g., upward and downward conveyors might be favored in a stable sediment as in IBIO in order to maintain their position in the sediment).

5. Conclusion and perspectives

The functional structure of the four habitats appeared to be relatively maintained over time although they showed different functional patterns. Indeed, IBAR was the least functionally rich but harbored high functional evenness. Moreover, the different species in IBAR showed strong dissimilarity in terms of functional richness but, on a regional scale, represented a large part of the regional species pool. IBIO covered dominant species with specialized traits and was unique with respect to the regional trait pool. However, the latter presented low equitability and redundancy. SBAR had a high functional evenness and an intermediate profile regarding the other functional indices. SBIO had the highest functional richness, a high proportion of species with unique traits and high functional redundancy. In this habitat, the sites were highly similar in space and time and represented all the traits of the regional pool.

When considering the mechanisms involved in the observed functioning stability, the high functional evenness in bare habitats as well as the high within-habitat β diversity in IBAR may have allowed the maintenance of the functional structure over the 15 years. In SBIO, the high functional redundancy could have allowed this stability. In IBIO, on the other hand, the preservation of functional traits might have been possible due to the environmental buffering effect of this habitat. One perspective might be to identify how unique or common traits are distributed between the Low Occurrences Low Abundances Species (LOLAS, *cf.* Chapter I) and the common ones. This would allow to better understand the response of communities to future changes, e.g., their resilience might be increased if LOLAS and common species share unique traits but they might be more affected if LOLAS support unique and essential functions.

Sediment characteristics closely linked to the type of habitat considered appeared to be the main drivers of the functional β diversity. Proxies of anthropogenic pressures also played a non-negligible role that should be better understood in order to set up effective management strategies. Analyses such as those conducted in Chapter II could be used to better disentangle the spatial, temporal and abiotic drivers and better understand the importance of each abiotic variable to the functional β diversity.

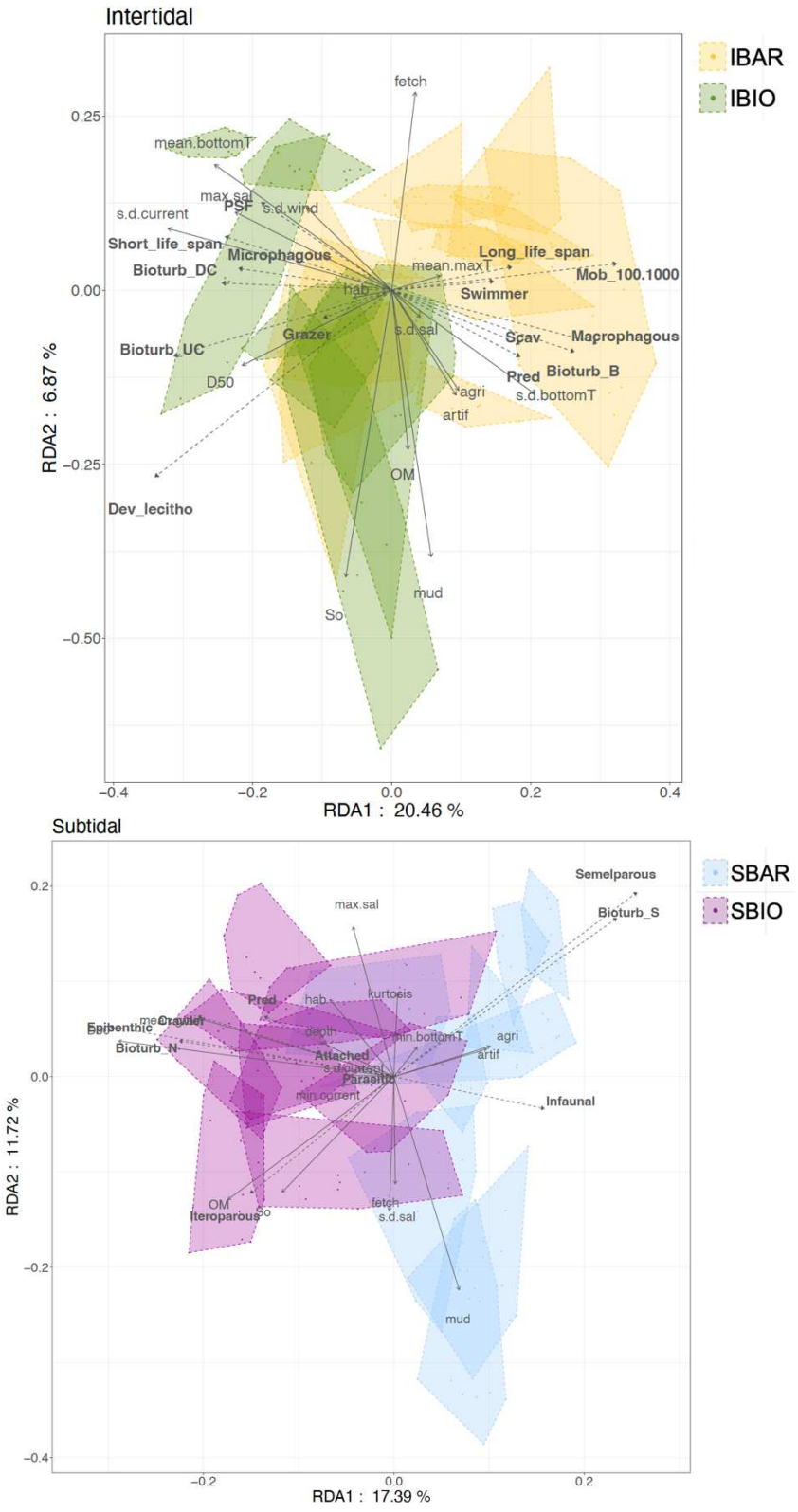
Appendices

Appendix 1: Fuzzy coding procedure of (Boyé et al. 2019) used in this study.

"In our coding procedure, a species expresses each modality of a given trait on a scale from 0 to 4, with 4 being an exclusive affinity for a modality (all other modalities of the trait being 0 for that species), 3 a strong affinity for a modality, 2 a mean or uncertain affinity for a modality, 1 an occasional behavior or observed value for the species, and 0 for the absence of the modality. When the species expressed several modalities of a trait without marked preferences, or with unknown preferences, it was coded 2 for all modalities expressed and 0 for those not expressed. On the other hand, when species expressed marked preferences for some modalities of a trait while expressing others occasionally, the preferred modalities were coded 3, the occasional modalities were coded 1 and those not expressed were coded 0. This coding procedure accounts to some extent for the plasticity of species and allows the incorporation of within-species variability in the functional analysis." (Boyé et al. 2019)

Appendix 2: List of observations with less than 5 taxa that were removed for the creation of the functional space and the computation of the different functional indices. IBAR = intertidal bare habitat.

Site	Year
IBAR – Blancs Sablons	All
IBAR – Saint Briac	All
IBAR – Baie du Mont Saint Michel	2009-2010-2011-2012-2013-2014
IBAR – Erdeven	2005-2011-2012-2014-2016-2017
IBAR – Kerjouanno	2009-2011
IBAR – Plage de l'Aber	2012-2013-2017
IBAR – Saint Efflam	2010-2011



Appendix 3: RDA triplots (sc – – linear combinations) for each tidal zone without fishing pressures, only the first two canonical axes are represented. The percentages represent the proportion of total variance explained by each axis. Solid arrows represent the abiotic variables. Dashed arrows represent a subset of trait modalities whose variances along these two axes represent more than 25% of their total variances along these two axes (assessed with the function "goodness" of the "vegan" package). Points represent the fitted observations, all observations from a single site are grouped within a convex hull. Full description of abbreviations can be found in Chapter II, Table 1. IBAR = intertidal bare habitat, IBIO = intertidal biogenic habitat, SBAR = subtidal bare habitat, SBIO = subtidal biogenic habitat.

Discussion & Perspectives

1. Discussion in English

1.1. Habitat-dependent mechanisms

Throughout the chapters, the study of the spatiotemporal dynamics of the four monitored habitats revealed different habitat-dependent mechanisms. Indeed, the dynamics highlighted were not specific to one tidal zone or one type of habitat (i.e., bare or biogenic) but specific to each habitat independently, even though some similarities appeared within tidal zone and habitat type. Although a regional-scale stability was demonstrated, Chapter I highlighted habitat differences in terms of taxonomic dynamics and drew up hypotheses concerning these differences. These latter might depend on the number of taxa and Low Occurrence and Low Abundance Species (LOLAS) in each habitat and whether these species are "rare" or "transient" as defined in Chapter I, the different biotic and abiotic interactions within each habitat and the nature of the habitat (i.e., bare or biogenic or the identity of the foundation species).

Chapter II showed that each habitat dynamic responded differently to environmental and anthropogenic drivers. In all habitat, the effect of space was greater than the temporal effect on macrofauna dynamics, and sediments and hydrodynamics were important drivers of these, as it was already demonstrated in the scientific literature (e.g., Snelgrove 1998; Veiga et al. 2017; Couce et al. 2020). However, Chapter II highlighted the importance of proxies of anthropogenic pressures on macrofauna dynamics in the intertidal zone and advanced the hypothesis that biogenic habitats might dampen the effect of extreme events on the communities rather than the effect of average environmental conditions. Moreover, this dampening effect might be more pronounced in habitats frequently exposed to stressful environments as the intertidal zone than in milder environments.

Chapter IV showed that each habitat presented specific functional structure and functional spatiotemporal dynamics that also responded differently to abiotic drivers. Although the difference of functional structure between bare and biogenic habitats was clearly marked, the way these functions were expressed within two same habitat types (i.e., bare/bare or biogenic/biogenic) also clearly differed. For example, with higher functional evenness and heterogeneous functional richness between sites in IBAR compared to SBAR, or with dominant taxa supporting distinct traits from the regional functional pool in IBIO compared to SBIO. The latter also expressed higher functional richness, redundancy and functional spatiotemporal stability. A gradient of within-habitat β diversity was observed from bare intertidal to biogenic subtidal habitats. IBAR being the habitat with the highest within-habitat β diversity mostly driven by functional richness differences between sites. We hypothesized this higher within-

habitat diversity might have allowed the maintenance of the functional regional pool of IBAR. We also suggested that functional stability might be driven by the high evenness of SBAR, principally by the environmental buffering of IBIO and by the high richness and redundancy in SBIO.

Over the chapters, 13 to 15 years were studied and no major changes in the dynamics of the monitored communities were detected. In each chapter, we tried to infer habitat-specific mechanisms that might participate in maintaining this stability. Our interpretations were, for the most part, set up in a habitat-wise manner. However, the monitored habitats are not isolated from each other as they are located in the same regional area, sometimes in the same water masses or in the same bays or beaches. Therefore, they are not fully independent from each other but interconnected in a mosaic of habitats (Gallon et al. 2017), and, in addition to intra-habitat mechanisms, this might play an important role in the depicted stability. Indeed, habitats might facilitate each other and an increasing diversity of habitats might enhance meta-ecosystem multifunctionality independently of species diversity (Alsterberg et al. 2017). In our case, the significant habitat diversity can be further multiplied if we consider the different physical settings encompassed by the four distinct habitats we studied as separate habitats, e.g., coarse sediment and muddy sediment could be considered distinct. Moreover, on a landscape scale, alternating patches with autogenic (e.g., seagrasses or maerl beds) and allogenic ecosystem engineers (e.g., bioturbators) are expected to produce the highest possible total diversity and species richness (Bouma et al. 2009a), which might enhance communities' stability through portfolio effects or the insurance hypothesis (Yachi and Loreau 1999).

Furthermore, we mostly considered the two biogenic habitats as structured by a single entity (i.e., the foundation species considered), however these habitats actually harbor nested foundation species (Angelini et al. 2011). Indeed, maerl and seagrass beds are associated with numerous epiphytes (e.g., Helias and Burel 2023). These species increase habitat complexity and facilitate different suites of organisms through habitat cascade, and are thus critical to maintaining communities' stability (Thomsen et al. 2010; Angelini et al. 2011). These foundations species not only shelter infaunal communities but also epifaunal ones. Epifauna can facilitate infauna through indirect effects. For example, the consumption of epiphytes by epifauna induces sedimentation of fecal pellets providing organic matter to infaunal communities (Jankowska et al. 2019). Epifaunal communities play an important role in the functioning of marine ecosystems as they provide a critical trophic link between benthic primary producers and higher order-consumers (Chen et al. 2021). Their spatiotemporal dynamics can be decoupled from those of the infaunal communities (Boyé et al. 2017), thus

one perspective could be to jointly consider the dynamics of these two communities in future work (Figure 1) in order to better characterize ecosystem dynamics, that might help to set more reliable management strategies.

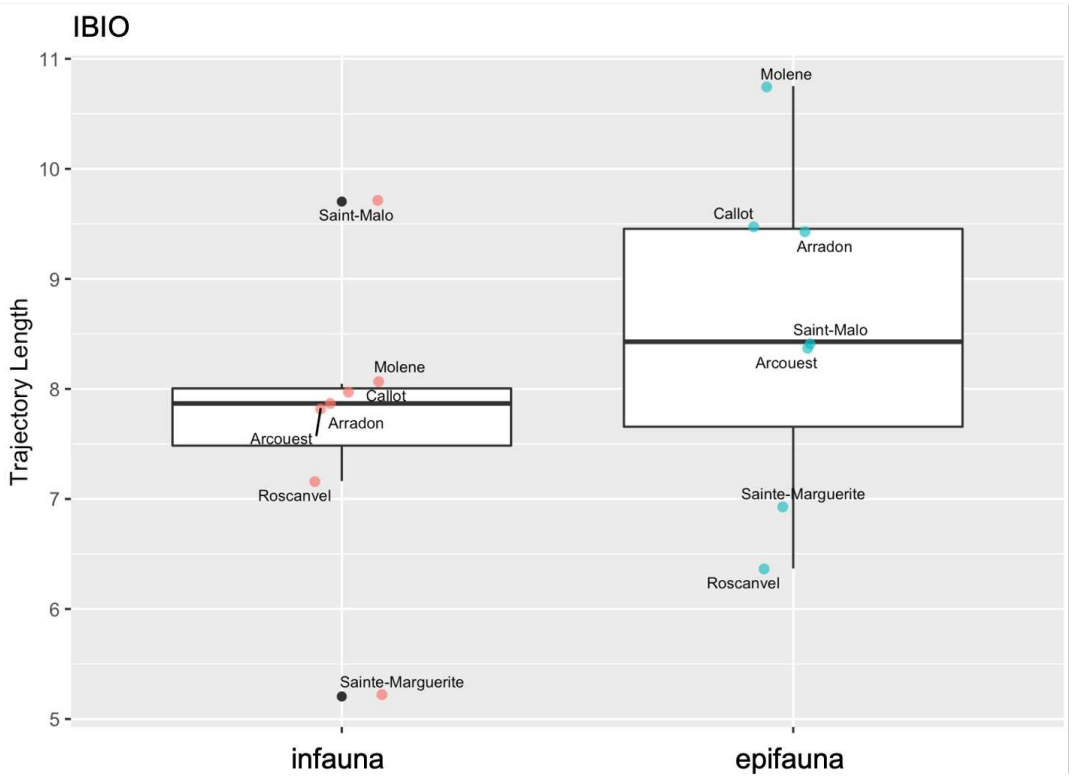


FIGURE 1: Comparison of trajectory lengths between infauna and epifauna communities in the intertidal biogenic habitat (IBIO). One point corresponds to the value for one site. Sites and years considered are the same as in Chapter I.

As a consequence, the stability patterns we depicted are certainly dependent on the location of our study. Bare habitats that are not embedded in a network of multiple biogenic or non-biogenic habitats might show different patterns, as already depicted by the various dynamics exposed worldwide by these habitats (e.g., Hinz et al. 2011; Frid 2011; Beukema and Dekker 2020). Moreover, the dynamics of the two biogenic habitats might also change depending on the stress gradient to which they are exposed. Indeed, according to the stress-gradient hypothesis, ecosystem engineers can alleviate physical stress in extreme physical environment while they can support ecosystem processes by providing competitor or predator free space in physically benign environment (Crain and Bertness 2006; Watt and Scrosati 2013). The identity of species forming these habitats might also have an effect on the macrofauna dynamics, as well as their patchiness or the complexity of their structures (Bouma et al. 2009b; Berlandi et al. 2012; Solano-Barquero et al. 2022), thus an intra-habitat variability in

macrofauna dynamics could also be investigated. In the light of these potential confounding effects, the question whether the outcomes of the different chapters are the norm remains open as they might, for example, be dependent on the regional and biogeographic context.

No regime shift or particular trends were found in the investigated natural environmental variables, therefore the depicted stability might also result from the general temporal stability of abiotic forces over time in the region. However, the mechanisms we highlighted might help us formulate hypotheses on the potential responses of habitats exposed to stronger stresses or disturbances. In facilitative habitats, response of communities to warming for example, might be undetectable until a tipping point is reached with the degradation or loss of the facilitative habitat (Jurgens et al. 2022). Thus, I expect the communities of maerl beds to be highly resilient in case of increasing environmental variability. However, in case of disturbances leading to habitat destruction, I hypothesize that, beyond a certain threshold, there would be no foreseeable return whereas this option might be more realistic in seagrass beds (Figure 2). Indeed, the slow-growth rate of rhodoliths and the way they reproduce (Foster 2001; Foster et al. 2013) renders the implantation of maerl beds on bare habitats difficult. On the other hand, the dispersal of seagrass seeds *via* hydrochory or zoochory for example (Orth et al. 2006), might facilitate their implantation. Moreover, I hypothesize that the destruction of these biogenic habitats will indirectly affect bare ones (Figure 2). Indeed, in the intertidal zone for example, IBAR sites sampled in the vicinity of IBIO showed higher species richness (e.g., see sites n° 5 and 9 in Appendix 2 of Chapter I) and more similar functional spaces (see Chapter IV), potentially because of exchanges between these two habitats (e.g., larval supply, colonists, resources supply, spillover). The “edge effect” has been conceptualized as an ecological change due to moving away from a core area of a habitat patch (Ries et al. 2004). It has already been demonstrated that edge habitats promote functional diversity (Gayer et al. 2019; Hu et al. 2022). Thus a potential habitat homogenization would decrease the diversity and multifunctionality of the meta-ecosystem (Alsterberg et al. 2017), negatively affecting exchanges between habitat patches, and potentially the stability of the communities.

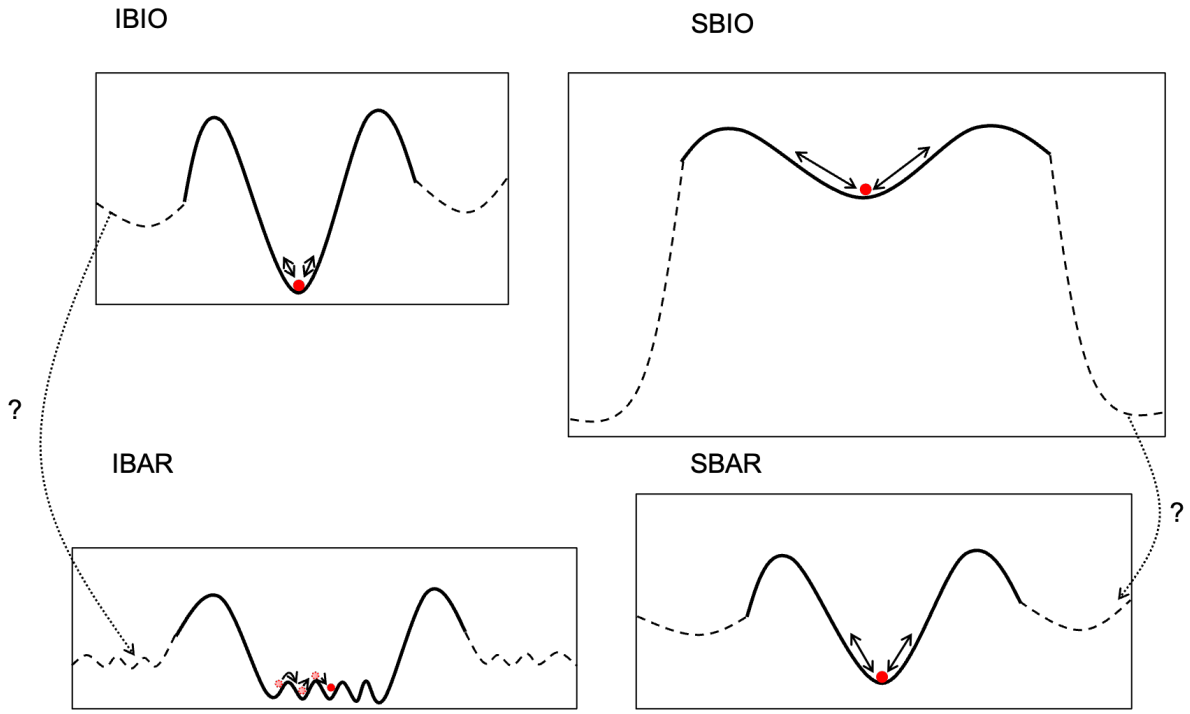


FIGURE 2: Ball and cup representation of each habitat state as depicted in Chapter I (solid lines) and hypothetical state (dashed lines) in case of biogenic habitat destruction. IBIO would shift in a less stable state (less narrow cup) with hypothetically more chance of return than SBIO. Destruction of biogenic habitats would hypothetically lead to shifts to less stable states in bare habitats (IBAR and SBAR). IBAR = intertidal biogenic habitat, IBIO = intertidal biogenic habitat, SBAR = subtidal bare habitat, SBIO = subtidal biogenic habitat.

Over the chapters, we mainly explained the dynamics observed with abiotic drivers or dbMEMs, and we briefly discussed how biotic interactions could affect these dynamics relying on existing scientific knowledge. In variation partitioning, the unique fraction modelled by spatial or temporal dbMEMs can be attributed to biotic interactions. In Chapter II, this fraction was significant, suggesting it would be fruitful to better apprehend these interactions in future work. The Hierarchical Modeling of Species Communities (HMSC) method offers a promising way to incorporate these biotic interactions (Ovaskainen et al. 2017a, 2017b; Violet et al. 2022). It decomposes observed species co-occurrences into those that can be explained by environmental covariates and those that cannot. Biotic assemblages are modeled through species-species association matrices that can be estimated at multiple spatial or temporal scales. In addition, this method allows for the consideration of species functional traits in estimating species response to environmental covariates. Species-species co-occurrence patterns and how they change in space and time is one of the tools that can sharpen our understanding of ecosystems dynamics and how it may affect their structure and function (Li et al. 2018).

1.2. Benthic ecology or the ecology of the rare?

Over the 14 years studied in Chapter I, on average 29 to 42% of species were detected only once at each site over the time series, while on average 2 to 7% were detected each year. Many names and interpretations have been given to these infrequently observed species, such as “accidental”, “occasional”, “transient” (Magurran and Henderson 2003; Snell Taylor et al. 2018). Rarity can be spatial, temporal or both and can take many forms (Violle et al. 2017). In Chapter I, we grouped these infrequently observed species as Low Abundances Low Occurrences Species (LOLAS) regarding their spatiotemporal occurrences and abundances in each habitat, and we decided to name as *rare* the species that might be always present but not always detected and *transient* the species that might be observed occasionally as a result of dispersal from adjacent habitats. Although we used graphical results to help us to set a threshold under which species were qualified as LOLAS and over which they were qualified as common, this threshold was still arbitrary and was mainly based on the occurrences of the species. Future work could investigate the way this threshold is set, for example by also using the abundances, as some taxa in our dataset had low occurrences but still high abundances. Moreover, we could strengthen our hypothesis that some species could be qualified as *rare* and other *transient.* One idea could be to look at the functional traits these species harbor as these species may have characteristics that differ from those that are common (Kunin and Gaston 1993). In addition, I hypothesize that *transient* species could harbor traits characteristic of opportunistic or colonist species (e.g., small size, high reproductive capacity and good dispersal) (Norkko et al. 2006). However, a limitation for the study of the LOLAS traits could be the accessibility to traits data since if these species are frequently rare, their functional traits might be less documented.

Rare or transient species are a predominant feature of ecological communities regardless of taxa or ecosystem (Hewitt et al. 2016b; Snell Taylor et al. 2018). In marine benthic ecosystems, they often represent approximately more than 50% and invertebrate communities tend to present higher proportion of these species than plankton or mammal communities (Snell Taylor et al. 2018). Moreover, their number can increase with both within and between-site heterogeneity, establishing an important link between habitat diversity and rarity (Ellingsen et al. 2007) The prevalence of these species renders the estimation of α diversity difficult. Rarefaction (Sanders 1968) and extrapolation methods (Chao et al. 2014) are often used in marine benthic studies to estimate the total number of species and those detected according to the number of individuals or samples. In the four monitored habitat, the number of taxa we detected was surely underestimated, moreover differences can appear depending on the scale of observation considered (Figure 3; note that in this figure, species and abundances of

replicates, points or sites and of 15 years were pooled which blur spatiotemporal differences). One solution could be to adjust the sampling effort in order to decrease bias in richness estimates (i.e., with higher sampling effort when there are many rare species) (Dornelas et al. 2013) or to extrapolate to estimate the asymptote of the accumulation curve (Chao et al. 2014). We could also improve our way of taking detectability into account by borrowing methods from Bayesian modeling (Iknayan et al. 2014).

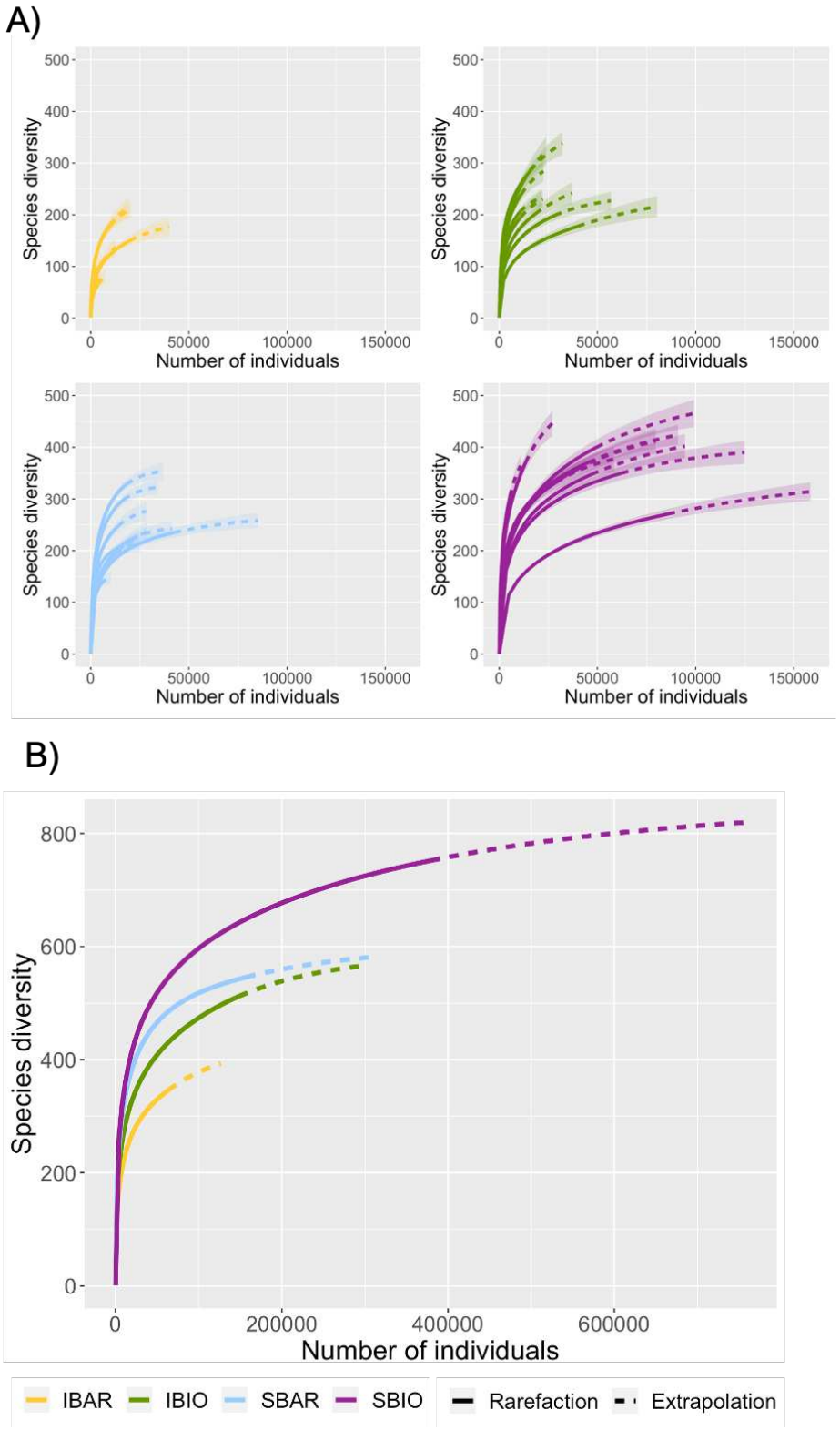


FIGURE 3: A) Rarefaction curves for each site taken into account in the analyses of Chapter II, species and abundances were pooled for the 15 monitored years (2005-2019). B) Rarefaction curves for each habitat taken, species and abundances were pooled for the monitored sites within each habitat and 15 monitored years (2005-2019). The ribbon around the curves which represents the standard error and confidence interval was removed to reduce computation time. For both graphs, the diversity order of Hill numbers used was q = 0 (i.e., species richness).

In Chapter I, we looked at the dynamics of the communities with and without LOLAS to understand the influence of these species on the temporal trajectories but we did not study the dynamics of the LOLAS. After adjusting our method to better detect these LOLAS, I believe that jointly looking at the dynamics and response of the common species and LOLAS, would greatly improve our understanding of ecosystem dynamics. Indeed, considering these species may help apprehend the fraction of LOLAS that can be attributable to detection errors (Iknayan et al. 2014) and quantify the noise it can induce in spatiotemporal dynamics. Moreover, it has been demonstrated that these species can have different dynamics than the core ones (Benedetti-Cecchi et al. 2008) and that they can play a major role in maintaining the stability and resilience of the communities (Henderson and Magurran 2014; Hewitt et al. 2016b). Considering these species in future studies will positively impact our understanding of how communities respond to environmental and anthropogenic constraints and increase the reliability of management strategies (Hewitt et al. 2016b; Snell Taylor et al. 2018).

Rarity is not only taxonomic but also functional. Violle et al. (2017) defined functional rarity as the extent to which species traits are more or less distinct or redundant within local communities or larger-scale. It combines species rarity and trait distinctiveness, where the functional rarest species have low abundance and the most distinct traits. In their framework they also proposed indices of functional distinctiveness (which assesses whether a species is more or less functionally close to the rest of the community) and functional uniqueness (which assesses the extent to which a species has no functional equivalent in the regional pool). Looking deeper into the traits supported by common species and LOLAS could be critical to understand the degree to which they share combination of their traits (Figure 4), thus how communities could respond to stresses or disturbances and if LOLAS could play a major role in this response (Mouillot et al. 2013a). Indeed, if LOLAS display relatively common functional traits, they would increase community functional redundancy, thus stability and resilience (Ellingsen et al. 2007). If they display distinct or unique traits, they might play important roles in the functioning of the ecosystem (Mouillot et al. 2013a; Murgier et al. 2021). In addition, assessing if species carry vulnerable traits would inform on the sensitivity of communities to shift after disturbances (McLean et al. 2019a). Examples of vulnerable traits for macrofauna could be sessile, low mobility and long life-span, as species supporting those traits have already showed a longer recovery after fishing than mobile species with shorter life-spans (Sciberras et al. 2018). Evaluating whether functionally distinct or unique species are vulnerable and if they are LOLAS or common species, could allow to better understand the future of the ecosystems

under increasing changes and better set up conservation management strategies (Mouillot et al. 2013a; Murgier et al. 2021).

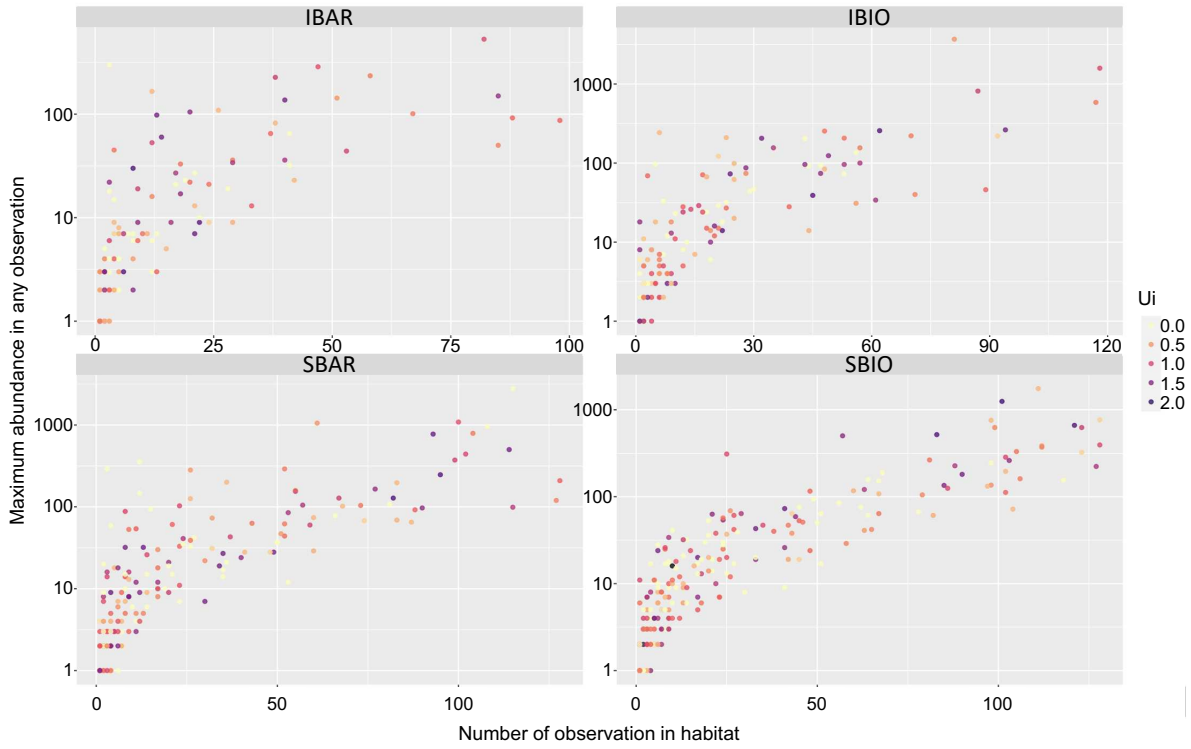


FIGURE 4: Functional uniqueness (Ui) of each Polychaeta species according to its taxonomic commonness or rarity in each habitat (i.e., its maximum abundance recorded in any observation (i.e., site and year) in each habitat according to the number of observations it was recorded). Sites and years taken into account were the same as in Chapter IV.

1.3. Considerations for long-term monitoring

One main element that emerged from each chapter of the thesis was the importance of the scale of observation in community dynamics. Indeed, community diversities and dynamics varied between habitats (Chapters I to IV), within habitats (i.e., between sites; Chapter I to IV) and even between taxonomic assemblages (Chapter III). Because there are still gaps in our knowledge about biodiversity change at different spatial and temporal scales (McGill et al. 2015), this thesis highlights the importance of considering multiple spatial scales in temporal studies, as well as the importance of large temporal and spatial scales monitoring programs as the REBENT to fill in these gaps. Indeed, the REBENT allows now to assess 21-years dynamics (2003-2023) of macrofauna communities from the scale of the replicate (i.e., core or grab) to that of the point, site, habitat, tidal zone and region, or at the scale of different compartments (e.g., infauna and epifauna) or taxonomic assemblages (and this list is not exhaustive as it can also include water masses, coasts of the North and South, etc.). Thus, the REBENT monitoring

program totally fulfills expectations of a robust monitoring program, that is long-term, multi-site and multi-species (Hughes et al. 2017; Kuebbing et al. 2018).

As demonstrated in Chapters II and IV, communities of the different tidal zones, sites and habitats did not respond similarly to abiotic constraints. As environmental forces and anthropogenic threats can be patchy in space and time, the spatial and temporal extent of monitoring programs is crucial. Indeed, biodiversity change in response to ecological drivers are strongly scale-dependent and can switch directions across scales (Chase et al. 2018). Moreover, a joint consideration of space and time allows for assessing the interaction of these two dimensions and how they are intrinsically related (Legendre et al. 2010; Collins et al. 2018). And more basically if, for example, we had concentrated only on the Trévignon site which presents an extremely persistent community because it is dominated by a single species, or if we had focused only on the first 4 years of monitoring in IBAR, our conclusions or hypotheses would have been very different. In addition, the importance of the spatial extent in time series particularly stood up in Chapter I and III when using Community Trajectory Analysis and comparing the shape of sites' trajectories. Indeed, in that case, the unit of observation is the trajectory and the number of observations is reduced to the number of sites, and when the latter is small, it can induce non-significant statistical results (e.g., RV coefficients in Chapter III).

Threats occur at all spatial scales and to assess how best to conserve biodiversity across spatial scales and over time, we need to understand the relationship between locally-collected monitoring data and regional diversity dynamics, and how the mechanisms that maintain diversity vary from local to regional spatial scales and over time (Socolar et al. 2016). The REBENT monitoring program provided the foundation on which this thesis could tackle these issues. Moreover, by focusing on β rather than α diversity, it allowed to address the integration of conservation issues across all scales (Socolar et al. 2016). Indeed, such studies based on a multi-scale monitoring, not only allow to link observations to ecological theory but are also potential support for implementing conservation strategies.

The temporal extent and frequency of monitoring programs are also important to detect trends. With its yearly sampling, the REBENT program can be qualified as a monitoring with "short term intervals", and is thus relevant for the measure of several Essential Biodiversity Variables (Pereira et al. 2013). However, the maximum temporal extent studied in this thesis was 15 years. Macrobenthic communities can exhibit different multi-years cycles (e.g., 3-9 years, 5-7 years, 10-12 years) (Thrush et al. 2021a) that we would not have been able to detect with a 15-years data series, as detecting cycles requires data series at least 2 to 3 times longer than the cycles. Moreover, oceanographic cycles can sometimes occur over decades making

long-term studies critical in marine ecosystems (Lindenmayer et al. 2012). Furthermore, the length of the cycles can differ depending of the species (e.g., oscillating dominance; Gray and Elliott 2009) and looking at the global trend of the community can sometimes blur them. Looking at some particular species or functional groups trends (e.g., Hewitt, et al. 2016a) could inform on the synchrony or asynchrony of species and better understand the response of the communities in the face of environmental or anthropogenic constraints, as well as the processes maintaining their stability (Hallett et al. 2016; Lamy et al. 2020).

A minority of the REBENT monitored sites are sampled twice a year (Fall and Spring sampling). This could allow future work to focus on seasonal dynamics and assess the finer variability of communities. Indeed, it could have an impact on the yearly dynamics studied here as some ecological processes in the monitored benthic macrofauna might be faster than the yearly sampling frequency. In the Chapters, we studied samples taken during Spring (i.e., between the end of February and the beginning of May), before the recruitment of most species in the region to avoid confounding effects. Yet, for some years or sites the sampling may sometimes have been postponed due to weather conditions. Exceptionally, sampling might overlap the recruitment period of some species and potentially induce a source of variability in the time series that could be investigated.

The REBENT monitoring program was set up in order to establish a baseline allowing us to better understand and quantify the effect of changing environmental conditions or catastrophic events such as those caused by oil spills. However, one major contingency in designating a state as a reference is our historical knowledge of what could have been the state of a “natural” and pristine ecosystem. Indeed, if the REBENT monitoring had begun just before the sinking of the Erika, these first observations might have been used as refence states. However, how can we know if at this moment the ecosystem was in a stable or a transitioning state? Pauly (1995) defined the “shifting baseline syndrome” as the fact that each generation tends to define what is “natural” or “normal” based on its experience, thus always adjusting the baseline to a new level. Actually, because of changing climate conditions at different time scales, the evolving nature and intensity of multiple interacting pressures on marine ecosystems and their non-linear and sometimes lagged responses, reference conditions are always dynamics (Duarte et al. 2009). Continuous long-term monitoring are certainly an essential tool to understand the complex dynamics of ecosystems and sharpen our vision of their historical dynamics, thus allowing a better characterization of the evolution of ecological states (Compton et al. 2017). Moreover, I believe that a short-term interval monitoring (1-5 years) is a bare minimum to provide a realistic view of ecosystems’ dynamics while fewer snapshots of

ecosystem states in time could maybe blur important dynamic changes and a higher frequency of observations could potentially highlight otherwise invisible variation.

Increasing the spatial and temporal extents of monitoring or the number of samples taken to adequately estimate diversity requires an additional effort and is costly and time consuming. In Chapter III, we proposed to use taxonomic surrogacy to study the dynamics of the overall macrofauna community only focusing on one surrogate taxon, which can drastically reduce the time and efforts needed for taxa identification (Olsgard and Somerfield 2000; Wodarska-Kowalczuk and Kedra 2007). However, to assess if surrogacy is consistent over time, a long time series where all the macrofauna is sampled is still needed. Moreover, as showed by Chapter III, the differences between the different taxa to act as surrogates were not always obvious depending on the habitats. This is why we recommended to refer to surrogacy studies on the same kind of environment or habitats before starting a surrogate-based monitoring program.

Barriers to fill in the gaps in our knowledge of biodiversity change at multiple scales are the collection and access to monitoring data. In addition to taxonomic surrogacy, inter-laboratory collaboration such as the one set up in the REBENT program is an example of other solution to make such an endeavor of acquiring such data. Furthermore, the data should be accessible from online databases, in supplementary materials when published or on demand (McGill et al. 2015), which is more and more the case nowadays. We could consider to add to the REBENT database (which already includes all the data collected in the field), data that have been collected *a posteriori* by engineers, interns or PhD students as me, that gather information on the functional traits of REBENT monitored taxa (which might imply a homogenization of the traits and modalities used by different teams). In addition, it might be possible to consider additional facets of biodiversity such as the phylogenetic diversity, which could be a relevant estimator of the productivity of ecosystems (Cadotte et al. 2012) as well as their functions since species of different lineages could perform different functions (Cadotte et al. 2008, 2009). This could be made possible by listing in the database the gene sequences of REBENT taxa that are available in online databases, although they might be rarer and not always well identified for invertebrates compared to vertebrates (Lavesque et al. 2019).

1.4. Methodological considerations

In the course of this thesis, the diverse methods used have raised questions, ideas of perspectives or have showed certain limits discussed in the following paragraphs.

Chapter I was principally based on CTA (De Cáceres et al. 2019), which was, at the time I started to explore and test this method on the REBENT data in the first year of my thesis, a very novel methodology which looked promising. Indeed, even though trajectory representations already existed (e.g., Clarke and Warwick 2014), CTA offered the possibility to quantify and compare community dynamics, taking into account the entirety of the multidimensional space with the possibility to manage missing data (only for some metrics). At the time, very few studies existed that used this method on real community datasets, making the comparison of results and interpretations between studies difficult. Since then, I have observed the growth of the CTA method, due to its more frequent use in research articles or by its extensions (i.e., Ecological Trajectory Analysis; Sturbois et al. 2021c, Stable Isotope Trajectory Analysis; Sturbois et al. 2022). Indeed, this method offers a multiplicity of possibilities as it can be also applied, for example, on the community functional structure or on the environmental matrix (Figure 5) or mixed with other multidimensional methods, as I can have tested by myself or through the supervision of an internship during these past 3 years.

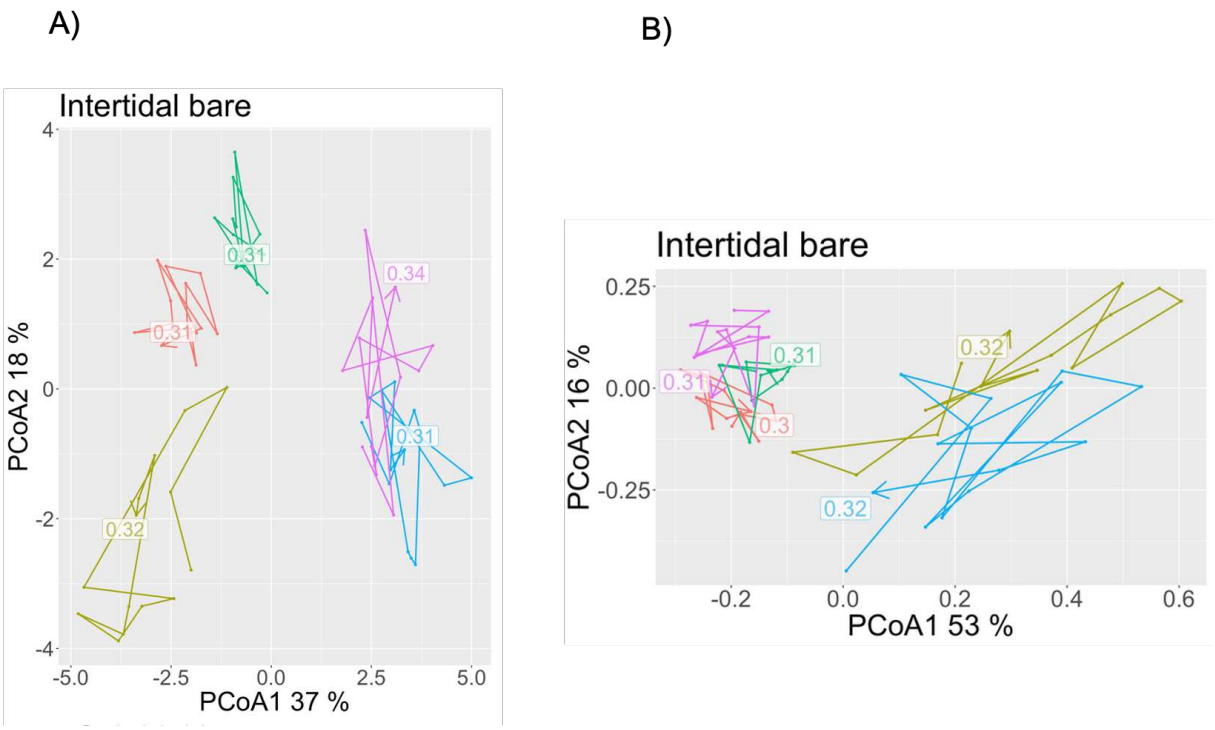


FIGURE 5: Examples of A) environmental trajectories for the intertidal bare sites considered in Chapter I and B) functional trajectories on Polychaeta communities of intertidal bare sites considered in Chapter I. The Euclidean distance was used for environmental trajectories and Hellinger distance for functional ones.

However, before interpreting all the possibilities of extensions of CTA, I focused on the metrics developed in the original method (De Cáceres et al. 2019). They were first developed on tree communities, but we applied and tested them on macrobenthic species and tried to interpret the observed patterns. In this Chapter, we concluded that communities followed habitat-dependent, non-directional and stable dynamics and we linked ecological trajectories to theoretical patterns, mainly following Lamothe et al. (2019). Several other metrics from the original CTA method that were not incorporated in Chapter I also hinted toward this conclusion. For example, distances between one observation and those à t+1, t+2, t+3, etc., did not show a marked trend (Figure 6) or convergence or divergence of the trajectories (i.e., if the distances between observations gradually decrease, reflecting a homogenization of the communities, or if they increase) were not significant.

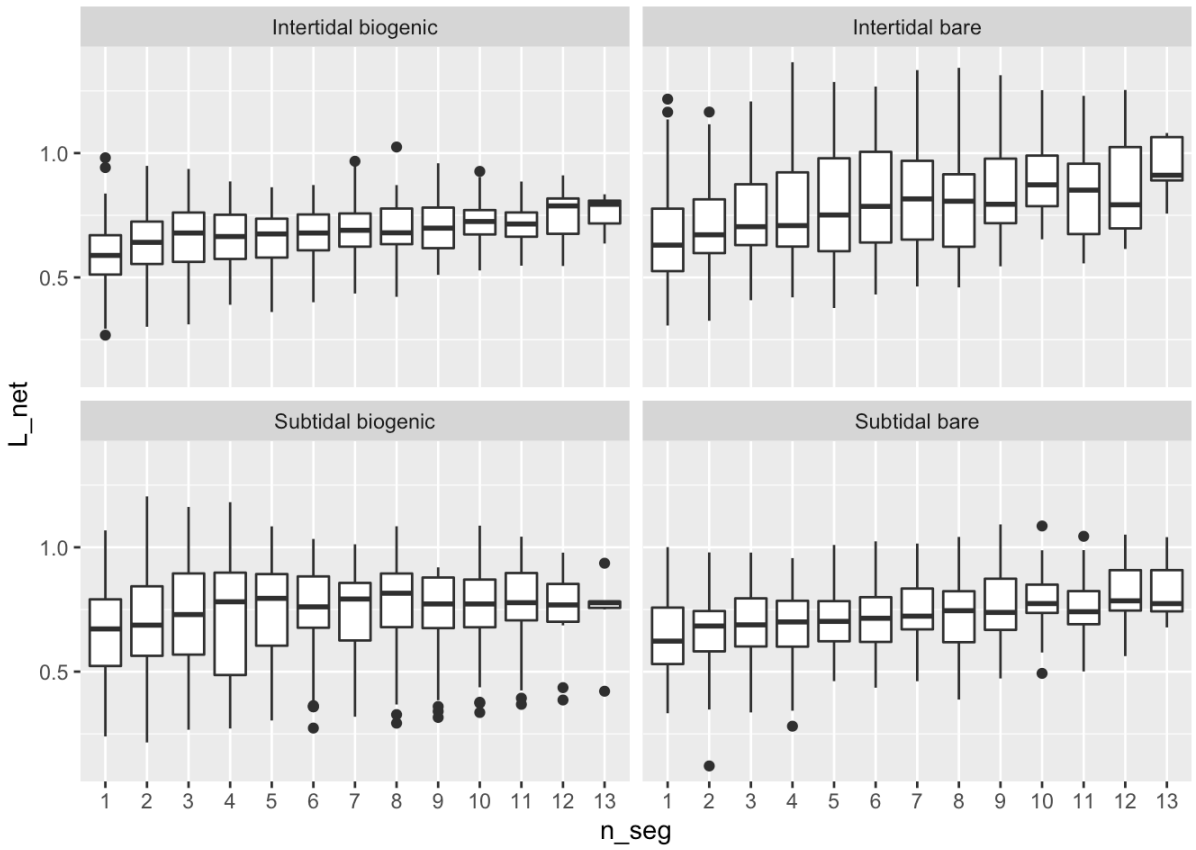


FIGURE 6: Net change (L_net, i.e., Hellinger distance here), between one observation and the one at t+1, t+2, etc. (i.e., n_seg = number of segments between the two observations considered), for each habitat. The number of sites and years considered are the same as in Chapter I.

However, as this method was quite new, we could have used other methods and indices that can quantify the temporal dynamics (Hallett et al. 2016; Buckley et al. 2021a) to compare CTA results. This is partly why I wanted to use other methods in the different parts of my thesis, and, in the end, the results generated by them supported the conclusions drawn with the CTA. We could also have used methods such as "tipping points" analyses (Andersen et al. 2009) to more precisely identify breaks in the time series (especially on the comparison of segment lengths between years; Chapter I, Figure 4) and the potential transition to new random stable states for example. However, these methods are highly dependent on the length and frequency of the time series (Hewitt and Thrush 2019).

One of the difficulties in interpreting trajectories was the lack of "reference" trajectories (i.e., community trajectory under a known dynamic) to which we could compare the observed trajectories to draw our conclusions. This is why we created simulated trajectories. Null models such as the one we set up can be a crucial tool in the evaluation of temporal β diversity (Magurran et al. 2019). However, the latter may show some limitations. Indeed, we first wanted

to set up a model simulating the processes (i.e., rather a neutral model than a null model; Gotelli and McGill 2006). Yet, simulating processes required to set parameters such as migration or individual extinction rates that are almost never measured directly. Given the complexity of elaborating such a model, we fell back on the simulation of the expected result, i.e., the simulation of completely non-directional trajectories. To build this null model, we used a randomization of the observed data. To do this, we combined all the taxa observed at all sites and all years of the time series into a "species pool" at the habitat scale (see the Appendices of Chapter I for more details). This approach has some limitations since species pool are not static and we might have simulated communities with species that are never found together in reality. Identifying the “correct” species pool is an important challenge in studies on spatial and temporal β diversity (Magurran et al. 2019), and an amelioration of this null model could be considered in future work.

Regarding the directionality metric, it showed very low and similar values between the different sites. We wondered in Chapter I if this was not due to the high richness and faster turnover of marine communities compared to terrestrial communities. However, I had the opportunity to apply CTA on less speciose foraminifera communities and surprisingly directionality values were almost identical to those found in Chapter I. This underlines the need to test this still recent method to better understand its limits, for example by meta-analysis grouping marine, terrestrial, rich or less rich ecosystems with already known dynamics, data from monitoring or experimental studies, but also by testing different ecological distances. Indeed, all CTA metrics are based on the distance used, which must be chosen carefully depending on their properties and the data and communities used (Legendre and De Cáceres 2013). These distances have different limits (i.e., different maximum value), and I would find it interesting to test if this could have an effect on directionality and more generally, I would find it instructive to look at how each of the metric react to these different distances. The other chapters of the thesis also confirmed that the fraction that models temporal structure plays a very small role in the variation of the communities. Moreover, when I computed the temporal linear trend of each site, most results were significant and explained approximately 10% of the variation in site community. This variation could be due to drift or stochastic changes in the 15 years monitored. It would be interesting in future work to simulate non-directional to completely directional trajectories (i.e., as it could be the case in successional dynamics) and estimate the proportion of variance of these linear trends, to assess whether a coherent relationship between these two could be found. In addition, a recent method for quantifying directional changes (Schmera et al. 2022) could be tested on the communities we studied in

Chapter I in order to compare the results or better understand them as it can inform if the turnover is dominated by species gain, loss or balanced between the two, although it was developed on presence-absence community data.

As already stated in the previous section, the number of trajectories taken into account can have an influence when comparing dynamics. The number of trajectories, and therefore of sites taken into account in Chapter I, could have been increased without sampling new sites. Indeed, in this chapter, we made a selection of sites in order to keep only those with complete time series to avoid confounding effects for the comparison of their dynamics and to avoid the effect that missing data could have on the metrics. Thus, assessing the effect of missing data, for example, by removing years one by one and looking at when a change is detected in the metrics evaluated on the complete trajectory, could allow us to increase the number of sites taken into account in the analyses, if CTA is not very sensitive to the lack of data.

A major prospect for CTA would be to be able to directly link environmental trajectories to community trajectories. This would involve a multidimensional space that can jointly represent environmental and community trajectories. The STATICO method allows this, by representing trajectories in a compromise space (Thioulouse et al. 2004). However, a drawback of this method is that it is not possible to quantify the proportion of community variance explained by the environment in this compromise space. An alternative, which I have tested, is to look at the correlation between the segment lengths of the environmental and community trajectories (i.e., if a long segment in the environmental trajectories, i.e., a strong change, also induces a long segment in the community trajectories). No correlation was found in the tests done, either because there is effectively no correlation or perhaps because of a lag between community response and environmental variation. Another hypothesis could be to test if there is a correlation between the potential number of extreme events between two years and the length of the segments.

Indeed, in Chapter II, we suggested that our environmental datasets did not adequately characterize the extreme events, these could be characterized in the same way as marine heat waves that are characterized by a period of 5 days above the 90th percentile, compared to a historical reference period (Hobday et al. 2016), or more simply by counting the number of days, of wind for example, above the last quartile. Moreover, apart from sediments characteristic, our environmental dataset is based on numerical models, for which it is often difficult to find a good compromise between spatial and temporal grain. Here we took models allowing to treat the entirety of our time series, despite the coarse spatial resolution of the models. For marine models, numerical models estimate the parameters of the water column but

may not be adequate to describe conditions on the seabed or inside a maerl bed for example. Ideally, in situ data would be more accurate, especially to better characterize the effect of environmental buffering of biogenic habitats. To better characterize the environmental data, we could also use polynomes, since RDAs only model linear relationships, this would allow us to characterize other forms of relationships.

The anthropogenic pressure variables we used were mainly proxies. These may have limitations since they were extracted (for the number of inhabitants and land use data) from terrestrial data that can better characterize intertidal than subtidal sites. Fishing pressure could also be better characterized, by evaluating more precisely the fishing effort by surveying a larger number of coastal stakeholders. The same could be done to evaluate the anthropic threats in general: a survey could be conducted among different coastal actors (e.g., fishermen, scientists, coastal conservatory). Another alternative would be to directly measure pressures (e.g., by measuring chemical elements in seawater, abrasion stress) or to take into account the presence of *Ulva* mats (that constitute green tides) as they have been shown to have an impact on the macrobenthic community structure of sandy beaches (Quillien et al. 2015).

Finally, concerning the functional traits, these have been defined during a previous thesis and following several inter-laboratory discussions. The search for traits in the literature may set certain limits since most species are relatively poorly described or for regions of the world far from our study area. The advantage of the fuzzy coding method used here, is to take into account the intra-specific or ontogenic variability, however in the analyses the modalities of each trait are considered as traits in their own right. This can cause problems for the interpretation of the results or the calculation of certain methods, such as RLQ and 4th corner analyses (Dray et al. 2014), which make possible to test the links between each trait (here modalities) and environmental parameters. One solution could be to summarize the number of modalities by fuzzy PCA axes (Chevenet et al. 1994; Beauchard et al. 2017) which would then be incorporated into the methods mentioned. This would present an interesting perspective since the RLQ and 4th corner methods also allow to take into account the effect of time and space (Wesuls et al. 2012). Concerning the computation of functional indices, a recent method proposed to assess them based on a probabilistic hypervolume rather than convex hull volumes (Figure 7; Mammola and Cardoso 2020). Interestingly, this method gave different results from the ones given by convex hulls (Figure 8). This raises the interesting question of whether or not this is an artefact of the method or revealing of actual underlying differences. I believe that testing the impact of LOLAS on these results should shed light on this question.

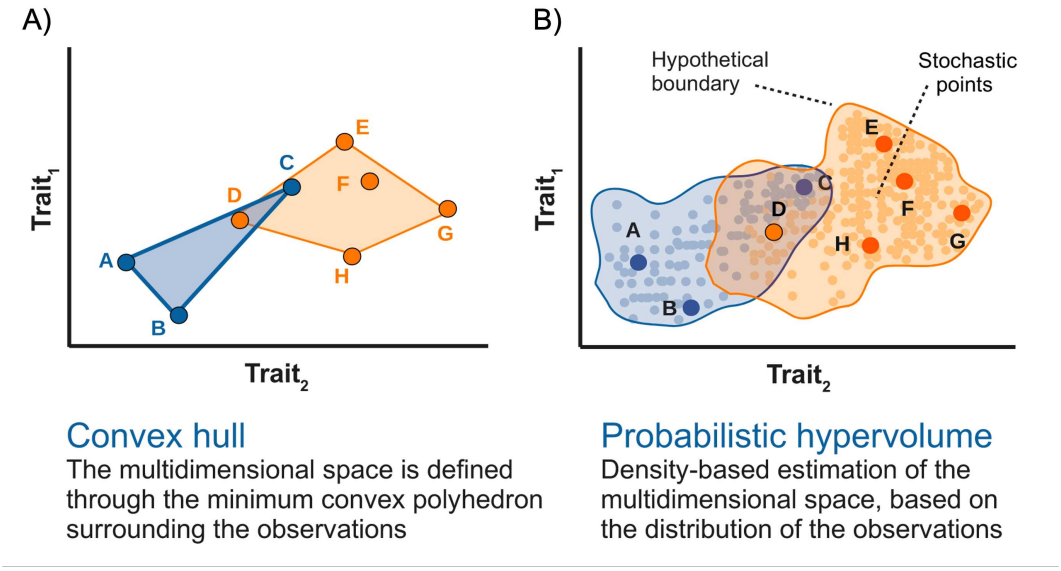


FIGURE 7: Examples of mathematical representations of functional diversity (FD) of communities. Examples are based on two hypothetical traits and two communities, represented in turquoise and orange. On letter corresponds to a species. A) The trait space can be represented as the minimum convex hull comprising the species occupying the trait space. The functional richness of a community is estimated as the area of the convex hull. B) The trait space can be constructed using kernel density hypervolumes, whereby it is approximated as a cloud of stochastic points sampled based on a set of observations (e.g., the traits of the species in the community). The functional richness of the community is estimated as the volume of the hypervolume delineated by the stochastic points. From Mammola and Cardoso (2020).

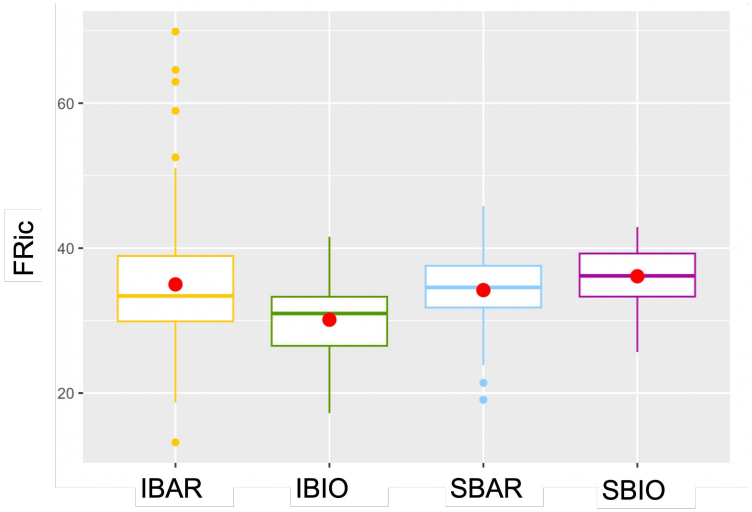


FIGURE 8: Functional richness (FRic) of the four habitats estimated using kernel density hypervolumes. Same sites, years and number of PCoA axes as in Chapter IV were used to compute it. Red points represent mean FRic in each habitat. We can notice a difference compare to FRic values computed in Chapter IV, which represented a clear gradient from IBAR to SBIO. IBAR = intertidal biogenic habitat, IBIO = intertidal biogenic habitat, SBAR = subtidal bare habitat, SBIO = subtidal biogenic habitat.

2. Discussion en français

2.1. Des mécanismes habitat-dépendants

Tout au long des chapitres de cette thèse, l'étude de la dynamique spatio-temporelle des quatre habitats suivis a permis de mettre en évidence des mécanismes différents dépendant de l'habitat. En effet, les dynamiques mises en évidence ne sont pas spécifiques à un étagement (i.e. intertidal ou subtidal) ou à un type d'habitat (i.e. nu ou biogénique) mais spécifiques à chaque habitat indépendamment, même si des similitudes apparaissent au sein d'un même étagement ou d'un même type d'habitat. Bien qu'une stabilité à l'échelle régionale ait été démontrée, le chapitre I a mis en évidence des différences entre les habitats en termes de dynamique taxonomique et a permis de dresser des hypothèses concernant ces différences. Ces dernières pourraient dépendre du nombre de taxons et d'espèces dites à « faible occurrence et faible abondance » (LOLAS dans le texte en anglais) dans chaque habitat et du fait que ces espèces sont "rares" ou "transitoires" (comme défini au chapitre I), des différentes interactions biotiques et abiotiques au sein de chaque habitat et de la nature de l'habitat lui-même (c'est-à-dire nu ou biogénique ou de l'identité des espèces fondations).

Le chapitre II a montré que la dynamique de chaque habitat réagissait différemment aux facteurs environnementaux et anthropiques. Dans tous les habitats, l'effet de l'espace était plus important que l'effet temporel sur la dynamique de la macrofaune benthique, et la granulométrie ainsi que l'hydrodynamisme étaient des facteurs jouant un rôle important dans cette dynamique, comme cela a déjà été démontré dans la littérature scientifique (e.g., Snelgrove 1998 ; Veiga et al. 2017 ; Couce et al. 2020). Toutefois, le chapitre II a souligné l'importance des proxys de pressions anthropiques sur la dynamique de la macrofaune dans la zone intertidale et a avancé l'hypothèse selon laquelle les habitats biogéniques auraient plutôt tendance à atténuer l'effet des événements extrêmes sur les communautés que l'effet des conditions environnementales moyennes. De plus, cet effet tampon pourrait être plus prononcé dans les habitats fréquemment exposés à des environnements stressants tels que la zone intertidale plutôt que dans des environnements plus doux.

Le chapitre IV a montré que chaque habitat présentait une structure fonctionnelle et une dynamique spatio-temporelle fonctionnelle spécifiques qui répondaient également différemment aux facteurs abiotiques. Bien que la différence de structure fonctionnelle entre les habitats nus et biogéniques soit clairement marquée, la manière dont ces fonctions sont exprimées au sein de deux mêmes types d'habitats (c'est-à-dire nu/nu ou biogéniques/biogénique) diffère également de manière évidente. Par exemple, avec une

régularité fonctionnelle plus élevée et une richesse fonctionnelle plus hétérogène entre les sites dans IBAR par rapport à SBAR, ou avec des taxons dominants soutenant des traits spécialisés par rapport au pool fonctionnel régional dans IBIO comparé à SBIO. Dans ce dernier cas, la richesse fonctionnelle, la redondance et la stabilité spatio-temporelle des fonctions sont également plus élevées. Un gradient de diversité β au sein de l'habitat a été observé depuis les habitats intertidaux nus jusqu'aux habitats subtidaux biogéniques. IBAR est l'habitat qui présente la plus grande diversité β intra-habitat, principalement en raison des différences de richesse fonctionnelle entre les sites. Nous avons émis l'hypothèse que cette plus grande diversité intra-habitat pourrait avoir permis le maintien du pool fonctionnel régional d'IBAR. Nous avons également suggéré que la stabilité fonctionnelle pourrait être due à la forte régularité des fonctions dans SBAR, principalement à l'effet tampon environnemental pour IBIO et à la forte richesse et redondance fonctionnelle dans SBIO.

Au fil des chapitres, 13 à 15 années ont été étudiées et aucun changement majeur dans la dynamique des communautés surveillées n'a été détecté. Dans chaque chapitre, nous avons essayé de déduire les mécanismes spécifiques à l'habitat qui pourraient participer au maintien de cette stabilité. Nos interprétations ont été, pour la plupart, établies en fonction de l'habitat. Cependant, les habitats surveillés ne sont pas isolés les uns des autres car ils sont situés dans la même zone régionale, parfois dans les mêmes masses d'eau ou dans les mêmes baies ou plages. Ils ne sont donc pas totalement indépendants les uns des autres mais interconnectés dans une mosaïque d'habitats (Gallon et al. 2017), et, en plus des mécanismes intra-habitats, cela pourrait jouer un rôle important dans la stabilité décrite. En effet, les habitats pourraient se faciliter mutuellement et une forte diversité d'habitats pourrait améliorer la multifonctionnalité du méta-écosystème, indépendamment de la diversité des espèces (Alsterberg et al. 2017). Dans notre cas, la diversité des habitats peut être multipliée si nous considérons les différents contextes physiques englobés par les quatre habitats distincts que nous avons considérés séparément, par exemple, les sédiments grossiers et les sédiments vaseux pourraient être considérés comme distincts. De plus, à l'échelle du paysage, l'alternance de parcelles autogènes (par exemple, les herbiers marins ou les bancs de maërl) et allogènes (par exemple, les bioturbateurs) devrait produire une diversité totale et une richesse en espèces élevées (Bouma et al. 2009a), ce qui pourrait renforcer la stabilité des communautés grâce à des effets portfolio ou d'après l'hypothèse d'assurance (Yachi et Loreau 1999).

De plus, nous avons principalement considéré les deux habitats biogéniques comme structurés par une seule entité (c'est-à-dire les espèces fondations considérées), alors que ces habitats abritent en réalité des espèces fondations imbriquées (Angelini et al. 2011). En effet,

le maërl et les herbiers sont associés à de nombreux épiphytes (e.g., Helias and Burel 2023). Ces espèces augmentent la complexité de l'habitat et facilitent les différentes suites d'organismes à travers une cascade d'habitats, et sont donc essentielles au maintien de la stabilité des communautés (Thomsen et al. 2010 ; Angelini et al. 2011). Ces espèces fondations abritent non seulement des communautés d'endofaune mais aussi d'épifaune. L'épifaune peut faciliter l'endofaune par des effets indirects. Par exemple, la consommation d'épiphytes par l'épifaune induit la sédimentation de boulettes fécales fournissant de la matière organique aux communautés d'endofaune (Jankowska et al. 2019). Les communautés d'épifaune jouent un rôle important dans le fonctionnement des écosystèmes marins car elles constituent un lien trophique essentiel entre les producteurs primaires benthiques et les consommateurs d'ordre supérieur (Chen et al. 2021). Leur dynamique spatio-temporelle peut être découplée de celle des communautés de l'endofaune (Boyé et al. 2017), ainsi une perspective pourrait être de considérer conjointement la dynamique de ces deux communautés dans de futurs travaux (Figure 1) afin de mieux caractériser la dynamique des écosystèmes, ce qui pourrait aider à mettre en place des stratégies de gestion plus fiables.

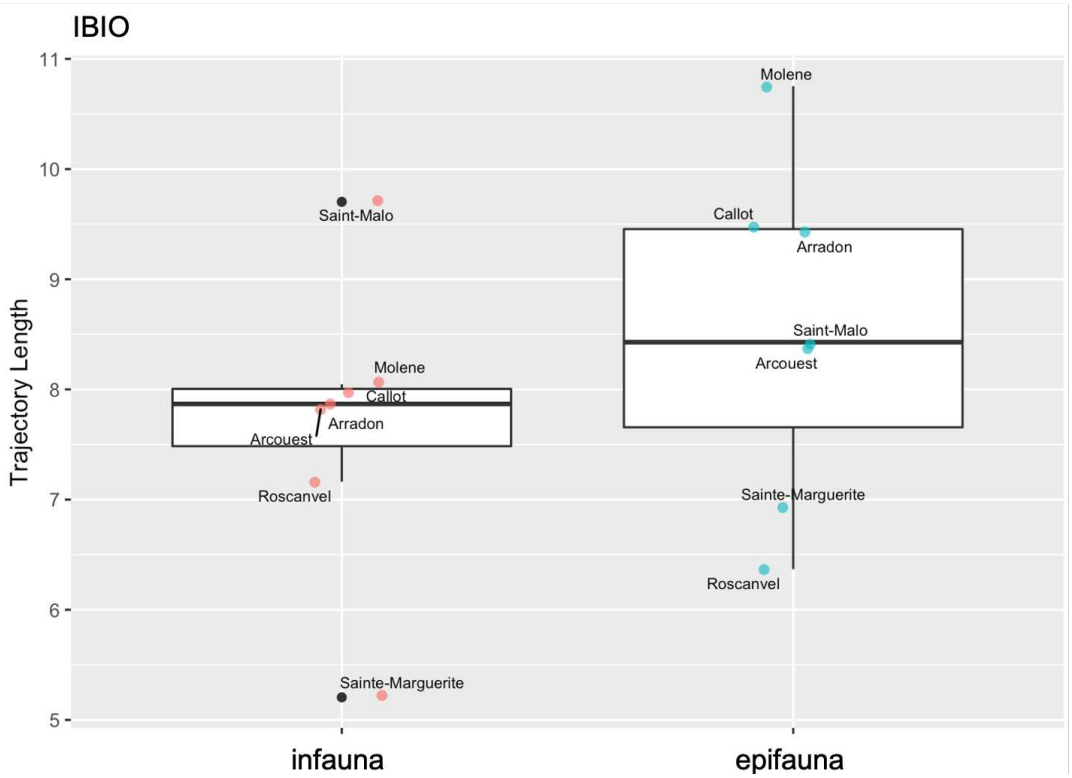


FIGURE 1 : Comparaison des longueurs de trajectoire entre les communautés d'endofaune et d'épifaune dans l'habitat intertidal biogénique (IBIO). Un point correpond à la valeur pour un site. Le nombre de sites et d'années considérés est le même que dans le Chapitre I.

Par conséquent, les modèles de stabilité que nous avons décrits dépendent certainement de l'emplacement de notre étude. Les habitats nus qui ne sont pas intégrés dans un réseau de multiples habitats biogéniques ou non biogéniques pourraient présenter des schémas différents, comme le montrent déjà les diverses dynamiques exposées dans le monde entier par ces habitats (par exemple, Hinz et al. 2011 ; Frid 2011 ; Beukema et Dekker 2020). De plus, la dynamique des deux habitats biogéniques pourrait également changer en fonction du gradient de stress auquel ils sont exposés. En effet, selon l'hypothèse du gradient de stress, les ingénieurs d'écosystème peuvent atténuer le stress physique dans un environnement physique extrême, tandis qu'ils peuvent soutenir les processus de l'écosystème en fournissant un espace libre pour les compétiteurs ou les prédateurs dans un environnement avec des conditions physiques plus atténuées (Crain et Bertness 2006 ; Watt et Scrosati 2013). L'identité des espèces formant ces habitats pourrait également avoir un effet sur la dynamique de la macrofaune, de même que leur disparité ou la complexité de leurs structures (Bouma et al. 2009b ; Berlandi et al. 2012 ; Solano-Barquero et al. 2022), la variabilité des dynamiques de la macrofaune pourrait également être étudiée au sein même d'un habitat. À la lumière de ces effets confondants potentiels, la question de savoir si les résultats des différents chapitres sont la norme reste ouverte car ils pourraient, par exemple, dépendre du contexte régional et biogéographique.

Aucun changement de régime ni aucune tendance particulière n'ont été constatés dans les variables environnementales naturelles étudiées, de sorte que la stabilité décrite pourrait également résulter de la stabilité temporelle générale des forceurs abiotiques au fil du temps dans la région. Toutefois, les mécanismes que nous avons mis en évidence pourraient nous aider à formuler des hypothèses sur les réponses potentielles des habitats exposés à des contraintes ou à des perturbations plus fortes. Dans les habitats facilitateurs, la réponse des communautés au réchauffement, par exemple, peut être indétectable jusqu'à ce qu'un point de basculement soit atteint avec la dégradation ou la perte de l'habitat facilitateur (Jurgens et al. 2022). Je m'attends donc à ce que les communautés des bancs de maërl soient très résilientes en cas d'augmentation de la variabilité environnementale. Cependant, en cas de perturbations conduisant à la destruction de l'habitat, j'émets l'hypothèse qu'au-delà d'un certain seuil, il n'y aurait pas de retour possible, alors que cette option pourrait être plus réaliste dans le cas des herbiers (Figure 2). En effet, la lenteur de la croissance des rhodolithes et leur mode de reproduction (Foster 2001 ; Foster et al. 2013) rendent difficile l'implantation de bancs de maërl sur des habitats nus. En revanche, la dispersion des graines d'herbiers via l'hydrochorie ou la zoochorie par exemple (Orth et al. 2006), pourrait faciliter leur implantation. De plus, je fais l'hypothèse que la destruction de ces habitats biogéniques affectera indirectement les habitats

nus (Figure 2). En effet, dans la zone intertidale par exemple, les sites d'IBAR échantillonnés à proximité d'IBIO ont montré une plus grande richesse en espèces (voir par exemple les sites n° 5 et 9 dans l'annexe 2 du chapitre I) et des espaces fonctionnels plus similaires (voir le chapitre IV), potentiellement en raison des échanges entre ces deux habitats (par exemple, approvisionnement en larves, colonisateurs, approvisionnement en ressources, spill-over). « L'effet de bordure » a été conceptualisé comme un changement écologique dû à l'éloignement d'une zone centrale d'une parcelle d'habitat (Ries et al. 2004). Il a déjà été démontré que cet effet de bordure favorisait la diversité fonctionnelle (Gayer et al. 2019 ; Hu et al. 2022). Ainsi, une homogénéisation potentielle des habitats diminuerait la diversité et la multifonctionnalité du méta-écosystème (Alsterberg et al. 2017), affectant négativement les échanges entre les parcelles d'habitat, et potentiellement la stabilité des communautés.

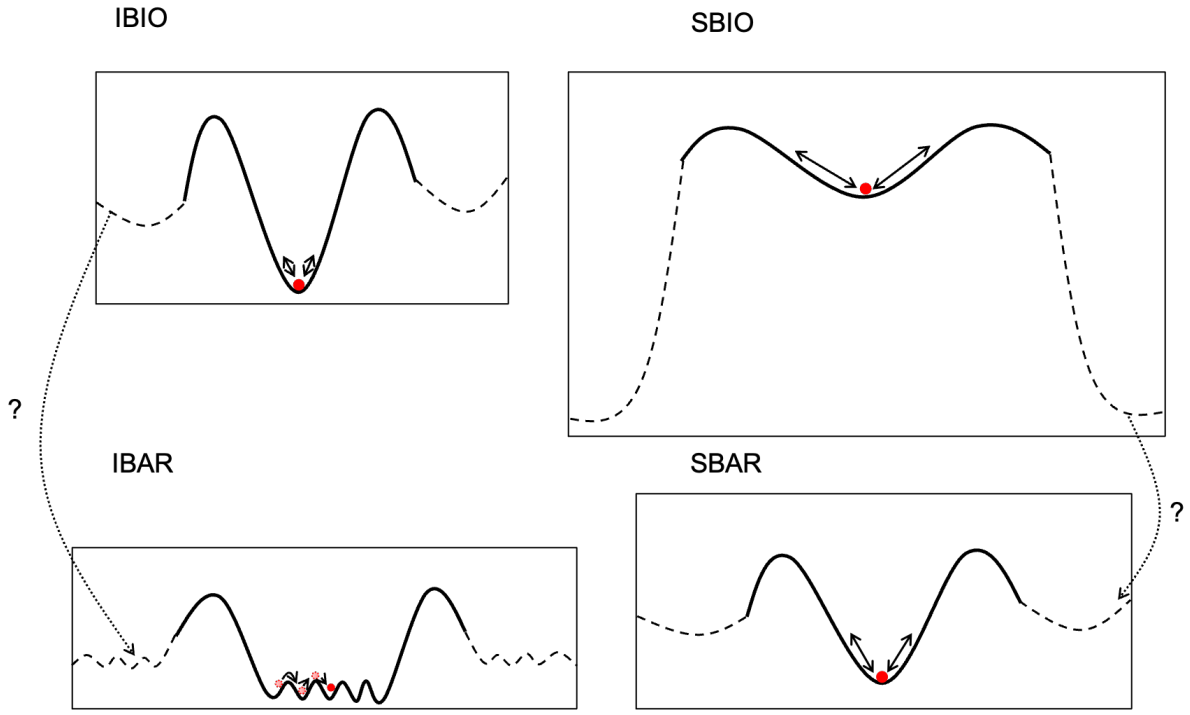


FIGURE 2 : Représentation selon le modèle "ball and cup" de l'état écologique de chaque habitat comme décrit dans le Chapitre I (ligne pleine) et l'état hypothétique (ligne pointillée) que les communautés des habitats pourraient prendre dans le cas d'une destruction des habitats biogéniques. IBIO pourrait passer dans un état moins stable (puit moins étroit) avec potentiellement plus de chance de retour à un état stable que SBIO. La destruction des habitats biogéniques pourrait mener à des changements vers des états moins stables dans les habitats nus (IBAR et SBAR). IBAR = habitat intertidal nu, IBIO = habitat intertidal biogénique, SBAR = habitat subtidal nu, SBIO = habitat subtidal biogénique.

Au fil des chapitres, nous avons principalement expliqué la dynamique observée avec des facteurs abiotiques ou les dbMEM, et nous avons brièvement discuté de la manière dont les

interactions biotiques pourraient affecter cette dynamique en se basant sur les connaissances scientifiques existantes. Dans le partitionnement de variance, la fraction unique modélisée par les dbMEM spatiaux ou temporels peut être attribuée aux interactions biotiques. Dans le chapitre II, cette fraction était significative, ce qui suggère qu'il serait fructueux de mieux appréhender ces interactions dans des travaux futurs. La méthode « Hierarchical Modeling of Species Communities » (HMSC) offre un moyen prometteur d'intégrer ces interactions biotiques (Ovaskainen et al. 2017a, 2017b ; Violet et al. 2022). Elle décompose les cooccurrences d'espèces observées en deux catégories : celles qui peuvent être expliquées par des covariables environnementales et celles qui ne le peuvent pas. Les assemblages biotiques sont modélisés par des matrices d'association espèce-espèce qui peuvent être estimées à plusieurs échelles spatiales ou temporelles. En outre, cette méthode permet de prendre en compte les traits fonctionnels des espèces dans l'estimation de la réponse des espèces aux covariables environnementales. Les patrons de cooccurrence d'espèces et leur évolution dans l'espace et dans le temps sont l'un des outils qui peuvent affiner notre compréhension de la dynamique des écosystèmes ainsi que la manière dont ils peuvent affecter leur structure et leur fonction (Li et al. 2018).

2.2. L'écologie benthique ou l'écologie du rare ?

Sur les 14 années étudiées dans le chapitre I, en moyenne 29 à 42% des espèces n'ont été détectées qu'une seule fois à chaque site tout au long de la série temporelle, tandis qu'en moyenne 2 à 7% ont été détectées chaque année. De nombreux noms et interprétations ont été donnés à ces espèces peu fréquemment observées, tels que "accidentel", "occasionnel", "transitoire" (Magurran et Henderson 2003 ; Snell Taylor et al. 2018). La rareté peut être spatiale, temporelle ou les deux et peut prendre de nombreuses formes (Violle et al. 2017). Dans le chapitre I, nous avons regroupé ces espèces peu fréquemment observées en tant qu'espèces à faible abondance et faible occurrence (LOLAS) concernant leurs occurrences spatiotemporelles et leurs abondances dans chaque habitat, et nous avons décidé de nommer *rares* les espèces qui pourraient être toujours présentes mais pas toujours détectées et *transitoires* les espèces qui pourraient être observées occasionnellement à la suite d'une dispersion à partir d'habitats adjacents. Bien que nous ayons utilisé les résultats graphiques pour nous aider à fixer un seuil en dessous duquel les espèces étaient qualifiées de LOLAS et au-dessus duquel elles étaient qualifiées de communes, ce seuil reste arbitraire et se base principalement sur les occurrences des espèces. Des travaux futurs pourraient mieux envisager la manière dont ce seuil est fixé, par exemple en utilisant également les abondances, étant donné que certains taxons de notre

ensemble de données avaient de faibles occurrences mais des abondances élevées. En outre, nous pourrions renforcer notre hypothèse selon laquelle certaines espèces pourraient être qualifiées de *rares* et d'autres de *transitoire*s. Une idée pourrait être d'examiner les traits fonctionnels que ces espèces supportent, car ces espèces peuvent avoir des caractéristiques différentes de celles qui sont communes (Kunin et Gaston 1993). De plus, j'émets l'hypothèse que les espèces *transitoires* pourraient présenter des traits caractéristiques des espèces opportunistes ou colonisatrices (par exemple, petite taille, capacité de reproduction élevée et bonne dispersion) (Norkko et al. 2006). Cependant, l'étude des traits des LOLAS pourrait être limitée par l'accessibilité des données sur les traits, car si ces espèces sont souvent rares, leurs traits fonctionnels pourraient être moins bien documentés.

Les espèces *rares* ou *transitoires* sont une caractéristique prédominante des communautés écologiques, quels que soient les taxons ou les écosystèmes (Hewitt et al. 2016b ; Snell Taylor et al. 2018). Dans les écosystèmes benthiques marins, elles représentent souvent environ plus de 50 % et les communautés d'invertébrés ont tendance à présenter une proportion plus élevée de ces espèces que les communautés de plancton ou de mammifères (Snell Taylor et al. 2018). De plus, leur nombre peut augmenter avec l'hétérogénéité intra et inter-sites, établissant donc un lien important entre la diversité des habitats et la rareté (Ellingsen et al. 2007). La prévalence de ces espèces rend l'estimation de la diversité α difficile. Les méthodes de raréfaction (Sanders 1968) et d'extrapolation (Chao et al. 2014) sont souvent utilisées dans les études portant sur le benthos marin pour estimer le nombre total d'espèces et celles détectées en fonction du nombre d'individus ou d'échantillons. Dans les quatre habitats suivis, le nombre de taxons détectés a sûrement été sous-estimé, de plus des différences peuvent apparaître selon l'échelle d'observation considérée (Figure 3 ; à noter que dans cette figure, les espèces et les abondances des réplicats, points ou sites et des 15 années ont été mises en commun ce qui estompe les différences spatio-temporelles). Une solution pourrait être d'ajuster l'effort d'échantillonnage afin de diminuer le biais dans les estimations de richesse (c'est-à-dire avec un effort d'échantillonnage plus élevé lorsqu'il y a beaucoup d'espèces rares) (Dornelas et al. 2013) ou d'extrapoler pour estimer l'asymptote de la courbe d'accumulation (Chao et al. 2014). Nous pourrions également améliorer notre façon de prendre en compte la détectabilité en empruntant des méthodes à la modélisation bayésienne (Iknayan et al. 2014).

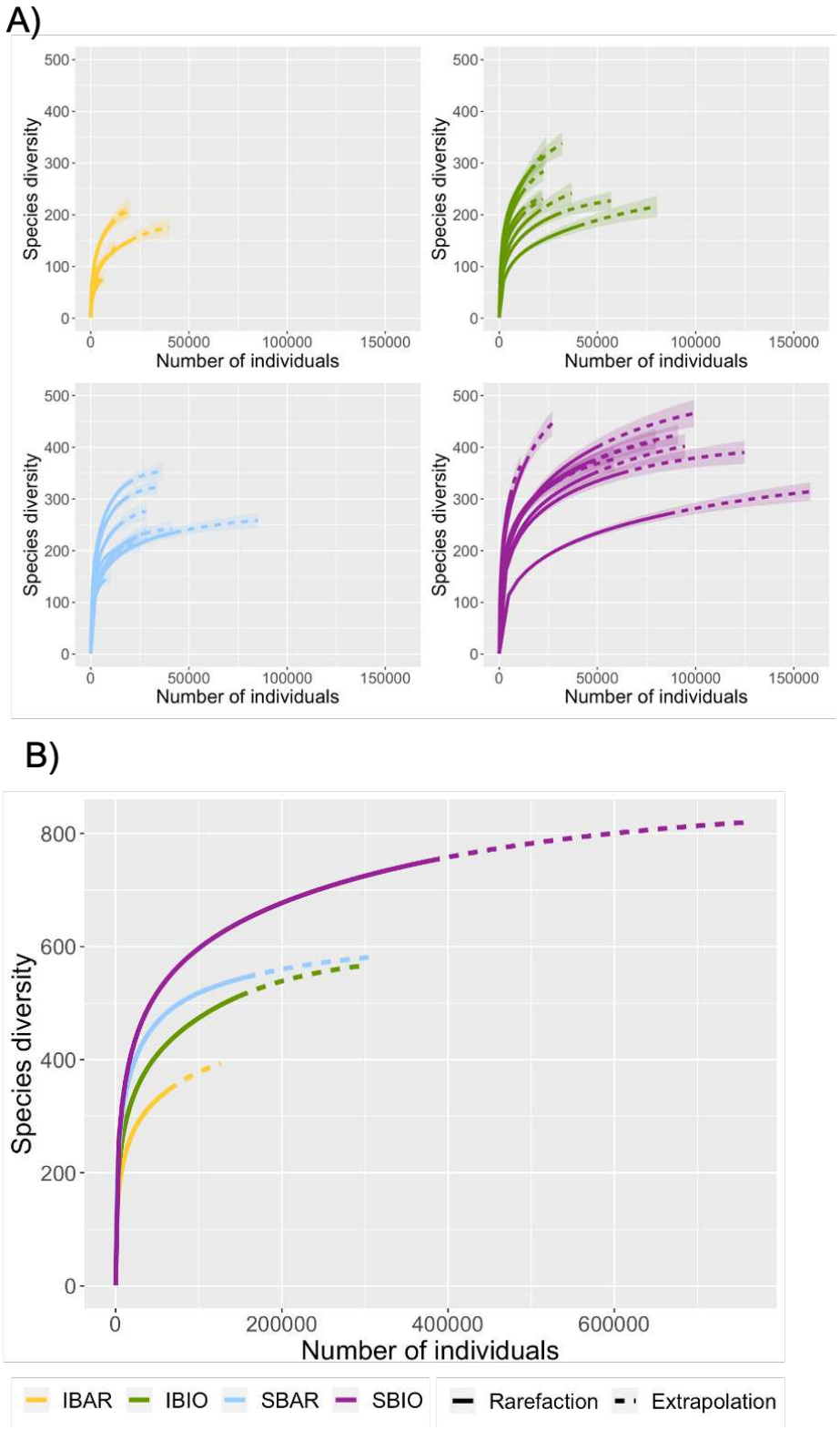


FIGURE 3 : A) Courbes de raréfaction pour chaque site pris en compte dans les analyses du Chapitre II, les espèces et les abondances ont été regroupées pour les 15 années du suivi (2005-2019). B) Courbes de raréfaction pour chacun des habitats étudiés, les espèces et les abondances ont été regroupées dans chaque habitat et pour les 15 années du suivi (2005-2019). Le ruban autour des courbes qui représente l'erreur standard et l'intervalle de confiance a été retiré afin de réduire le temps de calcul. Pour chaque graphique, le nombre de Hill utilisé était q = 0, c'est-à-dire basé sur la richesse spécifique.

Dans le chapitre I, nous avons examiné la dynamique des communautés avec et sans LOLAS pour comprendre l'influence de ces espèces sur les trajectoires temporelles, mais nous n'avons pas étudié la dynamique des LOLAS en elle-même. Après avoir ajusté notre méthode pour mieux détecter ces LOLAS, je pense que l'étude conjointe de la dynamique et de la réponse des espèces communes et des LOLAS améliorerait grandement notre compréhension de la dynamique des écosystèmes. En effet, la prise en compte de ces espèces peut permettre d'appréhender la fraction des LOLAS qui peut être attribuable aux erreurs de détection (Iknayan et al. 2014) et de quantifier le bruit qu'elles peuvent induire dans la dynamique spatio-temporelle des communautés. De plus, il a été démontré que ces espèces peuvent avoir des dynamiques différentes de celles des espèces communes (Benedetti-Cecchi et al. 2008) et qu'elles peuvent jouer un rôle majeur dans le maintien de la stabilité et de la résilience des communautés (Henderson et Magurran 2014 ; Hewitt et al. 2016b). La prise en compte de ces espèces dans des études futures aura un impact positif sur notre compréhension de la manière dont les communautés répondent aux contraintes environnementales et anthropiques et augmentera la fiabilité des stratégies de gestion (Hewitt et al. 2016b ; Snell Taylor et al. 2018).

La rareté n'est pas seulement taxonomique mais aussi fonctionnelle. Violle et al. (2017) ont défini la rareté fonctionnelle comme le degré selon lequel les traits des espèces sont plus ou moins distincts ou redondants au sein des communautés locales ou à plus grande échelle. Elle combine la rareté des espèces et le caractère distinctif des traits, où les espèces les plus rares sur le plan fonctionnel ont une faible abondance et les traits les plus distincts. Dans leur étude, ils ont également proposé des indices de « distinction » fonctionnelle (qui évaluent si une espèce est plus ou moins proche fonctionnellement du reste de la communauté) et d'unicité fonctionnelle (qui évalue à quel point une espèce n'a pas d'équivalent fonctionnel dans le pool régional). Un examen plus approfondi des traits supportés par les espèces communes et les LOLAS pourrait être essentiel pour comprendre dans quelle mesure elles partagent la combinaison de leurs traits (Figure 4), et donc comment les communautés pourraient répondre aux stress ou aux perturbations et si les LOLAS pourraient jouer un rôle majeur dans cette réponse (Mouillot et al. 2013a). En effet, si les LOLAS présentent des traits fonctionnels relativement communs, elles augmenteraient la redondance fonctionnelle de la communauté, donc sa stabilité et sa résilience (Ellingsen et al. 2007). Si elles présentent des traits distincts ou uniques, elles pourraient jouer des rôles importants dans le fonctionnement de l'écosystème (Mouillot et al. 2013a ; Murgier et al. 2021). De plus, évaluer si les espèces présentent des traits vulnérables permettrait d'informer sur la sensibilité des communautés face aux perturbations (McLean et al. 2019a). Des exemples de traits vulnérables pour la macrofaune pourraient être

les traits « sessile », « faible mobilité » et « longue durée de vie » par exemple, étant donné que les espèces présentant ces traits ont déjà montré une récupération plus longue après la pêche que les espèces mobiles ayant une durée de vie plus courte (Sciberras et al. 2018). Évaluer si des espèces fonctionnellement distinctes ou uniques sont vulnérables et s'il s'agit de LOLAS ou d'espèces communes pourrait permettre de mieux comprendre l'avenir des écosystèmes soumis à des changements croissants et de mieux mettre en place des stratégies de gestion de la conservation (Mouillot et al. 2013a ; Murgier et al. 2021).

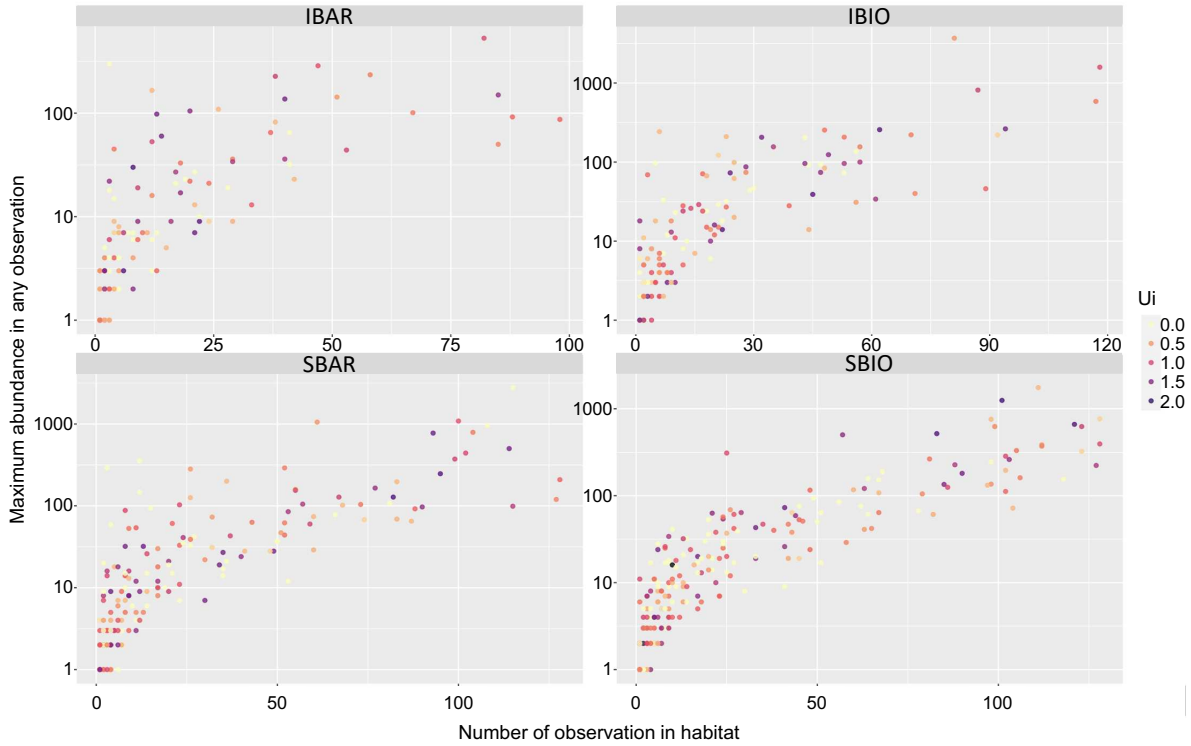


FIGURE 4 : Unicité fonctionnelle (Ui) de chaque espèce de Polychète selon qu'elle soit taxonomiquement commune ou rare dans chacun des habitats (i.e., son abondance maximale dans n'importe quelle observation (i.e., site et années) dans chaque habitat en fonction du nombre d'observation où cette espèce a été recensée). Les sites et années pris en compte sont les mêmes que dans le Chapitre IV.

2.3. Considérations pour les suivis à long terme

Un élément principal qui ressort de chaque chapitre de cette thèse est l'importance de l'échelle d'observation sur la dynamique des communautés. En effet, les diversités et dynamiques des communautés varient entre les habitats (Chapitres I à IV), au sein des habitats (c'est-à-dire entre les sites ; Chapitre I à IV) et même entre les assemblages taxonomiques (Chapitre III). Parce qu'il existe encore des lacunes dans nos connaissances sur les changements de la biodiversité à différentes échelles spatiales et temporelles (McGill et al. 2015), cette thèse souligne l'importance de considérer plusieurs échelles spatiales dans les études temporelles,

ainsi que l'importance des programmes de suivi à grande échelle temporelle et spatiale comme le REBENT pour combler ces lacunes. En effet, le REBENT permet aujourd'hui d'évaluer la dynamique sur 21 ans (2003-2023) des communautés de macrofaune depuis l'échelle du réplicat (i.e., carotte ou benne) jusqu'à celle du point, du site, de l'habitat, de la zone de marée et de la région, ou à l'échelle de différents compartiments (e.g., endofaune et épifaune) ou assemblages taxonomiques (et cette liste n'est pas exhaustive car elle peut aussi inclure les masses d'eau, les côtes du Nord et du Sud, etc.) Ainsi, le programme de suivi REBENT répond totalement aux attentes d'un programme de suivi robuste, c'est-à-dire long terme, multi-sites et multi-espèces (Hughes et al. 2017 ; Kuebbing et al. 2018).

Comme le démontrent les chapitres II et IV, les communautés des différentes zones de marée, sites et habitats n'ont pas réagi de la même manière aux contraintes abiotiques. Les forces environnementales et les menaces anthropiques pouvant être inégales dans l'espace et dans le temps, l'étendue spatiale et temporelle des programmes de surveillance est cruciale. En effet, les changements de biodiversité en réponse aux facteurs écologiques dépendent fortement de l'échelle et peuvent changer de direction d'une échelle à l'autre (Chase et al. 2018). En outre, une prise en compte conjointe de l'espace et du temps permet d'évaluer l'interaction de ces deux dimensions et la manière dont elles sont intrinsèquement liées (Legendre et al. 2010 ; Collins et al. 2018). Et plus fondamentalement si, par exemple, nous nous étions concentrés uniquement sur le site de Trévignon qui présente une communauté extrêmement persistante car dominée par une seule espèce, ou si nous nous étions concentrés uniquement sur les 4 premières années de suivi dans IBAR, nos conclusions ou hypothèses auraient été très différentes. De plus, l'importance de l'étendue spatiale dans les séries temporelles a été particulièrement mise en évidence dans les chapitres I et III lors de l'utilisation de l'analyse des trajectoires des communautés et particulièrement de la comparaison de la forme des trajectoires des sites. En effet, dans ce cas, l'unité d'observation est la trajectoire et le nombre d'observations est réduit au nombre de sites, et lorsque ce dernier est petit, il peut induire des résultats statistiques non significatifs (par exemple, les coefficients RV dans le chapitre III).

Les menaces se manifestent à toutes les échelles spatiales et pour évaluer la meilleure façon de conserver la biodiversité à travers les échelles spatiales et dans le temps, nous devons comprendre la relation entre les données de surveillance collectées localement et la dynamique de la diversité régionale, et comment les mécanismes qui maintiennent la diversité varient des échelles spatiales locales aux échelles spatiales régionales et à travers le temps (Socolar et al. 2016). Le programme de surveillance REBENT a fourni la base sur laquelle cette thèse a pu aborder ces questions. De plus, en se concentrant sur la diversité β plutôt que la diversité α, il a

permis d'aborder l'intégration des questions de conservation à toutes les échelles (Socolar et al. 2016). En effet, de telles études basées sur un suivi multi-échelle, permettent non seulement de relier les observations à l'écologique théorique mais sont également un support potentiel pour la mise en place de stratégies de conservation.

L'étendue temporelle et la fréquence des programmes de surveillance sont également importantes pour détecter des tendances. Avec son échantillonnage annuel, le programme REBENT peut être qualifié de surveillance avec des "intervalles à court terme", et est donc pertinent pour la mesure de plusieurs variables essentielles de la biodiversité (Pereira et al. 2013). Cependant, l'étendue temporelle maximale étudiée dans cette thèse était de 15 ans. Les communautés de macrofaune benthique peuvent présenter différents cycles pluriannuels (par exemple, 3-9 ans, 5-7 ans, 10-12 ans) (Thrush et al. 2021a) que nous n'aurions pas été en mesure de détecter avec une série de données de 15 ans, car la détection des cycles nécessite des séries de données au moins 2 à 3 fois plus longues que les cycles en question. De plus, les cycles océanographiques peuvent parfois se dérouler sur plusieurs décennies, ce qui rend les études à long terme essentielles dans les écosystèmes marins (Lindenmayer et al. 2012). Par ailleurs, la durée des cycles peut varier en fonction des espèces (e.g., changements de dominance ; Gray et Elliott 2009) et l'étude de la tendance globale de la communauté peut parfois les brouiller. L'examen des tendances de certaines espèces ou de certains groupes fonctionnels (e.g., Hewitt et al. 2016a) pourrait fournir des informations sur la synchronie ou l'asynchronie des espèces et permettre de mieux comprendre la réaction des communautés face aux contraintes environnementales ou anthropiques, ainsi que les processus qui maintiennent leur stabilité (Hallett et al. 2016 ; Lamy et al. 2020).

Quelques sites suivis par le REBENT sont échantillonnés deux fois par an (échantillonnage d'automne et de printemps). Cela pourrait permettre à l'avenir de se concentrer sur les dynamiques saisonnières et d'évaluer la variabilité plus fine des communautés. En effet, cela pourrait avoir un impact sur la dynamique annuelle étudiée ici, car certains processus écologiques de la macrofaune benthique suivie pourraient être plus rapides que la fréquence d'échantillonnage annuelle. Dans les chapitres, nous avons étudié des échantillons prélevés au printemps (c'est-à-dire entre la fin février et le début mai), avant le recrutement de la plupart des espèces dans la région, afin d'éviter des effets confondants. Cependant, pour certaines années ou certains sites, l'échantillonnage a parfois été reporté en raison des conditions météorologiques. Exceptionnellement, l'échantillonnage peut chevaucher la période de recrutement de certaines espèces et potentiellement induire une source de variabilité dans la série temporelle qui pourrait être étudiée.

Le programme de surveillance REBENT a été mis en place afin d'établir une base de référence nous permettant de mieux comprendre et quantifier l'effet des conditions environnementales changeantes ou des événements catastrophiques tels que ceux causés par les marées noires. Cependant, la désignation d'un état comme état de référence se heurte à une difficulté majeure : notre connaissance historique de ce qu'aurait pu être l'état d'un écosystème "naturel" et vierge. En effet, si le suivi REBENT avait commencé juste avant le naufrage de l'Erika, ces premières observations auraient pu être utilisées comme états de référence. Cependant, comment savoir si, à ce moment-là, l'écosystème était dans un état stable ou en transition ? Pauly (1995) a défini le « syndrome de la ligne de base changeante » comme le fait que chaque génération tend à définir ce qui est « naturel » ou « normal » en fonction de son expérience, ajustant ainsi toujours la ligne de base à un nouveau niveau. En fait, en raison de l'évolution des conditions climatiques à différentes échelles de temps, de la nature et de l'intensité changeantes des multiples pressions qui s'exercent en interaction sur les écosystèmes marins et de leurs réponses non linéaires et parfois décalées, les conditions de référence sont toujours dynamiques (Duarte et al. 2009). Les suivis continus à long terme sont certainement un outil essentiel pour comprendre la dynamique complexe des écosystèmes et affiner notre vision de leur dynamique historique, permettant ainsi une meilleure caractérisation de l'évolution des états écologiques (Compton et al. 2017). De plus, je pense qu'un suivi avec des intervalles courts entre les échantillonnages (1-5 ans) est un strict minimum pour fournir une vue réaliste de la dynamique des écosystèmes, alors que des aperçus moins fréquents de l'état des écosystèmes dans le temps pourraient peut-être estomper des changements de dynamiques importants et donc qu'une fréquence plus élevée d'observations pourrait potentiellement mettre en évidence des variations autrement invisibles.

L'augmentation de l'étendue spatiale et temporelle du suivi de surveillance ou du nombre d'échantillons prélevés pour estimer la diversité de manière adéquate nécessite un effort supplémentaire et est coûteuse que ce soit en temps ou en argent. Au chapitre III, nous avons proposé d'utiliser la substitution taxonomique pour étudier la dynamique de l'ensemble de la communauté de macrofaune en se concentrant uniquement sur un taxon de substitution, ce qui peut réduire considérablement le temps et les efforts nécessaires à l'identification des taxons (Olsgard et Somerfield 2000 ; Wodarska-Kowalczuk et Kedra 2007). Cependant, pour évaluer si la substitution est cohérente dans le temps, une longue série temporelle où toute la macrofaune est échantillonnée est encore nécessaire. D'ailleurs, comme le montre le chapitre III, les différences entre les différents taxons utilisés comme substituts ne sont pas toujours évidentes en fonction des habitats. C'est pourquoi nous avons recommandé de se référer à des

études de substitution portant sur le même type d'environnement ou d'habitats avant de lancer un programme de surveillance basé sur des substituts.

La collecte et l'accès aux données de surveillance constituent des obstacles pour combler les lacunes dans nos connaissances sur les changements de la biodiversité à plusieurs échelles. Outre la substitution taxonomique, la collaboration inter-laboratoires telle que celle mise en place dans le cadre du programme REBENT est un exemple d'une autre solution permettant de pondérer les efforts pour acquérir de telles données. Par ailleurs, les données devraient être accessibles à partir de bases de données en ligne, dans des annexes de travaux lorsque ceux-ci sont publiés ou sur demande (McGill et al. 2015), ce qui est de plus en plus le cas aujourd'hui. On pourrait envisager d'ajouter à la base de données REBENT (qui comprend déjà toutes les données collectées sur le terrain), des données qui ont été collectées a posteriori par des ingénieurs, des stagiaires ou des doctorants comme moi, qui rassemblent des informations sur les traits fonctionnels des taxons suivis par le REBENT (ce qui devrait impliquer une homogénéisation des traits et des modalités utilisés par les différentes équipes). De plus, il serait possible de considérer des facettes supplémentaires de la biodiversité telles que la diversité phylogénétique, qui pourrait être un estimateur pertinent de la productivité des écosystèmes (Cadotte et al. 2012) ainsi que de leurs fonctions, puisque des espèces de différentes lignées pourraient remplir différentes fonctions (Cadotte et al. 2008, 2009). Cela pourrait être possible en répertoriant dans la base de données les séquences génétiques des taxons répertoriés dans le REBENT qui sont disponibles dans les bases de données en ligne, bien qu'elles puissent être plus rares et pas toujours bien identifiées pour les invertébrés par rapport aux vertébrés (Lavesque et al. 2019).

2.4. Considérations méthodologiques

Au cours de cette thèse, les différentes méthodes utilisées ont soulevé des questions, des idées de perspectives ou ont montré certaines limites discutées dans les paragraphes suivants.

Le chapitre I était principalement basé sur la CTA (De Cáceres et al. 2019), qui était, au moment où j'ai commencé à explorer et tester cette méthode sur les données du REBENT dans la première année de ma thèse, une méthodologie très nouvelle qui semblait prometteuse. En effet, même si des représentations de trajectoires existaient déjà (e.g., Clarke et Warwick 1997), la CTA offrait la possibilité de quantifier et de comparer la dynamique des communautés, en prenant en compte l'intégralité de l'espace multidimensionnel avec la possibilité de gérer les données manquantes (uniquement pour certaines métriques). À l'époque, il existait très peu d'études utilisant cette méthode sur des ensembles de données de communautés réelles, ce qui rendait difficile la comparaison des résultats et des interprétations entre les études. Depuis lors, j'ai observé la croissance de cette méthode, en raison de son utilisation plus fréquente dans des articles de recherche ou de ses extensions (e.g., ETA ; Sturbois et al. 2021c, SITA ; Sturbois et al. 2022). En effet, cette méthode offre une multiplicité de possibilités puisqu'elle peut également être appliquée, par exemple, sur la structure fonctionnelle de la communauté ou sur la matrice environnementale (Figure 5), ou encore combinée avec d'autres méthodes d’analyses multidimensionnelles, comme j'ai pu le tester par moi-même ou à travers la supervision d'un stage au cours de ces 3 dernières années.

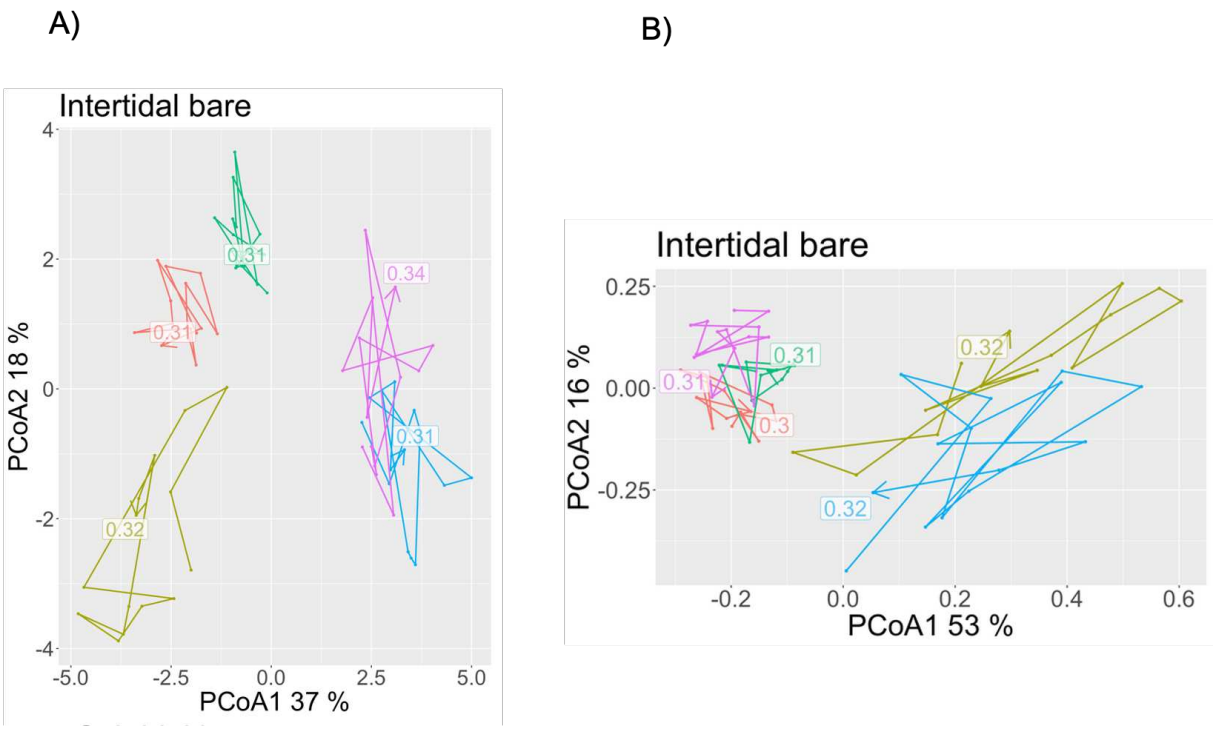


FIGURE 5 : Exemple de A) trajectoires environnementales pour les istes de l'habitat nu intertidal considérés dans le Chapitre I et de B) trajectoires fonctionnelles sur les communautés de Polychètes des sites de l'habitat intertidal nu considérés dans le Chapitre I. La distance euclidienne a été utilisée pour les trajectoires environnementales et la distance de Hellinger pour les fonctionnelles.

Cependant, avant d'interpréter toutes les possibilités des extensions de la CTA, je me suis concentrée sur les métriques développées dans la méthode originale (De Cáceres et al. 2019). Elles ont d'abord été développées sur des communautés d'arbres, mais nous les avons appliquées et testées sur des espèces de la macrofaune benthique et avons essayé d'interpréter les modèles observés. Dans ce Chapitre I, nous avons conclu que les communautés suivaient des dynamiques dépendantes de l'habitat, non directionnelles et stables, et nous avons lié les trajectoires écologiques à des modèles théoriques, principalement en suivant Lamothe et al. (2019). Plusieurs autres métriques de la méthode originale de la CTA qui n'ont pas été intégrées dans le Chapitre I ont également fait allusion à cette conclusion. Par exemple, les distances entre une observation et celles à t+1, t+2, t+3, etc. n'ont pas montré de tendance marquée (Figure 6) ou la convergence ou la divergence des trajectoires (c'est-à-dire si les distances entre les observations diminuent progressivement, reflétant une homogénéisation des communautés, ou si elles augmentent) n'étaient pas significatives.

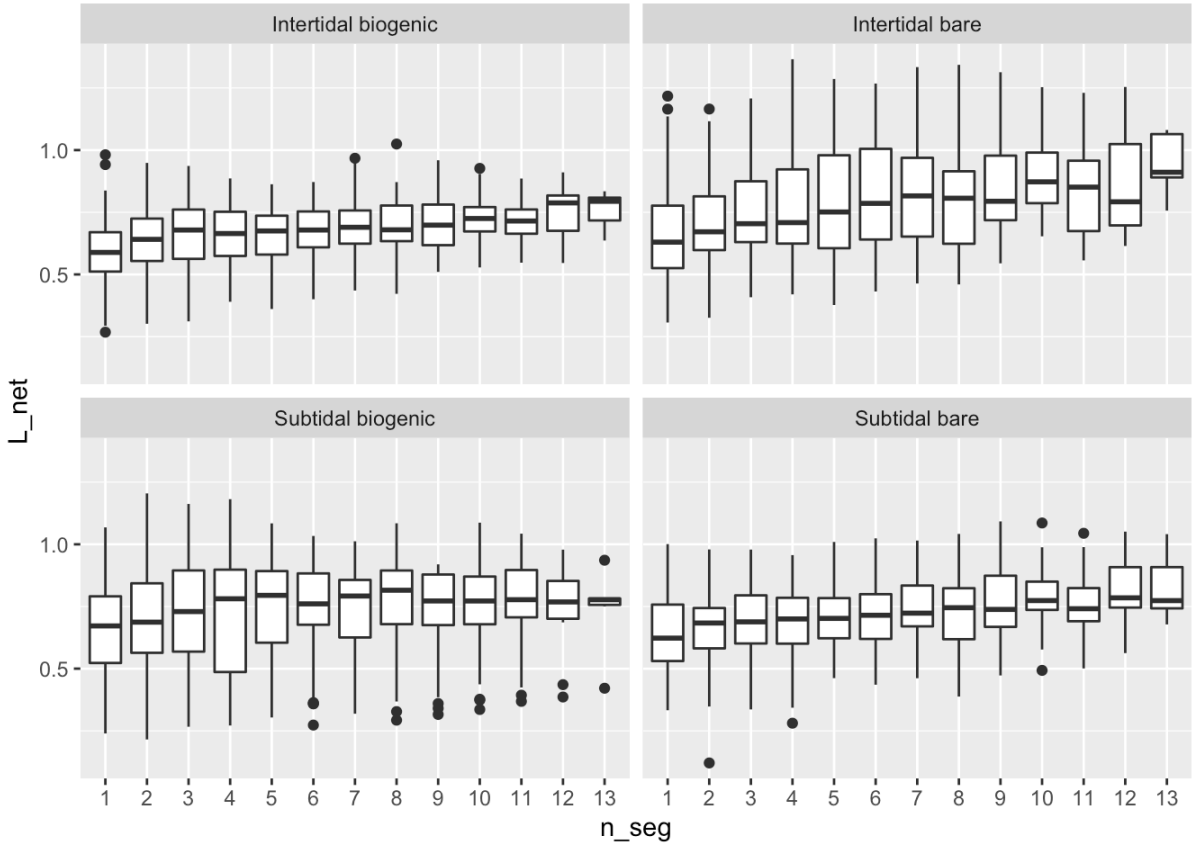


FIGURE 6 : Changement net (L_net, i.e., distance de Hellinger ici), entre une observation et celle à t+1, t+2, etc. (i.e., n_seg = nombre de segments entre deux observations considérées), pour chaque habitat. Le nombre de sites et d'années considérés est le même que dans le Chapitre I.

Cependant, cette méthode étant assez nouvelle, nous aurions pu utiliser d'autres méthodes et indices permettant de quantifier la dynamique temporelle (Hallett et al. 2016 ; Buckley et al. 2021a) pour comparer les résultats de la CTA. C'est en partie pour cette raison que j'ai voulu utiliser d'autres méthodes dans les différentes parties de ma thèse, et, au final, les résultats générés par ces méthodes ont soutenu les conclusions tirées avec la CTA. Nous aurions également pu utiliser des méthodes telles que les analyses de « points de basculement » (Andersen et al. 2009) pour identifier plus précisément les ruptures dans les séries temporelles (en particulier sur la comparaison des longueurs de segments entre les années ; Chapitre I, Figure 4) et la transition potentielle vers de nouveaux états stables aléatoires par exemple. Cependant, ces méthodes dépendent fortement de la longueur et de la fréquence de la série temporelle (Hewitt et Thrush 2019).

Une des difficultés dans l'interprétation des trajectoires était le manque de trajectoires « de référence » (c'est-à-dire la trajectoire d'une communauté avec une dynamique connue) auxquelles nous aurions pu comparer les trajectoires observées pour en tirer des conclusions.

C’est la raison principale pour laquelle nous avons simulé des trajectoires. Les modèles nuls tels que celui que nous avons mis en place peuvent être un outil crucial dans l'évaluation de la diversité β temporelle (Magurran et al. 2019). Cependant, ces derniers peuvent présenter certaines limites. En effet, nous avons d'abord voulu mettre en place un modèle simulant les processus (c'est-à-dire plutôt un modèle neutre qu'un modèle nul ; Gotelli et McGill 2006). Or, simuler des processus nécessite de fixer des paramètres tels que les taux de migration ou d'extinction individuelle qui ne sont presque jamais mesurés directement. Compte tenu de la complexité de l'élaboration d'un tel modèle, nous nous sommes rabattus sur la simulation du résultat attendu, c'est-à-dire la simulation de trajectoires totalement non-directionnelles. Pour construire ce modèle nul, nous avons utilisé une randomisation des données observées. Pour ce faire, nous avons combiné tous les taxons observés dans tous les sites et toutes les années de la série temporelle en un « pool d'espèces » à l'échelle de l'habitat (voir les annexes du chapitre I pour plus de détails). Cette approche présente certaines limites, car les pools d'espèces ne sont pas statiques et il est possible que nous ayons simulé des communautés avec des espèces qui ne se trouvent jamais ensemble dans la réalité. L'identification du « bon » pool d'espèces est un défi important dans les études sur la diversité β spatiale et temporelle (Magurran et al. 2019), et une amélioration de ce modèle nul pourrait être envisagée dans de futurs travaux.

En ce qui concerne la métrique de directionnalité, elle a montré des valeurs très faibles et similaires entre les différents sites. Dans le chapitre I, nous nous sommes demandé si cela n'était pas dû à la grande richesse et au turnover plus rapide des communautés marines par rapport aux communautés terrestres. Cependant, j'ai eu l'occasion d'appliquer la CTA à des communautés de foraminifères moins riches en espèces et, étonnamment, les valeurs de directionnalité étaient presque identiques à celles trouvées dans le chapitre I. Cela souligne la nécessité de tester cette méthode encore récente pour mieux comprendre ses limites, par exemple par une méta-analyse regroupant des écosystèmes marins, terrestres, riches ou moins riches dont la dynamique est déjà connue, des données provenant d'études de surveillance ou expérimentales, mais aussi en testant différentes distances écologiques. En effet, toutes les métriques de la CTA sont basées sur la distance utilisée, qui doit être choisie avec soin en fonction de ses propriétés et des données et communautés utilisées (Legendre et De Cáceres 2013). Les différentes distances écologiques ont des limites différentes (i.e., une valeur maximale différente), et je trouverais intéressant de tester si cela peut avoir un effet sur la directionnalité et plus généralement, je trouverais instructif de regarder comment chacune des métriques réagit à ces différentes distances. Les autres chapitres de la thèse ont également confirmé que la fraction qui modélise la structure temporelle joue un rôle très faible dans la

variation des communautés. De plus, lorsque j'ai calculé la tendance linéaire temporelle de chaque site, la plupart des résultats étaient significatifs et expliquaient environ 10% de la variation de la communauté du site. Cette variation pourrait être due à de la dérive écologique ou à des changements stochastiques au cours des 15 années suivies. Il serait intéressant, dans le cadre de futurs travaux, de simuler des trajectoires non directionnelles ou complètement directionnelles (comme cela pourrait être le cas dans de successions écologiques) et d'estimer la proportion de variance expliquée par ces tendances linéaires, afin d'évaluer si une relation cohérente entre ces deux éléments pourrait être trouvée. De plus, une méthode récente de quantification des changements directionnels (Schmera et al. 2022) pourrait être testée sur les communautés que nous avons étudiées dans le Chapitre I afin de comparer les résultats ou de mieux les comprendre, car elle peut indiquer si le turnover des communautés est dominé par le gain d'espèces, la perte d'espèces ou un équilibre entre les deux, bien qu'elle ait été développée sur des données de présence-absence.

Comme déjà indiqué dans la section précédente, le nombre de trajectoires prises en compte peut avoir une influence sur la comparaison des dynamiques. Le nombre de trajectoires, et donc de sites pris en compte dans le Chapitre I, aurait pu être augmenté sans échantillonner de nouveaux sites. En effet, dans ce chapitre, nous avons effectué une sélection des sites afin de ne garder que ceux dont les séries temporelles étaient complètes pour éviter de potentiels effets confondants pour la comparaison de leur dynamique et pour éviter le potentiel effet que les données manquantes pourraient avoir sur les métriques. Ainsi, l'évaluation de l'effet des données manquantes, par exemple en supprimant les années une par une et en regardant quand un changement significatif est détecté par rapport aux métriques calculées sur la trajectoire complète, pourrait nous permettre d'augmenter le nombre de sites pris en compte dans les analyses, si la CTA n'est pas très sensible au manque de données.

L'une des principales perspectives de la CTA serait de pouvoir établir un lien direct entre les trajectoires environnementales et les trajectoires des communautés. Cela impliquerait un espace multidimensionnel qui puisse représenter conjointement les trajectoires environnementales et des communautés. La méthode STATICO le permet, en représentant les trajectoires dans un espace compromis (Thioulouse et al. 2004). Cependant, un inconvénient de cette méthode est qu'il n'est pas possible de quantifier la part de variance de la communauté expliquée par l'environnement dans cet espace compromis. Une alternative, que j'ai testée, est de regarder la corrélation entre les longueurs des segments des trajectoires environnementales et des communautés (i.e., si un long segment dans les trajectoires environnementales, c’est-à-dire un fort changement, induit également un long segment dans les trajectoires des

communautés). Aucune corrélation n'a été trouvée dans les tests effectués, soit parce qu'il n'y a effectivement pas de corrélation, soit peut-être en raison d'un décalage entre la réponse de la communauté et la variation de l'environnement. Une autre hypothèse pourrait être de tester s'il existe une corrélation entre le nombre potentiel d'événements extrêmes entre deux années et la longueur des segments.

En effet, dans le Chapitre II, nous avons suggéré que nos jeux de données environnementales ne caractérisaient pas suffisamment les événements extrêmes, ceux-ci pourraient être estimés de la même manière que les vagues de chaleur marines qui sont caractérisées par une période de 5 jours au-dessus du 90ème percentile par rapport à une période de référence historique (Hobday et al. 2016), ou plus simplement en comptant le nombre de jours, de vent par exemple, au-dessus du dernier quartile. De plus, en dehors de la granulométrie, notre jeu de données environnementales est basé sur des modèles numériques pour lesquels il est souvent difficile de trouver un bon compromis entre grain spatial et temporel. Ici nous avons pris des modèles permettant de traiter l'intégralité de nos séries temporelles, malgré la résolution spatiale grossière des modèles. Pour les modèles marins, les modèles numériques estiment les paramètres de la colonne d'eau mais peuvent ne pas être adéquats pour décrire les conditions sur le fond marin ou à l'intérieur d'un banc de maërl par exemple. Idéalement, les données *in situ* seraient plus précises, notamment pour mieux caractériser l'effet tampon environnemental des habitats biogénique. Pour mieux caractériser les données environnementales, nous pourrions également utiliser des polynômes, puisque les RDA ne modélisent que les relations linéaires, ce qui nous permettrait de caractériser d'autres formes de relations.

Les variables que nous avons utilisées pour caractériser les pressions anthropiques étaient principalement des proxys. Celles-ci peuvent avoir des limites puisqu'elles ont été extraites (pour le nombre d'habitants et les données d'occupation du sol) de données terrestres qui peuvent mieux caractériser les sites intertidaux que les sites subtidaux. La pression de pêche pourrait également être mieux caractérisée, en évaluant plus précisément l'effort de pêche par le biais d'une enquête auprès d'un plus grand nombre d'acteurs du littoral. La même chose pourrait être faite pour évaluer les menaces anthropiques en général : une enquête pourrait être menée auprès de différents acteurs du littoral (par exemple, les pêcheurs, les scientifiques, le conservatoire du littoral). Une autre alternative serait de mesurer directement les pressions (e.g., en mesurant les éléments chimiques dans l'eau de mer, le stress d'abrasion, etc.) ou de prendre en compte la présence de marées vertes, car il a été démontré qu'elles ont un impact sur la structure de la communauté macrobenthique des plages de sable (Quillien et al. 2015).

Enfin, en ce qui concerne les traits fonctionnels, ceux-ci ont été définis au cours d'une précédente thèse et suite à plusieurs discussions inter-laboratoires. La recherche de traits dans la littérature peut poser certaines limites car la plupart des espèces sont relativement peu décrites ou pour des régions du monde éloignées de notre zone d'étude. L'avantage de la méthode de codage flou utilisée ici est de prendre en compte la variabilité intra-spécifique ou ontogénique, cependant dans les analyses, les modalités de chaque trait sont considérées comme des traits à part entière. Cela peut poser des problèmes pour l'interprétation des résultats ou le calcul de certaines méthodes, comme les analyses type RLQ et du 4ème coin (Dray et al. 2014), qui permettent de tester les liens entre chaque traits (ici modalités) et les paramètres environnementaux. Une solution pourrait être de résumer le nombre de modalités par des axes d'une « fuzzy PCA » (Chevenet et al. 1994 ; Beauchard et al. 2017) qui seraient ensuite intégrés dans les méthodes précédemment mentionnées. Cela présenterait une perspective intéressante puisque les méthodes RLQ et 4ème coin permettent également de prendre en compte l'effet du temps et de l'espace (Wesuls et al. 2012). En ce qui concerne le calcul des indices fonctionnels, une méthode récente a proposé de les évaluer sur la base d'un hypervolume probabiliste plutôt qu'à partir du volume de l'enveloppe convexe (figure 7 ; Mammola et Cardoso 2020). Il est intéressant de noter que cette méthode a donné des résultats différents de ceux donnés par les enveloppes convexes (Figure 8). Cela soulève la question intéressante de savoir s'il s'agit ou non d'un artefact de la méthode ou bien de différences sous-jacentes réelles. Je pense que tester l'impact de LOLAS sur ces résultats devrait permettre de répondre à cette question.

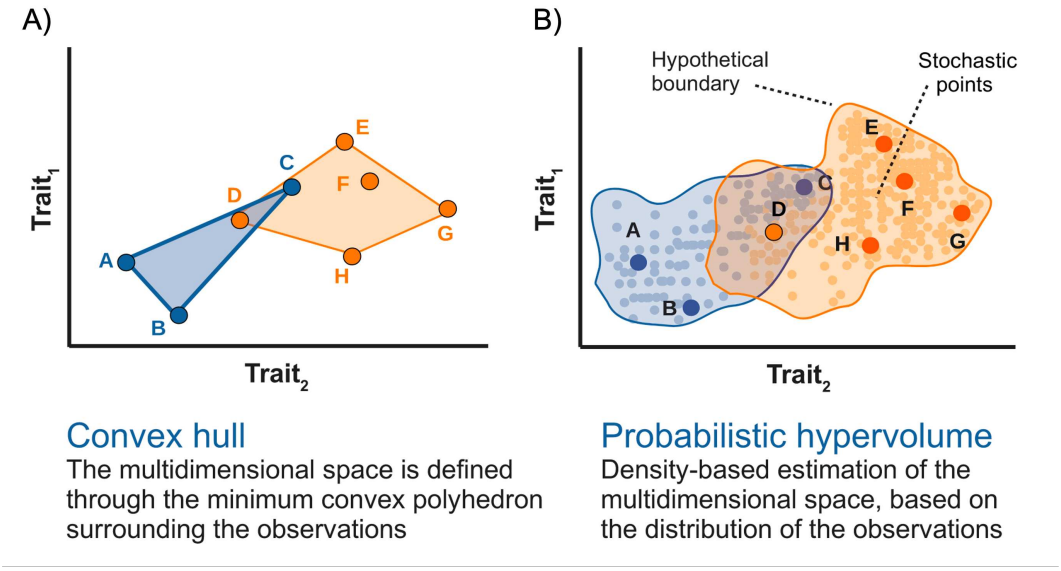


FIGURE 7 : Exemples des représentations mathématiques de la diversité fonctionnelle (FD) de communautés. Les exemples sont basés sur deux traits hypothétiques et deux communautés, représentées en turquoise et orange. Une lettre correspond à une espèce. A) L'espace de traits peut être représente par l'enveloppe convexe minimale comprenant toutes les espèces occupant l'espace de traits. La richesse fonctionnelle d'une communauté est estimée comme le volume de l'enveloppe convexe. B) L'espace de traits peut être construit à l'aide d'hypervolumes à densité de noyau, où il est approximé comme un nuage de points stochastiques échantillonnés sur la base d'un ensemble d'observations (e.g., les traits de l'espèce dans la communauté). La richesse fonctionnelle de la communauté est estimée par le volume de l'hypervolume délimité par les points stochastiques. D'après Mammola and Cardoso (2020).

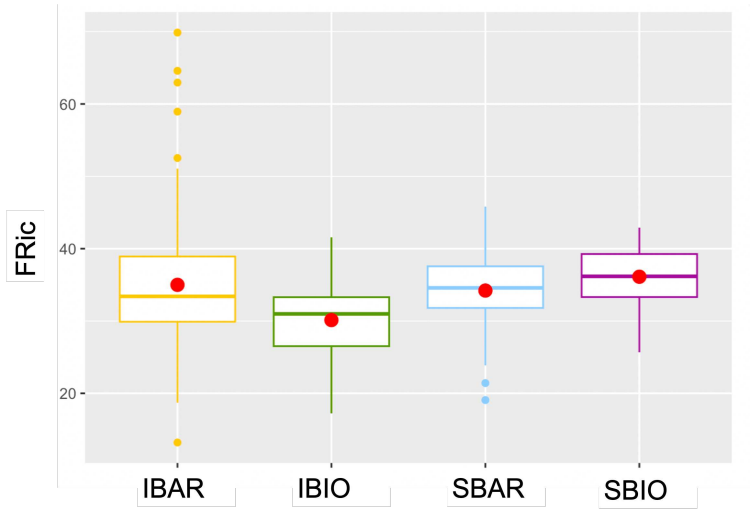


FIGURE 8 : Richesse fonctionnelle (FRic) de chacun des habitats estimée par hypervolume à densité de noyau. Le même nombre de sites, années et axes de la PCoA que le Chapitre IV a été utilisé pour le calcul. Les points rouges représentent la Moyenne de FRic dans chaque habitat. Nous pouvons observer une différence par rapport aux valeurs de FRic calculées dans le Chapitre IV, qui représentait un gradient marqué depuis IBAR vers SBIO. IBAR = habitat intertidal nu, IBIO = habitat intertidal biogénique, SBAR = habitat subtidal nu, SBIO = habitat subtidal biogénique.

Conclusion

Conclusion in English

In a context of global changes and increasing anthropogenic pressures on marine ecosystems, this thesis highlights the need to better understand the dynamics of ecological communities in order to detect, quantify and predict potential changes in biodiversity.

Based on long-term monitoring of benthic macrofauna communities at a regional scale, it has filled some gaps in our understanding of changes in biodiversity in the face of environmental variation at different spatial and temporal scales. Indeed, this work has allowed us to better understand the dynamics of benthic macrofauna communities at the spatial scales of sites, habitats and the region, on a temporal scale of about 15 years.

Over the 15 years studied, it has brought to light 1) variations in the structures and functions of the macrobenthic communities between sites, which are mainly dependent on space, 2) stability at the scale of the habitats supported by mechanisms depending on their nature and their tidal level, 3) remarkable stability at the regional scale. This demonstrates that significant heterogeneity at the local scale (e.g., site, bay, sub-region) can be included in a system with highly homogeneous behavior over time.

"Stable" does not mean "static" and the demonstrated stability does not preclude rapid change, especially under habitat destruction scenarios. Moreover, in addition to highlighting various habitat-dependent ecological mechanisms, this thesis emphasizes the importance of key environmental and anthropogenic factors in the variation of benthic macrofaunal community structure and function.

Bringing these findings together allows us to hypothesize how these habitats will respond to potential threats and thus adjust or implement appropriate conservation strategies. Rather than focusing solely on the conservation of biogenic habitats (whose overall positive effect on local biodiversity this thesis confirms), this thesis work highlights the value of conserving β-diversity, both within a habitat but also between habitats (e.g., habitat diversity at a regional scale), as an essential ingredient in maintaining stability.

Indeed, as biodiversity is a multi-faceted and multi-scale concept, its characterization and conservation should tend to take these multiple dimensions into account. While this thesis has focused on taking into account multiple scales and the taxonomic and functional facets of diversity, future work could consider the study of other facets (e.g., phylogenetic, seascapes, etc.). Another major perspective raised by this work is to better understand the respective roles of "rare" and common species in maintaining or not the stability of communities. Ultimately,

this thesis is firmly situated at the crossroads between observation, theoretical ecology and conservation, which are the direct benefits that can be derived from long-term monitoring.

Conclusion en français

Cette thèse s'inscrit dans un contexte de changements globaux et de pressions anthropiques croissantes sur les écosystèmes marins, soulignant la nécessité de mieux comprendre les dynamiques des communautés écologiques afin de détecter, quantifier et prédire de potentiels changements dans la biodiversité.

En s'appuyant sur un suivi à long-terme des communautés de macrofaune benthique à une échelle régionale, elle a permis de combler certaines lacunes dans notre compréhension des changements dans la biodiversité face aux variations de l'environnement, à différentes échelles spatiales et temporelles. En effet, ce travail a permis d'appréhender les dynamiques des communautés de macrofaune benthique aux échelles spatiales des sites, des habitats et de la région, sur une échelle temporelle d'environ 15 années.

Il a mis en lumière, sur les 15 années étudiées, 1) des variations des structures et fonctions des communautés macrobenthiques entre les sites, qui sont principalement dépendantes de l'espace, 2) une stabilité à l'échelle des habitats supportée par des mécanismes dépendant de leur nature et de leur étagement, 3) une remarquable stabilité à l'échelle régionale. Ce qui démontre qu'une importante hétérogénéité à l'échelle locale (e.g., site, baie, sous-région) peut être incluse dans un système au comportement fortement homogène dans le temps.

« Stable » ne signifie pas pour autant « statique » et la stabilité démontrée n'exclut pas qu'un changement rapide pourrait advenir, surtout dans le cas de scénarios de destruction de l'habitat. D'ailleurs, en plus d'avoir mis en évidence différents mécanismes écologiques dépendants de l'habitat, cette thèse met l'accent sur l'importance de facteurs environnementaux et anthropiques clés dans les variations de structure et fonctionnement des communautés de macrofaune benthique.

Rassembler ces conclusions permet de dresser des hypothèses quant à la réponse de ces habitats face à de potentielles menaces et donc d'ajuster ou de mettre en place des stratégies de conservation adaptées. Plutôt que de se pencher uniquement sur la conservation des habitats biogéniques (dont cette thèse confirme l'effet positif général sur la biodiversité locale), ce travail de thèse met en évidence l'intérêt de conserver la diversité β, à la fois au sein d'un habitat mais également entre habitats (e.g., diversité des habitats à l'échelle régionale), en tant qu'ingrédient essentiel au maintien de la stabilité.

En effet, la biodiversité étant un concept abritant une multitude de facettes et d'échelles, sa caractérisation ainsi que sa conservation devraient tendre à prendre en compte ces dimensions multiples. Si cette thèse s'est appliquée à prendre en compte, au-delà de multiples échelles, les facettes taxonomique et fonctionnelle de la diversité, les travaux à venir pourraient considérer l'étude d'autres facettes (phylogénétique, paysages marins, etc.). Une autre perspective majeure que soulève ce travail est à l'avenir de mieux appréhender les rôles respectifs des espèces « rares » et des espèces communes dans le maintien ou non de la stabilité des communautés. En fin de compte, cette thèse se situe résolument au carrefour entre observation, écologie théorique et conservation, qui constituent les bénéfices directs pouvant être tirés des suivis à long-terme.

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COLLEGE SCIENCES DOCTORAL DE LA MER BRETAGNE ET DU LITTORAL

UBO Université de Bretagne Occidentale

Titre : Influence de l'habitat sur les dynamiques spatiotemporelles des structures taxonomique et fonctionnelle des communautés de macrofaune benthique sous contraintes naturelles et anthropiques.

Mots clés : écologie des communautés – suivis à long-terme – habitats benthiques – dynamiques spatiotemporelles – β diversité – facettes taxonomiques et fonctionnelles

Résumé : Dans un contexte de changements globaux et de pressions anthropiques croissantes sur les écosystèmes côtiers, comprendre la dynamique et la réponse des communautés écologiques face à ces changements devient primordial. Pour ce faire, cette thèse s'appuie sur le suivi à long-terme des communautés de macrofaune benthiques, mené à une échelle régionale, dans le cadre du RÉseau BENThique (REBENT). Elle vise à mieux comprendre l'influence de l'habitat sur les dynamiques spatiotemporelles de ces communautés en s'appuyant sur les facettes taxonomique et fonctionnelle de la biodiversité. En effet, quatre habitats côtiers distincts sont comparés : les plages de sables, les herbiers intertidaux, les fonds meubles subtidaux et les bancs de maërl. Cette étude appréhende en premier lieu les dynamiques temporelles des communautés de macrofaune au sein de chacun des habitats. Elle s'attèle ensuite à comprendre la nature des facteurs contrôlant les dynamiques spatiotemporelles des communautés, en prenant en compte à la fois variables environnementales et proxys de pressions anthropiques. Cette étude aborde enfin la compréhension des déterminants des dynamiques fonctionnelles des communautés.

Cette thèse a par ailleurs permis de tester l'efficacité de la substitution taxonomique pour décrire les dynamiques spatiale et temporelle des communautés, une méthode pouvant réduire l'effort engendré par les suivis à long-terme. Ce travail fait progresser notre compréhension des changements de la biodiversité à différentes échelles spatiales et temporelles. Il démontre une hétérogénéité des dynamiques à l'échelle des sites, une importante stabilité à l'échelle des habitats et révèle différents mécanismes de stabilité dépendant de l'habitat. Enfin, il montre une remarquable stabilité temporelle (15 ans) de ces communautés à l'échelle régionale. Ces considérations soulignent la nécessité d'appréhender les différentes échelles et facettes de la biodiversité afin de mieux caractériser les dynamiques et permettre de prendre les mesures de conservation les plus pertinentes. En particulier il est primordial de veiller à conserver la diversité β intra et inter habitats, ingrédient essentiel au maintien de la stabilité. Finalement, cette thèse souligne l'importance des suivis à long-terme en tant qu'outils d'acquisition de connaissance à l'interface entre observation, écologie théorique et conservation.

Title: Influence of habitat in structuring spatiotemporal taxonomic and functional dynamics of benthic macrofauna under natural and anthropogenic constraints.

Keywords: community ecology - long-term monitoring - benthic habitats - spatiotemporal dynamics - β diversity - taxonomic and functional facets

Abstract: In a context of global changes and increasing anthropogenic pressures on coastal ecosystems, understanding the dynamics and response of ecological communities to these changes becomes essential. To do so, this thesis is based on the long-term monitoring of benthic macrofauna communities, conducted at a regional scale, within the RÉseau BENThique (REBENT). It aims to better understand the influence of the habitat on the spatiotemporal dynamics of these communities based on the taxonomic and functional facets of biodiversity. Indeed, four distinct coastal habitats are compared: sandy beaches, intertidal seagrass beds, subtidal soft bottoms and maerl beds. This study firstly apprehends the temporal dynamics of macrofauna communities within each of the habitats. It then focuses on understanding the nature of the factors controlling the spatiotemporal dynamics of the communities, taking into account both environmental variables and proxies of anthropogenic pressures. Finally, this study addresses the identification of the determinants of community functional dynamics.

This thesis also tested the effectiveness of taxonomic surrogacy to describe spatial and temporal community dynamics, a method that can reduce the effort required for long-term monitoring. This work advances our understanding of biodiversity changes at different spatial and temporal scales. It demonstrates heterogeneity of dynamics at the site scale, significant stability at the habitat scale, and reveals different habitat-dependent stability mechanisms. Finally, it shows a remarkable temporal stability (15 years) of these communities at the regional scale. These considerations underline the need to understand the different scales and facets of biodiversity in order to better characterize its dynamics and to allow for the most relevant conservation measures. In particular, it is essential to ensure the conservation of intra- and inter-habitat β-diversity, an essential ingredient for maintaining stability. Finally, this thesis highlights the importance of long-term monitoring as a knowledge acquisition tool at the interface between observation, theoretical ecology and conservation.