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Research article

Habitat complexity promotes species richness and community stability: a case study in a marine biogenic habitat

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Habitat complexity (HC) promotes species richness and abundance. Aquatic environments are faced with intense pressures that threaten the 3D structure of the seafloor, with cascading effects on ecosystem functioning and biodiversity. Maerl or rhodolith beds are marine biogenic habitats created by few species of free-living non-geniculate coralline algae that aggregate and form complex structures. Although their high biodiversity has been attributed to the HC provided by coralline algal nodules, the mechanisms through which HC modification affect associated communities remains uncertain in face of numerous confounding factors. Hence, we tested how changes in the extent and nature of maerl complexity drive changes in biodiversity. Using long-term monitoring data from ten maerl beds in Brittany (France) over 12 years, we investigated the links between structural complexity, environmental conditions and benthic macrofaunal communities. HC was quantified at the coralline algal nodule and bed level, through morphometrics and density, and its effects on local diversity and on communities spatial and temporal variability were evaluated. HC promoted species richness and density of most taxa regardless of other environmental factors. These relationships were linear and no limiting threshold of complexity was found at a regional scale. HC played a more important role in driving regional diversity patterns than other measured environmental constraints individually, and beds with relatively lower HC were the most distinct in terms of community composition and structure. Species replacement was the main component of temporal variability and HC promoted community stability. While overall facilitative, the effects of HC might be taxa and trait-dependent, justifying comprehensive trait-based approaches. Our results reiterate the need to protect complex biogenic habitats.

Keywords: complexity–diversity relationships, foundation species, habitat diversity, maerl, rhodolith, structural complexity

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Introduction

Habitat complexity (HC) is defined by the spatial arrangement and features (diversity, size, density) of physical structuring elements (SEs) at different scales (Tokeshi and Arakaki 2012, Loke and Chisholm 2022). The role of HC in driving and maintaining biodiversity remains a fundamental question in ecology since MacArthur and MacArthur (1961) first demonstrated that the diversity of birds increased with variation in vegetation height: trees were the SEs and height variation a measure of SEs diversity, one aspect of HC. Since, numerous studies reported similar relationships between aspects of HC provided by a variety of SEs and the diversity of several taxa across habitats, including birds (Melles et al. 2003, Ghadiri Khanaposhtani et al. 2012, Watson 2015), fish (Almany 2004, Gratwicke and Speight 2005, Knudby et al. 2010, 2011, Nagelkerken et al. 2010), terrestrial (Díaz et al. 2012, Nooten et al. 2019), freshwater (Brown 2003, Barnes et al. 2013, Huttunen et al. 2022, Wu et al. 2022a) and marine macroinvertebrates (Johnson et al. 2003, Kelaher and Castilla 2005, McAbendroth et al. 2005, Warfe et al. 2008, Jankowska and Włodarska-Kowalczuk 2022, Vozzo et al. 2021, Navarro-Barranco et al. 2022). Hence, the habitat heterogeneity hypothesis that structurally complex habitats promote species richness by providing more niches and, therefore, more ways of exploiting resources, has been a cornerstone of ecology for decades (Tews et al. 2004).

While numerous, most empiric studies are based on the effects of a single aspect of HC on local (α) diversity and the importance of HC for spatial and temporal community variability has received little attention so far (Smith et al. 2014). Alpha diversity, usually expressed as the number of species (richness) and the abundance, density or biomass of individuals in communities, allows for testing hypotheses on the state of a community at a point in time and space (Whittaker 1960). Spatial and temporal β diversity can be respectively defined as the variation in community composition and structure among sites within a geographical area of interest or among times in a single site. Beta diversity allows for testing hypotheses regarding the processes that generate and maintain biodiversity in ecosystems (Legendre and De Cáceres 2013, Legendre 2014, Boyé et al. 2017). It can elucidate how differences in HC drive regional community patterns (spatial β diversity) and help unravel the effects of HC on community dynamics (temporal β diversity).

Temporal β diversity may also aid in unveiling the ecological processes leading to community stability, as the total variance of the community composition can be decomposed into richness difference and species replacement components (Legendre 2014). Increasing HC could either lead to higher stability by reducing both richness differences and species replacement through dampening environmental variability (Kovalenko et al. 2012), or to lower stability, as higher fine-scale spatial heterogeneity can lead to higher temporal variability (Collins et al. 2018). Alternatively, the relative contribution of both components could vary differently along an HC gradient. For instance, a dynamic stability with high species replacement but mostly invariant richness, might be maintained through portfolio effects – in which diverse communities support ecosystem properties that are less variable, leading to stable community sizes regardless of the variability in composition (Schindler et al. 2015, Gotelli et al. 2017). This would be expected in more complex habitats if HC promotes niches and resource diversity, leading to higher species replacement (Magurran and Henderson 2018) while maintaining stable community sizes regardless of the niche space structure (Storch and Okie 2019).

Quantifying HC is an arduous task because all aspects of complexity cannot be described by a single metric: density, diversity (as assessed through SEs richness and evenness), size and the arrangement of SEs in space are necessary to fully describe complexity (Loke and Chisholm 2022). SEs might also change with scale (Tokeshi and Arakaki 2012): at the scale of a forest, trees might be the SEs, but at the scale of a single tree, the SEs become its branches and leaves. In this sense, different SEs might present dissimilar complexities, and it is difficult to predict if a high density of simple SEs provides more HC and niches than a low density of complex SEs.

Interpreting causal relationships in HC–diversity studies is also challenging as few integrate confounding environmental constraints (Kovalenko et al. 2012). These difficulties may explain a recent lack of consensus on the HC–diversity relationships, with contrasting results being documented across habitats and taxa (Romero et al. 2015, Pygas et al. 2020). The area-dependency of the HC–richness relationship has also been subject to debate (Johnson et al. 2003, Kostylev et al. 2005, Loke and Todd 2015, Loke et al. 2019, LaRue et al. 2023), with studies reporting non-monotonic responses. These relationships can be explained by the area–heterogeneity tradeoff hypothesis, in which richness may initially increase with HC but decrease after reaching an HC threshold due to an increase in the likelihood of stochastic extinctions of highly specialized species (Kadmon and Allouche 2007, Allouche et al. 2012).

Maerl beds are biogenic habitats founded on a few species of free-living non-geniculate coralline algae that form structurally complex nodules called rhodoliths or maerl (herein used as synonyms) that can aggregate to high densities in soft substrates. These worldwide distributed habitats present high macrofaunal diversity and abundance (Barbera et al. 2003, Grall et al. 2006, Riosmena-Rodríguez et al. 2017, Schubert et al. 2020) as well as rich algal communities (Qui-Minet et al. 2018, Helias and Burel 2023), harbouring around 30% of the macroalgae diversity of the NE Atlantic (Peña et al. 2014). However, maerl beds face several conservation challenges globally due to anthropogenic threats (Barbera et al. 2003, Grall and Hall-Spencer 2003, Wilson et al. 2004, Ragueneau et al. 2018). With average growth rates of around 0.4 mm × a^{0-1} maerl HC is highly static in the absence of disturbances (Foster 2001). Consequently, they also have low and slow resilience and high sensitivity to physical impacts (Bernard et al. 2019).

Maerl beds are particularly abundant in Brittany (northwest France) where they are mainly formed by *Phymatolithon* *calcareum* and *Lithothamnion corallioides* and found in a wide range of environmental conditions (Grall and Hall-Spencer 2003). Maerl beds in the region are great candidates for exploring complexity–diversity relationships as their macrofaunal communities have been monitored for most of the last two decades (Derrien 2003). Studies in the area have shown that maerl-associated communities are richer and more stable than those in bare sediments and seagrass meadows (Boyé et al. 2019, Toumi 2023, Toumi et al. 2023, 2024), but the underlying mechanisms are still to be investigated. Recently, HC in Breton maerl beds was quantified using different metrics and shown to vary at both local and regional scales and be partially driven by the environment (Jardim et al. 2022). Identifying the isolated effect of HC on biodiversity is quite challenging as it is also dependent on environmental constraints, human impacts (Bernard et al. 2019) and even community diversity itself (Thomsen et al. 2018). The gradient in physical environmental constraints and HC found in Brittany allows for testing different hypotheses on the main mechanisms driving maerl-associated communities.

The main goal of this study is to understand the role of the HC provided by coralline algal nodules in driving and maintaining maerl-associated benthic faunal diversity. We investigate how variations in HC at the nodule and the habitat scale drive local (α) and regional (spatial β) diversity, as well as community dynamics and stability (temporal β diversity). First, we explore how different aspects of HC may influence regional community variability. Then, we verify whether the HC–richness relationship in maerl beds is linear and positive as historically reported and proposed by the habitat heterogeneity hypothesis (Tews et al. 2004), or unimodal, following the more recent area–heterogeneity tradeoff hypothesis (Allouche et al. 2012). Finally, we explore how HC may influence temporal community stability.

Material and methods

Study area, sampling design and data acquisition

In the ongoing REBENT (Réseau Benthique, (Derrien 2003) monitoring programme (2003–present; http://www.rebent.org), macrofaunal benthic communities of 10 subtidal maerl beds along Brittany's coast are monitored yearly. Sites were chosen to encompass most of the environmental settings found along Brittany's coast, from very shallow (< 5 m) to deeper beds (up to 22 m), with differing hydrological and sedimentological characteristics (Boyé et al. 2019, Jardim et al. 2022). Every year, three fixed points at least 200 m apart are sampled at each site using three Smith–McIntyre grabs of 0.1 m^2. In this study, the three grabs were pooled to estimate abundances at the point level (hereafter an observation). Accordingly, macrofaunal densities were estimated based on the surfaces sampled per point (usually 0.3 m^2, but see exceptions below).

For this study, 12 years were chosen (2007–2018) in order to encompass the largest time-span without compromising sampling balance, as gaps usually happen in long-term monitoring programs. Sampling was systematically performed once a year around the spring equinox, between the end of February and the beginning of May, following winter storms and before recruitment of most benthic species (Boyé et al. 2017, 2019). Sampling was mostly consistent throughout the study, with only a few points not being sampled in all years, and all observations containing only two grabs in 2012 (Supporting information), resulting in 348 observations in total.

Sediment samples were collected yearly at each sampling point for grain size distribution and organic matter content assessment, as an additional Smith–McIntyre grab was taken and subsampled with 12.5 × 12.5 cm box-corers (n = 348). The same protocol was followed once for sampling coralline algal nodules for complexity estimation in all beds monitored in the study between 2019 and 2020 (n = 30). All sampled nodules with at least one axis greater than 10 mm were selected and 12 of them were randomly selected at each sampling point, for a total of 360. Additional grab samples were taken in April 2022 and subsampled with 12.5 × 12.5 cm box-corers at each sampling point to estimate maerl densities.

Ideally HC would have been measured yearly for the duration of the study. However, a single estimation for each sampling point for HC was made from nodule samples collected between 2019–2022. Nevertheless, both *P. calcareum* and *L. corallioides* have very low growth rates with an accepted average of 0.4 mm a^{-1} (Foster 2001). For *L. corallioides,* annual growth rates have been estimated to range from 0.10 to 0.14 mm a^{-1} in European waters, with a rate of 0.13 mm a^{-1} for the maerl in the bay of Morlaix, included in this study (Piazza et al. 2022). Additionally, subarctic maerl beds of *Lithothamnion glaciale*, which present similar growth rates and growth forms to *L. corallioides,* are structurally stable over a year, with no significant seasonal changes in maerl densities or morphometrics (Bélanger and Gagnon 2023). Therefore, the nodules analysed in this study (> 10 mm in diameter) most likely reflect the conditions of the sites for at least the 12 years of macrofaunal monitoring considered.

Macrofaunal diversity

Grab samples were sieved over a 1 mm mesh and fixed in 4% formalin. Taxa were identified at the lowest taxonomic level possible by several specialists over the years. To avoid methodological bias and ensure consistent resolution across sites and years, taxonomic homogenization was performed, as described in Boyé et al. (2017). Taxa were corrected using the latest accepted names in the World Register of Marine Species by July 2022 (WoRMS Editorial Board 2023).

In order to investigate if HC affected macrofaunal compartments differently, information on the position of each identified taxa in the sediment was collected from an extensive survey of specialized literature as well as existing trait-databases, including *Polytraits* (Faulwetter et al. 2014), the Marine Bivalve Shells of the British Isles (Oliver et al. 2016) and the Biological Traits Information Catalogue by MarLIN

(MarLIN 2006). Species were divided in three categories: epifauna, living mostly in the maerl-water column interface, endofauna, living mostly in sediments, and interstitial fauna, occupying mostly the complex matrix formed by maerl and sediment. Data was collected at the lowest possible taxonomic level and inferred when missing from data available from other species from the same genus.

Habitat complexity quantification

The authors have recently quantified and documented HC for the studied maerl beds and all nodule complexity metrics used in the present study were acquired as described in Jardim et al. (2022). Nodule complexity was estimated through classic coralline algae morphometrics – nodule size measured as the largest diameter (L), sphericity metrics, containing sphericity and three other diameter ratios DR1, DR2 and DR3 (Sneed and Folk 1958, Graham and Midgley 2000) and branching density (Steller et al. 2003). All algae larger than 0.5 mm sampled in April 2022 were counted in order to estimate maerl densities at the point level (nodules m^{-2}).

Physical environmental data

Bathymetry, exposure, granulometry and hydrological data were acquired for the whole study period, and imputed when missing, as detailed in Jardim et al. (2022). Bathymetric data was downloaded from the EMODnet Digital Terrain Model 2020 (EMODnet Bathymetry Consortium 2020, https://www.emodnet-bathymetry.eu/data-products). Exposure was quantified as the unobstructed distance that wind can travel over a surface in a constant direction (fetch) using land polygon data for the study area acquired through QGIS (QGIS Development Team 2021) and the 'fetch' R package (Seers 2020). For granulometry, sediments were dried for 48 h at 60°C and separated into 15 fractions that were measured for masses. Fractions were afterward grouped in mud (< 63 μm), sand (63 μm to 2 mm) and gravels (> 2 mm, which in our study are very often dead maerl fragments) and several descriptive statistics were computed with R package 'G2Sd' (Fournier et al. 2014). Hydrological data were extracted from the Atlantic – Iberian Biscay Irish – Ocean Physics Reanalysis Product (ver. 3.3) issued by the E.U. Copernicus Marine Service Information (Iberia Biscay Irish Monitoring Forecasting Centre 2020). Yearly average, maximum and minimum values of temperature at the bottom and current velocity were calculated from daily averages ($n = 348$).

Data analysis

Redundancy analysis (Rao 1964) of the log-chord transformed community abundance data as a function of HC and the physical environment was performed to understand the effects of HC on regional biodiversity. The log-chord transformation was chosen as it down-weights the importance of very abundant species and does not give excessive weight to rare ones (Legendre and Borcard 2018). The median standardized Box–Cox transformed (Box and Cox 1964) complexity values of each sampling point were used. Median values were chosen as macrofaunal data are at the sampling point level and could not be directly linked to single nodules. Removing colinear variables in each explanatory variable set lead to: HC (containing branching density, sphericity and diameter ratio DR3, nodule diameter, and maerl density), hydrodynamics (containing mean current velocities and exposure), granulometry (containing the percentage of mud in sediments and the content of organic matter) and temperature (containing mean temperature at the bottom and their standard deviation). Models for each set were tested and forward selection performed on the significant ones. RDA significance was evaluated through a free permutation test under a reduced model with 9999 permutations, and the adjusted R^2 was calculated to evaluate model fit (Peres-Neto et al. 2006). Sites were added as a fixed factor in order to control for site-dependent omitted confounders, and year was added as a continuous variable. Variation and hierarchical partitioning were performed to further explore the contributions of each selected variable or variable set to overall diversity. Variation partitioning quantifies the unique and shared fractions of explained variance (semi-partial R^2s) by each variable set (Borcard et al. 2018). The relative importance of any set of predictors can also be estimated as its unique contribution to the total model plus its average shared contributions with the other predictors through hierarchical partitioning (Lai et al. 2022).

PCA was performed as a means of dimension reduction for describing HC with only two variables (the two first principal components) in subsequent univariate analysis. The median standardized Box–Cox transformed (Box and Cox 1964) complexity values of each sampling point were used. principal component (PC) scores from median values were highly correlated with those of the centroids of each sampling point when all individual nodule observations were taken into account (Pearson correlation > 0.95, $RV = 0.87$, Supporting information).

To describe local (α) diversity, observed species richness (S), the total density of individuals, Simpson's inverse, and Pielou's evenness J (Pielou 1966) were calculated for each observation. Simpson's inverse, which is Hill's diversity number N_2, was used for further down-weighting rare species (Hill 1973). Linear models (LMs) of α-diversity metric as a function of complexity (represented by the two first PCs) were performed. Both linear and quadratic functions of complexity metrics were evaluated in order to test for non-linear relationships. This was done for the whole macrofaunal community as well as for each main phyla and each faunal compartment (endo, epi and interstitial fauna) individually. Whenever any of the complexity components were significant, multiple linear regression was performed with the additional physical environmental data. Relationships between HC metrics and physical environmental variables are well described in Jardim et al. (2022), but correlations were verified before variable selection (Supporting information). Forward selection of explanatory variables was performed in order to obtain more parsimonious models. Year was added as a continuous variable to assess temporal trends. Finally, linear mixed models (LMMs) with random intercepts were performed to control for site-dependent differences not necessarily considered by environmental variables. To do so, site was treated as a random factor and all other previously selected continuous variables were treated as fixed. Additionally, since within-site variation in complexity is lower than among-sites variation (Jardim et al. 2022), adding sites as a random factor accounts for possible pseudoreplication in case intra-site observations are indeed not independent. LMMs pseudo-R^2s were computed as in Nakagawa and Schielzeth (2013), with standard errors and p-values calculated using Kenward–Rogers approximation (Kenward and Roger 1997).

Temporal β diversity was computed as the total variance of the presence–absence community matrix (BD_{total}) to quantify community stability as the inter-annual variability in species composition. Temporal β diversity was calculated individually for each sampling point comprising the 12 years. Jaccard dissimilarity (which varies from 0 to 1) was used in order to compare sites regardless of their intrinsic and highly-variable dominance shifts (Legendre and De Cáceres 2013). Temporal β diversity was further partitioned into replacement and richness difference components using the Podani family indices (Podani and Schmera 2011), as described by Legendre (2014). All metrics were calculated for the total macrofaunal community as well as for the main phyla and for each compartment separately. LMs of each temporal diversity metric (BD_{total}, richness difference and replacement) as a function of HC were performed to understand the effects of HC in community stability. Site was not added as a random factor in this analysis as there were only three observations in each group.

All analyses were performed using R ver. 4.2.2 (www.r-project.org) and the following packages: 'EnvStats' (Millard 2013, Box Cox transformation), 'adespatial' (Dray et al. 2022, forward selection and total community variance decomposition), 'rdacca.hp' (Lai et al. 2022, variation partitioning), 'UpSetVP' (Liu 2022, visualization of fractions), 'lme4' (Bates et al. 2015), 'gvlma' (Peña and Slate 2006), 'jtools' (Long 2022, LMMs fitting, evaluation), and 'vegan' (Oksanen et al. 2020, all other analysis).

Results

Effects of HC on regional macrofaunal diversity

Regional biodiversity is explained through the RDA of log-chord transformed community data. Models for all variable sets were significant and all variables in each set were kept after forward selection (Supporting information). Selected physical environment constraints, HC, year and site, explained 43% of beta diversity ($R^2_{adj} = 0.43$, $F = 12.29$, $p = 0.001$). The first 13 canonical axes were significant ($p = 0.001$), and the first unconstrained component contained only 1.91% of variance, less than that explained by each of the first four canonical axes, indicating no relevant residual structure. The first axis explained 12.45% of regional community variability, and was mainly related to nodule complexity and granulometry. Beds characterized by spheroidal and branched nodules, found in rich and mixed sediments, were mainly dominated by mobile predators eunicids (Polychaeta) and porcelain crabs (Decapoda, Malacostraca). On the other hand, surface deposit feeding corophiid amphipods (Malacostraca), tube dwelling suspension feeding serpulids (Polychaeta), and the subsurface deposit feeding knot worms (Polygordidae, Polychaeta) were dominant in beds with simple and discoidal nodules, found in coarser sorted sediments. The second axis explained 7.56% of the regional diversity, reflects a latitudinal gradient and is driven by depth and hydrodynamics, with northern, more exposed, deeper and less dense beds being the most dissimilar (Supporting information).

Variation and hierarchical partitioning (Fig. 1) highlight that site (21.43%) had the highest individual contribution, followed by complexity metrics (6.99%). The unique effect of sites was again most important (10.06%) followed by its shared effect with complexity and granulometry (5.83%) and its shared effect with complexity (3.44%). Among quantitative variables, complexity had the highest unique contribution to explained variance (0.88%). Nodule complexity, composed of sphericity metrics (Sphericity and DR3) and branching density, explained over twice more variance (4.93%) than bed complexity, composed of maerl density and nodule size (2.1%; Supporting information). Year explained the least amount of variance, suggesting that spatial variability was more important.

Effects of HC on local diversity

The first two axes of the PCA of median complexity values represent over 66% of the regional variance and are used to describe complexity at two scales in subsequent analysis (Supporting information). The first PCA axis (PC1) was mainly driven by nodule complexity: sphericity metrics (Sphericity and DR3) and branching density. PC2 was mainly driven by bed complexity: maerl densities and nodule size (largest diameter, L). Therefore, highly complex beds present a high density of small, spheroidal and branched nodules, and consequently, high values of PC1 and PC2.

Complexity–richness relationships

Complexity at the bed level (PC2) had a positive effect on species richness (Fig. 2A). Quadratic terms for bed and nodule (PC1) complexity were never significant (Supporting information). Beds with the highest values of bed complexity and species richness (S) often reached values twice those from the poorest and less complex beds. This was also observed within beds: those with highly variable maerl densities exhibited lower species richness in their less complex sampling points. The first LM indicated a significant positive effect of HC at both scales, explaining 32% of variation in species richness ($R^2_{adj} = 0.32$, $F = 55.56$, $p < 0.001$). Adding environmental factors confirmed this (model 2, $R^2_{adj} = 0.42$, $F = 32.69$, $p < 0.001$) but revealed the effect of HC was overestimated by

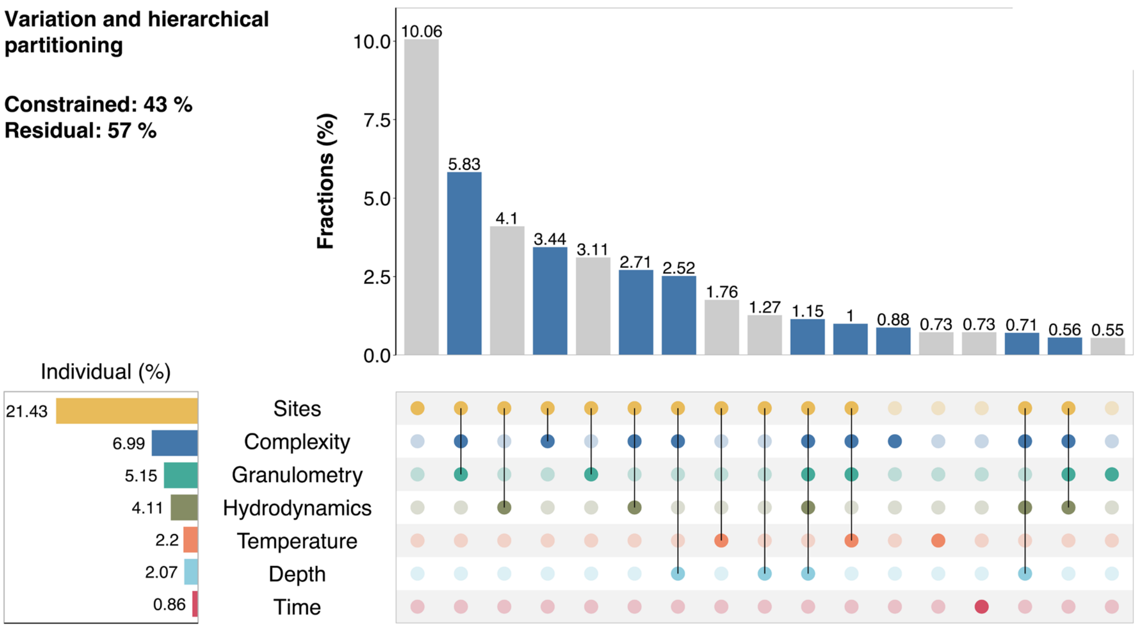

Figure 1. Variation and hierarchical partitioning of the log-chord transformed community matrix by selected explanatory variable sets. The different variable sets explained 43% of the spatio-temporal variations in communities. The bottom-left bar chart shows the relative individual importance of each explanatory variable set. The top bar chart shows the percentage of variation explained by the different sets and their shared fractions, based on adjusted R^2s. All fractions containing metrics of HC are coloured in blue. The lower panel indicates which variable sets were taken as explanatory (opaque circles) and conditional (translucent circles) for each fraction. Fractions < 0.5% are not shown.

the first model (Fig. 2B). The second model also revealed that depth and exposure to wind-generated waves had a negative effect on S, while S increased with mean bottom temperature and sediment organic matter content. Adding site as a random factor (model 3) left only bed complexity, organic matter content and year as significant, but highlighted a marginal effect of the interaction of both scales, which was also significant for annelids only (Table 1). Indeed, nodule complexity appears to have little influence on species richness until high levels of bed complexity are reached, when both become additive (Fig. 2A). Fixed factors alone explained 29% of variance (marginal R^2), while together with random factors they accounted for 43% (conditional R^2). The positive effect of year was marginal. Similar HC–richness relationships were found for phyla and compartments analysed separately (Table 1) and for Pielou's evenness and Simpson's inverse diversity index (N2; Supporting information).

Complexity–density relationships

HC had an intricate taxa-dependent effect on macrofaunal densities (Fig. 2B). Selected fixed models showed a positive effect of nodule complexity on total macrofaunal densities ($R^2_{adj} = 0.48$, $F = 33.22$, $p < 0.001$), which reflects a positive effect on arthropod abundances ($R^2_{adj} = 0.36$, $F = 24.94$, $p < 0.001$). Bed complexity had a significant positive effect on mollusc and annelid abundances, but not on arthropods or total macrofaunal densities. The interaction between both complexity scales (PC1:PC2) had a significant negative effect on total macrofaunal and arthropod densities. Macrofaunal densities decreased with mean current velocities (namely for arthropods), depth (mainly for molluscs and annelids) and exposure to wind-generated waves (only for annelids), but overall increased with mean bottom temperature, organic matter content and percentage of gravel in sediment (Fig. 2B). Model coefficients were not affected by correlations between the PCA axes and physical environmental variables (Supporting information). Adding sites as a random factor made most predictors nonsignificant. Nevertheless, the effects of bed complexity remained positive and significant for molluscs. Overall, densities either increased (annelids, arthropods) or showed no significant relationship with year. Relationships were also compartment-dependent, with only the interstitial fauna being positively affected by bed complexity (Table 1).

Complexity–stability relationships

Temporal β diversity ranged from 0.32 to 0.39 in the less stable beds, while it ranged from 0.26 to 0.29 in the most stable. Decomposition of temporal β diversity indicates that replacement systematically trumps richness differences (Fig. 3A): replacement constitutes at least 60% of BD_{total} in all cases, reaching 89% in the most stable bed (Supporting information). Replacement was also dominant for faunal compartments and phyla considered separately.

Stability significantly increased with nodule complexity (PC1), which had a negative effect on temporal β diversity (Fig. 3B). This was found for the entire community

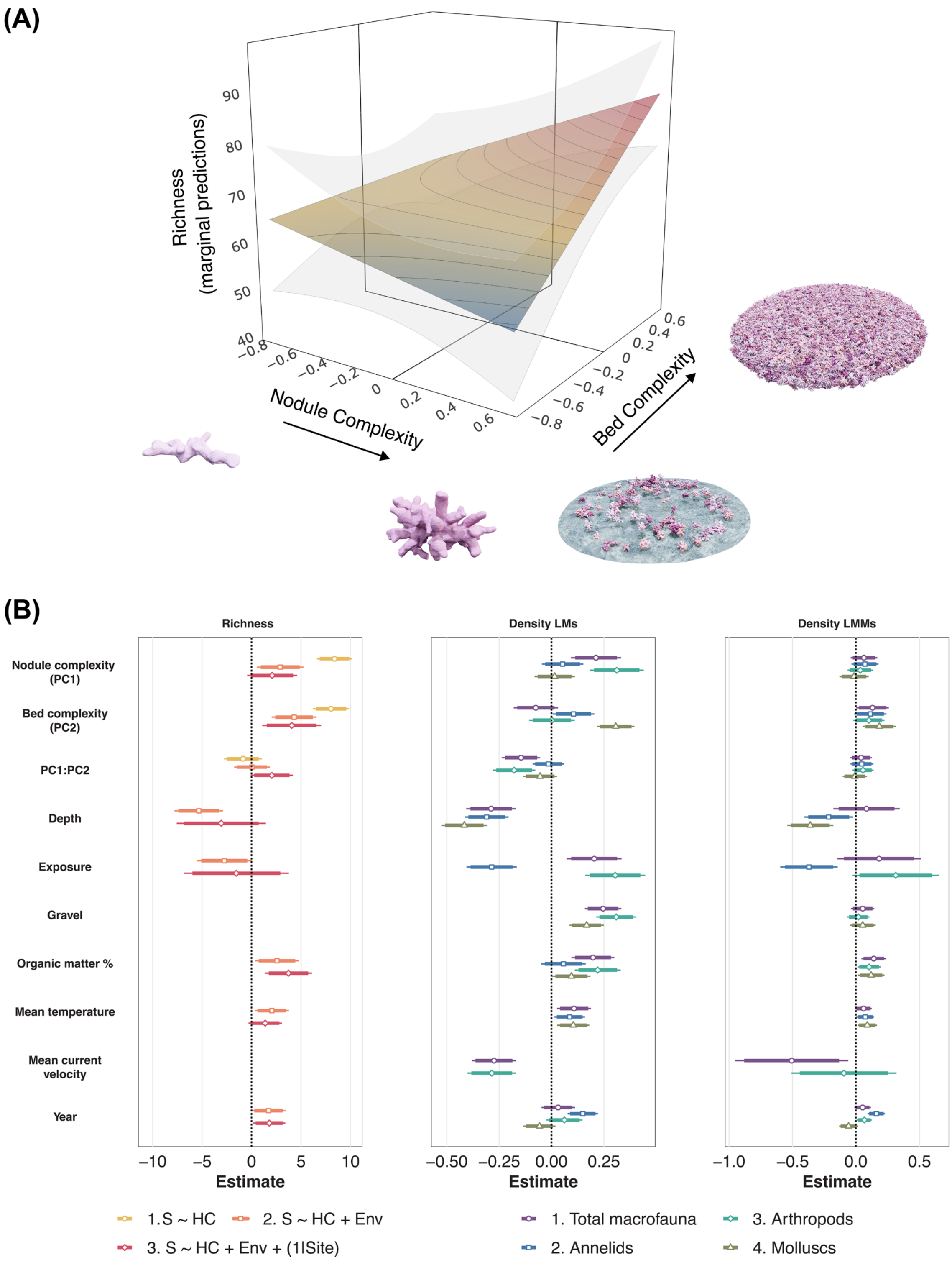

Figure 2. Effects of habitat complexity on local diversity. (A) Marginal predictions of species richness as a function of bed and nodule complexity when all other covariables are kept at mean regional values. Different levels of bed and nodule complexity are exemplified. (B) Standard regression coefficients of selected linear models (LMs) and LMMs with site as random factor of species richness and macrofaunal density as a function of habitat complexity and physical environmental variables. Year was added as a continuous variable to evaluate temporal trends. All continuous variables are standardized (including the response in density models). Confidence intervals for LMMs are computed through Kenward–Roger approximation.

Table 1. Marginal effects of bed and nodule complexity as well as their interaction on entire macrofaunal communities, as well as each main phyla and faunal compartment, under linear mixed models. Positive (pos), negative (neg) and null effects are shown on both species richness (S) and density of individuals (D). Bold effects are significant, with standard errors and p values calculated using Kenward–Roger approximation.

Complexity	Annelids		Arthropods		Molluscs		Epifauna		Infauna		Interstitial		Total	
	S	D	S	D	S	D	S	D	S	D	S	D	S	D
Nodule	**pos**	null	pos	null	neg	null	pos	null	pos	null	**pos**	null	pos	null
Bed	**pos**	pos	pos	pos	pos	**pos**	pos	pos	pos	pos	**pos**	**pos**	**pos**	pos
Interaction	**pos**	null	pos	null	null	null	pos	null	pos	null	pos	null	pos	null

($R^2_{adj}=0.31$, $F=3.55$, $p=0.015$), infauna ($R^2_{adj}=0.48$, $F=6.30$, $p < 0.001$) and interstitial fauna ($R^2_{adj}=0.25$, $F=2.92$, $p=0.034$). A non-linear relationship was identified for infauna, with an initial smaller decrease in temporal β diversity until intermediate nodule complexity levels followed by a steeper decrease at higher nodule complexity levels. A negative linear relationship between temporal β diversity and bed complexity was observed for interstitial fauna. Similar results were obtained for annelids (Supporting information).

The effects of HC on the replacement and richness difference components were mostly consistent with those seen for the BD_{total}, although less pronounced. Reduction in species replacement at high HC was best seen in the infaunal, interstitial and annelid communities (Fig. 3, Supporting information). Bed and nodule complexity interaction was not significant.

Discussion

Effects of HC on regional macrofaunal diversity

Site effect aside, HC is the main driver of community structure in our study area, driving species identities and possibly traits. These differences are mostly driven by nodule, rather than bed complexity, suggesting that available space provided by nodules with different complexities allows different species to colonize the environment, such as has been proposed for other macroalgae (McAbendroth et al. 2005, Ware et al. 2019). Similarly fine, rather than large scale habitat features were also important in predicting different bird species incidences (Melles et al. 2003). In our study, the dominance of mobile predator worms and porcelanid crabs in beds with complex nodules in contrast with the dominance of tube-dwelling filter feeding serpulid worms in beds with simple nodules, may indicate that different microhabitats benefit different feeding strategies. Indeed, predator success is higher in habitats with complex SEs, as interstitial spaces are ampler and predators have easier access to prey (Alexander et al. 2013, Mocq et al. 2021).

Finally, the most dissimilar beds were those with low bed complexity under higher environmental stress. This is in line with among-habitat diversity in Brittany, in which bare sediments were highly dissimilar among each other, while biogenic, hence more complex, habitats were less variable at a regional level (Boyé et al. 2019, Toumi et al. 2024). In these studies, the authors attribute the higher dissimilarity of less complex sediments to their sensitivity to extreme events when compared to complex habitats, which are believed to act as environmental buffers. Our findings indicate that this is also the case in a within-habitat complexity gradient, and that the facilitative effect of biogenic species (or other SEs) is dependent on their density and arrangement (Tokeshi and Arakaki 2012, McCloskey and Unsworth 2015, Martins Neto et al. 2021, Loke and Chisholm 2022, Navarro-Barranco et al. 2022).

Effects of HC on local macrofaunal diversity

Complexity–richness relationships

The classic paradigm that HC promotes species richness was corroborated. Whereas nodule complexity drives species identity, increasing levels of bed complexity led to an increase in species richness, as expected by the habitat heterogeneity hypothesis. This has been observed for numerous habitats (McCoy and Bell 1991, Johnson et al. 2003, Tews et al. 2004, Thomaz et al. 2007, St. Pierre and Kovalenko 2014, Navarro-Barranco et al. 2022). We did not identify unimodal HC–richness relationships, as has been more recently suggested by the area-heterogeneity tradeoff hypothesis (Kadmon and Allouche 2007). This hypothesis is based on the assumption that higher heterogeneity or complexity leads to a reduction in the effective area available for organisms, but, in aquatic systems, increasing complexity usually results in more available space in terms of refuge as they are usually under strong environmental selection (Tokeshi and Arakaki 2012, Sadchatheeswaran et al. 2019, Boyé et al. 2019, Kindeberg et al. 2022). Additionally, this tradeoff between HC and effective available area is thought to be dependent on niche width (Allouche et al. 2012), which could also explain why a unimodal effect was not observed, as maerl communities are composed of many generalist species and have high functional redundancy (Boyé et al. 2019). Therefore, as no unimodal relationship was observed, we believe high HC might rarely limit species richness in maerl beds, and possibly other complex marine habitats, due to the extreme importance of shelter and enhanced available space provided by 3D structures. Ultimately, considering the breadth of environmental conditions considered here, we argue that HC has an overall positive effect on richness in maerl beds, and do not expect it to limit or stop promoting diversity at higher HC levels.

The facilitative effect of HC on species richness was clearer when taking into account bed-level complexity, here mainly represented by maerl densities and median nodule size. This

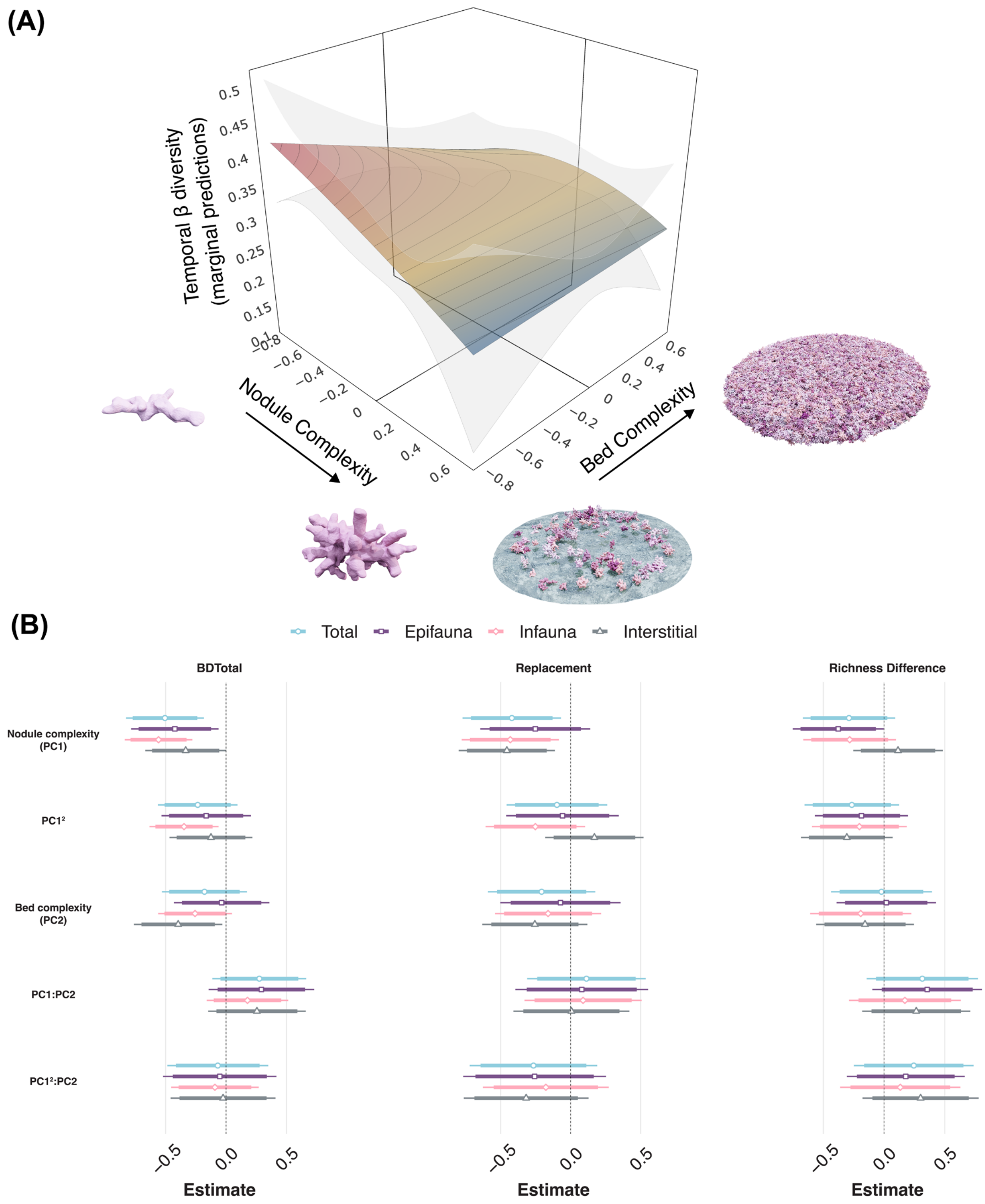

Figure 3. Effects of HC on community stability. (A) Marginal predictions of temporal β diversity under different bed and nodule complexity levels. (B) Standard regression coefficients of linear models (LMs) of BDtotal and its both components, replacement and richness difference, as a function of habitat complexity. All continuous variables (including the response) are standardized.

was clear among beds, but also evidenced within beds with highly variable bed complexities. High richness associated with higher maerl densities has been observed in maerl beds worldwide and considered a main driver of biodiversity in this habitat (Martins Neto et al. 2021, Solano et al. 2022). Richness has been found to increase with nodule size when considering epibionts only (Steller et al. 2003, Veras et al. 2020, Solano et al. 2022). Here, however, the opposite was found, which may be related to differences in nodule complexity, as complex nodules were usually small, whereas larger nodules were mostly simple. Thus suggesting that the effective available refuge for species is highly dependent on nodule branching and shape as opposed to their size (Hesterberg et al. 2017, Ware et al. 2019).

Indeed, while the effect of bed complexity on species richness seems universally positive, the sign and magnitude of the effect of nodule complexity appear context and taxa dependent. While more complex nodules were usually associated with higher annelid richness, nodule complexity had weaker to negative effects on arthropod and mollusc richness, respectively. This could be related to differences in the mobility, body shape and size of these organisms, and therefore their capacity to access highly heterogeneous and complex habitats, as suggested by Ware et al. (2019). In our study, mobile polychaetes can move through intricate interstitial spaces due to their soft bodies, whereas microhabitat access may be limited to littorinomorph gastropods, crabs and amphipods due to their size and hard shells or carapaces.

Complexity–density relationships

The effects of HC on macrofaunal densities were also taxa and trait-dependent, with molluscs, as well as interstitial and epifaunal densities increasing with bed complexity. Similarly, the density of different taxonomic and functional groups of epi and infaunal invertebrates, macroalgae, and fish, responded differently to complexity loss in coralline algal beds and seagrass meadows (Gartner et al. 2013, Gabara et al. 2018). Nodule complexity had no effect on macrofaunal densities, suggesting that the total available refuge, rather than the refuge quality, determine community sizes. Nodule complexity seems to mediate population sizes instead, as it was the main driver of species identities. While the density of some higher-level taxonomic groups may respond to complexity, the abundance of different species within a community reflect the amount of resources secured by each species (or functional group) and, therefore, can be highly variable among species depending on their traits (Tokeshi 1993).

Drivers and mediating effects of HC

As in other habitats, the local–regional diversity relationship is also dependent on depth, hydrodynamics and sediment (Boyé et al. 2017, Counsell et al. 2018, Burel 2020, Toumi 2023). Here, shallow, sheltered and muddy beds promote species richness. Likewise, maerl HC is also higher in these conditions (Jardim et al. 2022). Physical environmental conditions seem to affect species richness both directly and indirectly by driving HC, as is the case for oyster-dominated habitats (Vozzo et al. 2021). Most predictors had no significant effect on local diversity after adding site as a random factor: sites are environmentally very distinct but within-bed variability remains low, however, bed complexity retained a strong positive effect.

Effects of HC on community stability

Temporal variability in community composition

As in other aquatic habitats, complex beds were more stable. In freshwater streams, short-term (seasonal) temporal variability in macroinvertebrate communities was reported to decrease with sediment heterogeneity (Brown 2003, Huttunen et al. 2022). Similarly, longer-term stability (over four years) in 32 Finnish streams also increased with HC estimated as macrophyte cover (Mykrä et al. 2011). Recent studies in the sites analysed here have shown that, compared to subtidal bare sediments, maerl beds had slightly lower temporal variability, although these differences were less pronounced than those detected among maerl beds in our study (Boyé 2018, Toumi 2023).

Nodule complexity had a significant negative effect on temporal beta diversity. Higher stability related to fine-scale HC could be related to species functional responses, as nodule complexity might determine the quality of the available space for species. For example, differences in HC can change the strength of trophic links and affect predator–prey interactions (Almany 2004, Alexander et al. 2013, Hesterberg et al. 2017, Mocq et al. 2021). This improved available space might also lead to higher colonization by secondary foundation species, also thought to promote species richness and densities, hence increasing stability (Thomsen et al. 2018). Whereas bed complexity drives the number of species and the densities of some taxonomic groups, nodule complexity seems to play a more important role in driving species composition.

Processes driving temporal variability

Species replacement was the main process behind temporal beta diversity. This could indicate that even if higher HC leads to higher niche differentiation (Bar-Massada 2015), the great functional redundancy in maerl benthic communities, with numerous broad-niched species, leads to competition and higher replacement, and that compensatory dynamics may be at work (Lamy et al. 2015, Boyé et al. 2019). Replacement was also the main component of temporal diversity in intertidal seagrass beds (Boyé et al. 2017), intertidal and subtidal bare sediments (Boyé 2018), freshwater streams (Wu et al. 2022b) and coral reef fish communities (Lamy et al. 2015). Greater richness differences can indicate disturbed communities that do not have the ability to reorganize their compositions to maintain their pre-disturbance richness (Lamy et al. 2015, Mathers et al. 2022). This might indicate that maerl beds in our study are resilient.

The effects of HC on the richness difference and replacement components were intricate. Although negative trends were observed for both components in most compartments and taxonomic groups, these were rarely significant. Boyé (2018), comparing seagrass meadows and intertidal bare habitats, found significant difference in stability among habitats, but not for the individual components. They argue that seagrasses modify resource supply without affecting community size, because they provide shelter from stochastic physical constraints in the intertidal. Within maerl beds, we found a similar relationship between complexity and stability. This might indicate that higher HC levels play a more important role in providing shelter from environmental stress than in changing species interactions in maerl beds. Indeed, the high functional redundancy among Breton maerl beds (Boyé et al. 2019) might explain this pattern.

The effects of HC were more evident for infaunal communities, which might be related to the fact that more complex beds are usually associated with less sorted and more stable sediments, leading to a highly complex sediment–maerl matrix benefiting this compartment (Bernard et al. 2019, Jardim et al. 2022). For infaunal communities, replacement was significantly reduced in more complex beds, but we lack evidence to determine whether stability increases with HC due to a reduction in replacement or richness differences. Instead, it seems that HC reduces both components, and its effects are more evident in the component that contributes the most to total variance.

Due to limited sample size, we were not able to investigate the site effects nor that of other physical environmental variables potentially impacting stability. However, no significant relationship between stability and depth or stability and exposure was previously found in the studied beds (Boyé 2018). Nevertheless, other site-specific factors could play an important role. Eutrophication and fishing activities (mainly dredging) could lead to less stable communities in some sites (Grall and Hall-Spencer 2003, Dutertre et al. 2015, Qui-Minet et al. 2018, Tauran et al. 2020). Finally, other stability metrics could further improve our understanding of complexity–stability relationships: community trajectory analysis (Cáceres et al. 2019, Sturbois et al. 2021), the decomposition of β diversity into pairwise pattern components (Schmera et al. 2022) and synchrony (Cusson et al. 2015, Craven et al. 2018, Lamy et al. 2020).

Implications for conservation

HC is affected by human activities, and extraction and fishing through dredging and trawling can directly destroy coralline algal nodules, impact bed structure, or increase mortality due to higher deposition (Bernard et al. 2019, Tauran et al. 2020, Labrune et al. 2021). Direct maerl extraction has been banned in France since 2012 due to important conservation efforts, greatly motivated by the BIOMAERL project (Barbera et al. 2003, Grall and Hall-Spencer 2003). Nonetheless, fishing still poses a great threat to maerl complexity and vitality (Bernard et al. 2019). This has recently been shown to directly affect macrofaunal communities (Tauran et al. 2020). In this study, we empirically demonstrate that HC is the main driver of maerl beds benthic macrofaunal communities in Brittany. This brings further light to the negative impacts of destructive fishing gear as they will affect benthic communities not only with the initial direct impact on the organisms but in the long-term by reducing maerl HC, as the damages caused by such activities can persist for several years (Cabanellas-Reboredo et al. 2018, Tauran et al. 2020).

Maerl beds may work as sources of biodiversity to neighbouring less structurally complex habitats, such as bare sediments (Boyé et al. 2019). We argue that this hypothesis might be true within habitats as well, with more complex maerl beds helping to maintain regional diversity levels by exporting species to adjacent, less complex beds. In this sense, intermediate to highly complex beds should receive even more conservation attention, as they might support biodiversity at large scales. That being said, even impacted and less complex beds seem to harbour more diverse communities than bare habitats and could contribute to regional biodiversity (Boyé et al. 2019, Costa et al. 2021, Kindeberg et al. 2022).

Conclusions

To our knowledge, we explicitly and quantitatively investigate for the first time the relationship between HC and macrofaunal diversity patterns in maerl beds at a regional scale. Beyond this, we provide new insights into which mechanisms are behind the extensively reported effects of HC on biodiversity in the marine environment, as we: 1) demonstrate that HC is the main driver of macrofaunal diversity at local and regional scales even when taking into consideration depth, hydrodynamics, sediment characteristics and temperature; 2) provide evidence that different aspects of HC may affect distinct aspects of diversity, with nodule complexity mainly driving species identity, while bed-level complexity drives community size in terms of richness and abundance; 3) found the effects of HC on abundance to be taxa-dependent, which might also have implications for ecosystem functioning; 4) found that, at the regional level, community stability increased with HC, with less differences in terms of community composition in more complex beds.

Although further studies are encouraged to test the hypotheses brought up by our results, our findings point out the great importance of HC at different levels to biodiversity. We argue that HC is deeply involved with the generation and maintenance of local and regional biodiversity in maerl beds, and possibly marine habitats in general. This is of great conservation relevance and should be taken into account by stakeholders in the future.

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Author contributions

Victor Leite Jardim: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Investigation (lead); Methodology (equal); Resources (equal); Software (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Aurelien Boyé**: Conceptualization (equal); Validation (equal); Visualization (supporting); Writing – review and editing (supporting).

Vincent Le Garrec: Data curation (equal); Investigation (supporting); Methodology (equal); Resources (equal). **Marion Maguer**: Data curation (equal); Investigation (supporting); Methodology (equal); Resources (equal). **Adeline Tauran**: Data curation (equal); Investigation (lead); Methodology (equal); Resources (equal). **Olivier Gauthier**: Conceptualization (equal); Supervision (equal); Validation (equal); Writing – review and editing (supporting). **Jacques Grall**: Conceptualization (equal); Funding acquisition (lead); Resources (equal); Supervision (equal); Writing – review and editing (supporting).

Data availability statement

Data and original code are available from the Zenodo Repository: https://doi.org/10.5281/zenodo.7966423 (Leite Jardim et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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