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Functional convergence in macroalgal assemblages of isolated coral reefs in the Mozambique Channel

Nicolas Loiseau^{1,2}, C. E. Payri³, L. Mattio^{4,5}, S. Andréfouët³, M. Grellier¹, M. Zubia¹

The understanding of macroalgae functions and processes requires a good understanding of the spatial distribution of the functional diversity of macroalgae. In coral reef environments, this information remains fragmentary. Here, based on 314 species sorted according to a set of 10 functional traits, the functional niches of macroalgae at three remote coral reefs of the Îles Éparses in the Indian Ocean (Europa, Glorioso, and Juan de Nova) are described. For the comparison of intra- and inter-reef functional structures, we characterized both taxonomic and functional beta diversities, and their turnover and nestedness-resultant components. Within the three reefs, we observed strong taxonomic and functional dissimilarities across sampling sites, mainly determined by turnover. Null models highlighted several processes, which structured macroalgal assemblages across sites: a combined effect of environmental variables (geomorphology and wave exposure), limiting similarity and stochastic effects. At the inter-reef scale, the three reefs only shared a small number of species, but the functional beta diversity between Glorioso and Juan de Nova was weak. This suggested that although assemblages were different, fairly similar environmental conditions may have homogenized macroalgae functions through both ecological and evolutionary scale processes. Our results support the idea that macroalgal assemblages can provide similar functional trait portfolios, despite distinct species composition. We stress the need to focus on macroalgae life-history traits for a better understanding of the processes structuring their communities.

Introduction

Coral reefs are highly complex ecosystems that shelter an exceptional biodiversity and provide critical goods and ecological services (Moberg and Folke 1999; Cinner et al. 2012; Mora et al. 2016). Macroalgae are key components of coral reef communities providing essential ecological functions such as primary production, provision of trophic resources, nutrient retention and recycling, stabilization of the reef structure through calcification, contribution to sand formation, and provision of habitats, including nursery areas for juvenile fish (Fong and Paul 2011; Koch et al. 2013; Evans et al. 2014).

Coral reefs worldwide are in serious decline owing primarily to overfishing (Paddack et al. 2009), pollution (De'ath and Fabricius 2010), invasive species (Kulbicki et al. 2012), and climate change (Munday et al. 2008; Graham et al. 2013). Phase shifts towards macroalgae-dominated system have followed coral loss in several areas (Diaz-Pulido et al. 2011; Koch et al. 2013; Ainsworth et al. 2016). Investigating the ecological processes that may facilitate these changes is of key importance (Bittick et al. 2016) and these macroalgal

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phase shifts have been fairly well documented in some cases (Done 1992; Carassou et al. 2013; Doropoulos et al. 2016). Most studies dedicated to the description of macroalgal communities have been based on taxonomical inventories and analyses of species richness (Payri et al. 2012; Keith et al. 2014; Mattio et al. 2016). However, it is now widely acknowledged that functional diversity is a great addition to the traditional taxonomical approaches for assessing species assemblages (Diaz and Cabido 2001; Violle et al. 2007; Stuart-Smith et al. 2013; Loiseau and Gaertner 2015). Functional diversity has the potential to link morphological, physiological, and phenological variations at the individual level (i.e. functional traits) to ecosystem processes and patterns (Violle et al. 2007) but also to reveal the impact of disturbances on community (Mouillot et al. 2013).

The capacity of each macroalgal species to contribute to ecosystem processes depends on several biological traits related to growth, primary productivity, fixation to the substrate, and reproduction (Littler 1980; Littler and Littler 1980; Littler et al. 1983; Steneck and Dethier 1994; Lotze and Schramm 2000; Griffin et al. 2009).

Most flora trait-based studies have targeted terrestrial plants, while the analysis of functional traits in marine vegetated ecosystems, particularly macroalgal communities, is still in its infancy (see Jänes et al. 2016 for temperate macrophytes). In addition, a few studies that focused on macroalgal functional diversity have only grouped together species sharing broadly similar physiological or morphological characteristics (Littler and Littler 1980, 1984; Littler et al. 1983; Steneck and Watling 1982; Steneck and Dethier 1994; Cheal et al. 2010; Balata et al. 2011). This method assumes that all species belonging to the same functional group interact the same way with the ecosystem, although these broadly defined groups may include species with significant differences that were not taken into account (i.e., groups ignores all the differences between species belonging to the same group, whereas these differences may be important, Petchey et al. 2004; Ricotta 2005; Petchey and Gaston 2006). Assessing the functional diversity using pre-defined functional groups can be problematic, because the user's choices can be subjective (Chapin et al. 1996; Diaz and Cabido 2001). Hence, the defining group and the number of groups from an arbitrary grouping protocol can produce non-desirable variabilities. This method distorts the representation of the functional diversity (Petchey and Gaston 2002) and the conclusions that are made about the processes structuring communities. In macroalgae, all *Halimeda* species belong to the same functional group (calcareous group, Littler and Littler 1980), while some of them have very different ecological niches (e.g., sandy areas vs hard substratum). Describing the functional niche of macroalgal species and assemblages requires the consideration of an exhaustive set of functional traits. Only a few studies (and none to our knowledge in

coral reef ecosystems) have assessed the structure of functional diversity using a macroalgal functional trait database (Griffin et al. 2009).

In this paper, we address this gap by applying a functional trait-based approach to coral reef macroalgal communities at three remote coral reefs characterized by a preserved environment. We first describe the coral reef macroalgae functional niches using the selected categorical traits as a proxy of continuous measurement for their functional niches. We then apply a multicomponent approach to beta diversity (taxonomic and functional beta diversity) for investigating the structure of functional traits at two spatial scales: among reefs and among sites (within reefs). This two-scale approach has been shown to reveal the spatial scaling of ecological factors and to provide useful information for conservation planning. In doing so, we also assess the relationship between beta diversities and geomorphology, depth and swell exposure. Finally, we discuss how functional traits can be used to better understand macroalgae distribution and how these results could help with the management of conservation area.

Materials and methods

Study area

Three coral reefs of the Îles Éparses (Scattered Islands) were sampled: Europa, Glorioso (*Glorieuses*), and Juan de Nova (Fig. 1). With an exceptional biodiversity and preserved ecosystems, the Îles Éparses offer a unique opportunity to analyze the distribution and structure of functional traits in macroalgal communities' (for a thorough description of the Îles Éparses protection status, environmental conditions, and species inventories, see the special issue: Quézel et al. 2016.).

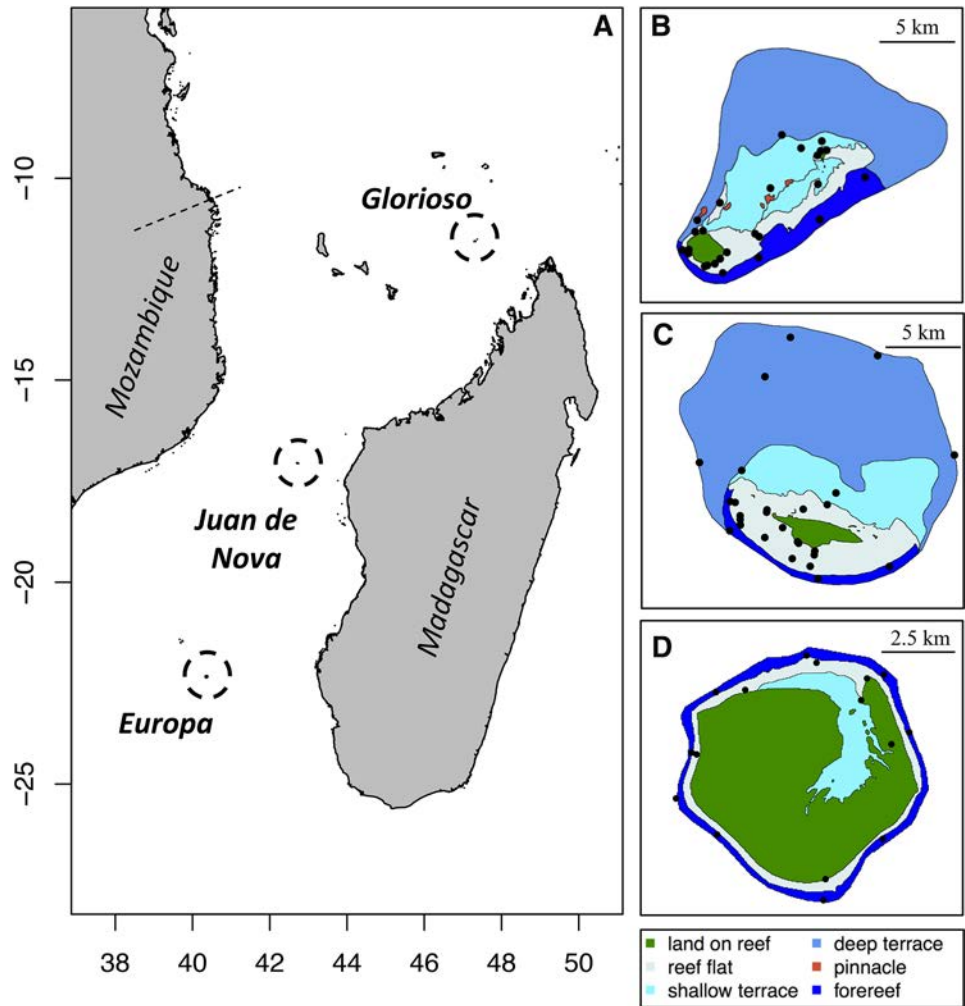
The Îles Éparses are among the last sanctuaries of marine and terrestrial tropical biodiversity in the South Western Indian Ocean. Their geographic isolation and very limited past human occupation have largely preserved these territories (Quézel et al. 2016). Together, Europa, Glorioso and Juan de Nova harbor 2% and 7% of the reefs' geomorphological unit's diversity, worldwide, and in the western-central Indian Ocean, respectively (Andréfouët et al. 2009).

Sampling strategy

We used data from the taxonomic inventory of the three reefs published by Mattio et al. (2016).

Macroalgae were collected from a total of 16 sites at Europa (December 2011), 26 sites at Glorioso (December 2012), and 27 sites at Juan de Nova (December 2013) (Mattio et al. 2016, Fig. 1). All collections were made during the

Fig. 1 Location of the Îles Éparses in the SW Indian Ocean (a) and sampling sites (black dots) at Europa (b), Glorioso (c), and Juan de Nova (d). Mapping data were extracted from the Millennium Coral Reef Mapping Project (Andréfouët et al. 2009). Different colors indicate geomorphological classes. At Europa, the site that appears inland is a mangrove site



same season (Austral summer) to produce comparable data sets. Sites were chosen based primarily on satellite images to include most of the major geomorphological units (geomorphological habitats) found between the intertidal zone and 20 m deep (see Payri et al. 2012 for a description of methods). Specimens were collected from the following geomorphological units: forereef, mangrove, reef flat, shallow terrace, and deep terrace (Fig. 1). Only reef flat and forereef habitat were present at the three reefs, the “deep terrace” habitat was found at Glorioso and Juan de Nova only, and Europa was the only reef with mangroves (Zubia et al. 2016, Table S1). In addition to the geomorphological information, we recorded depth and interpreted swell exposure from the geographical position of each site considering the direction of the dominant swell (see supplementary material Table S1).

At each site, the sampling effort was standardized by searching during 60 min over a 10×50 m surface area within the same habitat (Mattio et al. 2016). During this time, we randomly searched all the possible species and all the different encountered species were collected. Samples

were sorted, photographed, labeled with a preliminary field identification, and pressed the same day. The available taxonomic inventories accounted for a total of 316 macroalgae, 134 for Europa, 170 for Glorioso, and 157 for Juan de Nova (Mattio et al. 2016).

Macroalgae functional traits

Based on the literature and our taxonomic expertise, we compiled a functional trait database using ten traits that describe the main aspects of macroalgal ecology. These traits were selected for their relevance in the investigation of the functional diversity of macroalgae, but also because they were available or could be inferred for a wide range of species (Table 1), providing proxies of the functional niche of each taxonomic unit. Following Kissling et al. (2018), we selected traits related to four of the five critical functions that describe the functional diversity of species: phenology, morphology, physiology, and movement. Because continuous value was unavailable for most species, we choose to use categorical traits as a proxy of continuous measurement for

Table 1 Functional traits of macroalgae and their modalities

Traits	Modalities	Main functional significance
Life-history traits		
Growth	S: Slow F: Fast	Food web (primary producer) Contribution to seascape
Mean height	Small species: < 2 cm Medium species: 2–5 cm Large species: > 5 cm	CO ₂ bio-fixation Ability to create habitat (nurseries, recruitment) Tolerance to disturbance
Longevity	A: annual P: perennial	
Primary productivity	1: < 2 mgC/g dw/day 2: 2–8 mgC/g dw/day 3: 9–20 mg C/g dw/day 4: > 40 mg C/g dw/day	
Calcification	No: non-calcified macroalgae Low: < 50% dw CaCO ₃ Medium: 50–80% dw CaCO ₃ High: > 80% dw CaCO ₃	Reef construction and stabilization Sand formation Capacity to create habitat and new surface for benthic colonization Defense against herbivory
Ecological traits		
Substratum	No: epiphyte HS: hard substratum (corals, dead corals, rubbles) S: soft substratum (sand or sediments) HS/S: hard and soft substrata	Contribution to seascape Substratum consolidation CO ₂ bio-fixation Resistance to environmental condition Canopy resilience
Fixation strength	Low: weak fixation Medium: intermediate strength of fixation High: strong fixation	
Interactions	Epiphyte: interactions with macroalgae 1: < 25% contact (erect thalli) 2: 25–50% contact (tangled mat or shelf-like forms like procumbent, decumbent, or anastomosing) 3: 50–100% contact (tangled mat or shelf-like forms like procumbent, decumbent, or anastomosing) 4: 100% contact (crustose species)	Coral resilience Ability to create habitat Defense against herbivory
Ability to proliferate	No: no proliferation record was found in the literature Yes: some records of proliferation.	Food web (primary producer) Coral resilience
Repellent molecules	No: no production of repellent molecules Yes: production of repellent molecules	Defense against herbivory Regulation of competition

all traits. If no data are available for a specific species, we first used similarities across taxonomic levels. When trait information was not well known or not reported in the literature (e.g., production of repellent molecules), it was reported as “NA” in the database. We describe these traits below and provide the final database as a supplementary material (see Table S2 and Figure S2 for an illustration of assignment of functional traits).

Growth

It is an important component of macroalgal niches. Relative growth rate depends on the CO₂ assimilating capacity, carbon-use strategy (Ho and Carpenter 2017), and photosynthetic activity of the species. Macroalgae can be rapid and efficient initial colonizers of space on almost any area of coral reefs after disturbance (Fong and Paul 2011). Two

main contrasted strategies have been observed: (1) opportunistic species with fast growth (F), high productivity, and high reproductive capacity, which are characteristics of pioneer macroalgae communities (e.g., turf); and (2) slow growing macroalgae (S) such as calcareous macroalgae (including Rhodophyta and Chlorophyta) or fleshy brown macroalgae (Littler and Littler 1980). These modalities have been assigned based on anatomical and morphological characteristics proposed by Littler (1980), Littler and Littler (1980), Littler et al. (1983), and Steneck and Dethier (1994).

Mean height

The size has a primary role in defining the ecological niche of macroalgae (Littler and Littler 1980; Steneck and Dethier 1994). Size determines the energy requirements and the primary production of each species (Littler and Littler 1980).

Size also determines the capacity of a particular species to provide a canopy that can be a habitat for other species (Steneck and Dethier 1994). The size of a macroalgal species can also be an asset in the competition for space in coral reefs through coral–algae interactions. For the purpose of the present study, three modalities have been defined for this functional trait: small (< 2 cm), medium (2–5 cm), and high (> 5 cm) species.

Longevity

The role of macroalgae longevity in mediating marine biodiversity and ecosystem functioning has often been neglected (Bracken and Williams 2016). However, the longevity of macroalgae is closely related to their productivity (carbon fixed per gram of dry mass per hour) with generally greater longevity corresponding to lower productivity (Steneck and Dethier 1994). Two modalities have been defined to represent this functional trait: annual (A) and perennial (P) species.

Primary productivity

Photosynthetic organisms harvest photons using pigments and use the excitation energy to fix CO₂ into biomass (Bertotti et al. 2016). The productivity of macroalgae plays an important role through the regulation of nutrient cycling and carbon cycling. Primary production is affected by many factors including physiological conditions, environmental characteristics, and season, but also by intrinsic factors of the organisms themselves. Hence, there is a very strong functional relationship between species morphology and primary production (Littler and Littler 1980; Payri 2000). For this trait, four modalities were defined based on daily carbon production (e.g., 1 = low < 2mgC/g dw/day to 4: high > 40 mg C/g dw/day) following Payri (2000) (Table 1).

Calcification

The level of calcification is an important component that determines the ability to (1) avoid or limit grazing by fish or invertebrate, (2) cement fragmented rubbles or create rocky intertidal zones like algal crest, and (3) provide critical habitat for numerous other organisms (Steneck and Watling 1982; Littler et al. 1983; Pennings and Paul 1992; McCoy and Kamenos 2015). For instance, non-geniculate coralline macroalgae (massive forms, e.g., *Hydrolithon* spp.) contribute to the cementation of reefs, while geniculate coralline macroalgae (articulated forms, e.g., *Jania* spp., *Amphiroa* spp.) or some green calcareous macroalgae (e.g., *Halimeda* spp.) contribute to the formation of sand (Montaggioni and Braithwaite 2009). The mode and extent of calcification vary widely among the calcareous macroalgae, from low to

heavily calcified species, which results in different functions. For this trait, we defined four modalities relating to the level of calcification: “no”, “low”, “medium”, and “high” following Payri (2000) (see Table 1).

Substratum

The substratum preferentially occupied by macroalgae is critical for determining macroalgal ecological niches. Each species has specific substratum affinities (bedrock, coral rubble, dead coral, live coral, and sand). Vieira et al. (2014) also recently pointed out that different substrata create niche partitioning between the major lineages of the genus *Lobophora* spp. This trait is directly correlated with habitat characteristics and also influences the interaction and, potentially, the competition with other sessile species. For the purpose of this study, we distinguished three main substratum types: no substratum (epiphyte species), and hard and soft substratum (see Table 1).

Fixation strength

Macroalgae are attached (except for rare holopelagic species) to a substratum which can be hard (e.g., rocks) or soft (e.g., sand and rubbles). Some species are strongly attached (e.g., large brown macroalgae *Sargassum* spp. or tiny filamentous turf like Gelidiales) or loosely attached (e.g., *Cladophora* spp. and *Boodlea* spp.). The strength of fixation to the substratum has important implications for the species life histories as it can vary depending on the developmental stages and depth (e.g. *Sargassum hornerii*, Xu et al. 2016). Strong attachment, which can maintain macroalgae for long periods, provides three-dimensional habitat-building capacity like in brown macroalgae or *Halimeda* spp., which can form large meadows (Rossier and Kulbicki 2000). Low fixation strength helps in species dispersal. We based this trait on the different fixation ways of species (e.g., bulbous holdfast, stupose holdfast, etc.). Considering the high diversity of holdfast type, we chose to use a proxy of “fixation strength”. We distinguished three modalities corresponding to different strength of fixation (“low”, “medium”, and “high”) using taxonomical descriptions and observations. Fixation strength was derived from each species’ fixation type, assuming that, e.g., an encrusting calcified attachment to rocky substratum was stronger than, e.g., rhizoids in soft sand.

Interactions with substratum or benthic organisms

This trait is critical for determining the ecological niche of macroalgal species. It is directly correlated with habitat characteristics and macroalgal growth forms. The latter are associated with ecological features, particularly the level of interactions with other sessile organisms like corals. For

example, encrusting growth forms are often found in interaction with live corals (e.g., *Lobophora hederacea*, Vieira et al. 2015). We distinguished four modalities for this trait: (1) whether they are “epiphyte” or not, and (2–4) depending on the shape of the species, four modes of epilithic interactions ranging from low contact (<25%) when the contact zone is limited to the holdfast region (e.g., erect plants), to full contact (100%) for flat and encrusting species fully adhering to the substratum (see Table 1).

Ability to proliferate

Phase shifts to macroalgal dominance have been described worldwide (cf. introduction), pinpointing to the ability of macroalgae to proliferate following coral loss. Several species belonging to many different groups have been reported to proliferate, including mostly large brown macroalgae like Dictyotales (*Lobophora* spp., see Vieira et al. 2015 for a review) or Fucales (*Turbinaria* spp. and *Sargassum* spp., Stiger and Payri 1999a, b; Andréfouët et al. 2017), but also green (*Caulerpa* spp., *Ulva* spp., *Codium* spp., Lapointe et al. 2005; Machendiranathan et al. 2016) and red macroalgae (e.g. *Asparagopsis taxiformis*, Greff et al. 2017). The ability of species to proliferate has a direct impact on the fitness of reef organisms (recruitment, reproduction, etc.) and the resilience of coral reefs. Two modalities (no or yes) have been defined for this trait by considering the ecology of the species and by building a bibliographic synthesis.

Capacity of production of repellent molecules

The production of metabolite is a critical trait in macroalgae. Many macroalgae produce chemical defenses in response to herbivory, or against competitors and pathogens (Hay and Fenical 1988). The ability of macroalgae to avoid herbivory using allelopathic compounds has implication in the food web through both bottom-up and top-down controls (Rasher and Hay 2010; Rasher et al. 2011; Rasher and Hay 2014). Two modalities (no or yes) have been defined for this trait by building a bibliographic synthesis and using the database MarinLit.

Out of the 316 macroalgal species recorded in this study, functional trait information was completely lacking for only two species, which were excluded from the analyses (*Kallymenia* sp. and *Rhodopeltis* sp). Further analyses were performed using the ten functional traits: five traits in relation to life-history strategy (growth, mean height, longevity, primary productivity, and calcification) and five ecological traits (substratum, fixation strength, interactions with substratum and benthic organisms, ability to proliferate, and repellent molecule production) (see Table 1).

Macroalgae functional space

Pairwise functional distances between functional entities (unique combination of functional trait modalities) were computed using the Gower distance, which allows mixing different types of variables while giving them equal weight (Gower 1971; Podani 1999). A Principal Coordinates Analysis (PCoA) was then performed using this functional distance matrix. Maire et al. (2015) demonstrated that the quality of the functional space (used to compute the functional beta diversity indices) can vary according to the number of dimensions/axes, the number of functional traits, and/or the nature of functional traits (quantitative or qualitative). They showed that using a poorly defined functional space could lead to erroneous ecological conclusions (Maire et al. 2015; Loiseau et al. 2017). To avoid these biases, we used the mean squared deviation (mSD) index (Maire et al. 2015) to select the optimal functional space and, therefore, prevent the misinterpretation of beta functional diversity patterns. In our study, five dimensions provided the best balance between true distances and computing time for functional space.

Diversity indices

To reveal the functional structure of communities, we graphically represented the functional space of the three reefs (Europa, Glorioso, and Juan de Nova) and the distribution of species within this functional space. To investigate the structure of functional traits in macroalgal communities, we computed the mean trait value of a community weighted by the number of species (CWM, which remains robust when facing missing data, Májeková et al. 2016). CWM reflects the values of the most dominant traits in a given community. It was calculated using the modified equation of Lavorel et al. (2008):

$$CWM_j = \sum_i^n p_{ij} T_{ij},$$

where p_{ij} is the number of species i in the community j , and T_{ij} is the mean trait value of the species i in the community j . For qualitative traits (or binary), the modality that was the most represented in the community was considered as the dominant traits in the community.

Finally, to investigate the spatial distribution pattern of species and functional traits, we also computed the taxonomic and functional beta diversity at two spatial scales: among reefs and among sites (within reefs). To determine the relative contribution of turnover and nestedness-resultant to overall beta diversity (taxonomic and functional),

we used the additive partitioning of the pairwise Jaccard dissimilarity proposed by Baselga (2010, 2012) and Villéger et al. (2013) based on functional space representation. Overall taxonomic and functional beta diversities ($S\beta_{tot}$ and $F\beta_{tot}$, respectively) were decomposed into two components: turnover ($S\beta_{tur}$ and $F\beta_{tur}$, respectively) and nestedness-resultant ($S\beta_{nes}$ and $F\beta_{nes}$, respectively). Spatial turnover implies the replacement of some species by others as a consequence of environmental sorting and/or spatial and historical constraints (Qian et al. 2005). The nestedness-resultant component measures differences in richness between assemblages nested to some degree (Baselga and Leprieur 2015; Legendre 2014). At large spatial scale (between reefs), to avoid biases on the value of beta diversity indices because of differences in sampling effort (Cardoso et al. 2009; Beck et al. 2013), we standardized the survey effort by randomly selecting 16 sites per reefs, 999 times. For each iteration, we computed beta diversity indices and used the average value of the indices. To graphically represent the values of beta diversity indices, we used principal coordinate analysis (PCoA). Standard deviation ellipses were projected on the ordination plot to visualize the multivariate dispersion in community composition in function of reefs.

Null model

We used a null model to investigate the potential presence of ecological factors that could drive the pattern of taxonomic and functional beta diversity. The null model simulated the compositional dissimilarity that would be expected in the absence of factors that would cause the clumping of species or species traits (Chase et al. 2011; Kraft et al. 2011). Null models were applied at two spatial scales, among reefs and among site (within reefs). For taxonomic beta diversity, we randomly assigned species to site holding constant both row sums (species incidences) and column sums (site species richness) as in the observed presence/absence matrix (Ulrich and Gotelli 2007). For functional beta diversity, we applied a randomization of functional traits (i.e., we reshuffled the species traits matrices). We reassigned randomly the observed trait combinations to species. This permutation process allowed keeping the following constant: (1) the species richness at each site or reef, (2) the taxonomic beta diversity and its components at each pair of reef/site, and (3) the pool of functional strategies (i.e., trait combinations). We then calculated a P value from the 999 iterations of null models (Veech 2012). More specifically, we derived the P value as the proportion of the null distribution of beta diversity that is more extreme than the observed beta diversity. If deterministic factors are absent or weak, we expect the observed beta diversities to range between 5 and 95% of the null distribution. In contrast, if niche-based processes prevail (limiting

similarity), the observed beta diversity should be significantly different from the null distribution. Typically, beta diversity should be lower than expected at random (lower than 5% of the null distributions) if environmental filtering occurs. In contrast, if limiting similarity occurs, we expect the observed beta diversities to be higher than 95% of the null distribution. At large spatial scale, the observed beta diversities that are higher than the null distribution highlight a shift due to biotic or abiotic selections.

Data analysis

Beta diversity for both diversity components (taxonomic and functional) were analyzed with a permutational multivariate analysis of variance (PERMANOVA, 9999 permutations). For each reef, geomorphology, depth, and swell exposure were analyzed as the source of variation in beta diversity. All statistical analyses and data manipulations were carried out in R 3.3.1 (R Development Core Team 2016). In addition to the core software, the ‘vegan’ (Oksanen et al. 2016), ‘betapart’ (Baselga and Orme 2012), ‘plyr’ version 1.8.3 (Wickham et al. 2011), and ‘ecodist’ (Goslee and Urban 2007) packages were used.

Results

Among reefs, the overall taxonomic beta diversity ranged from 0.77 ± 0.07 (mean \pm SD) and was essentially due to turnover (96%) (see Fig. 2 and Table S1 for the number of species per station).

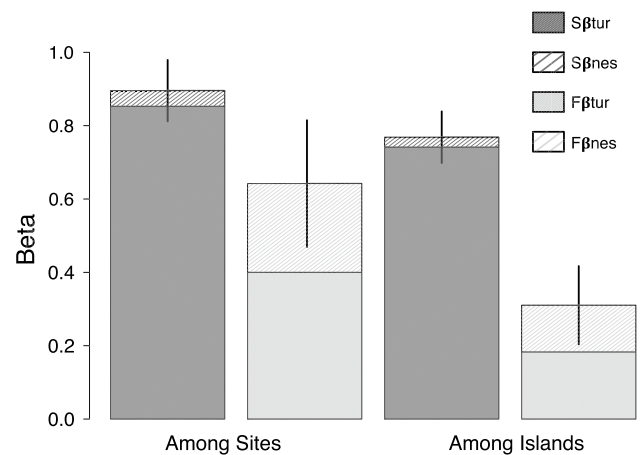


Fig. 2 The multiple-site beta diversities and their partitioning components of turnover (dark gray) and nestedness-resultant (light gray). Computed from the Îles Éparses macroalgal data set for taxonomic ($S\beta_{tur}$ and $S\beta_{nes}$) and functional ($F\beta_{tur}$ and $F\beta_{nes}$) facets at small spatial scale (among sites) and at high spatial scale (among reefs). Vertical bars represent standard deviation of the overall beta diversity

In contrast, functional beta diversity was lower than taxonomic beta diversity (0.31 ± 0.1). The taxonomic beta diversity between Europa and Glorioso and Juan de Nova was higher than the null expectation (P value = 0.993 and 0.999, respectively). Similarly, the functional beta diversity was higher than the null expectation (mean P value = 0.992 and 0.999, respectively). Conversely, the taxonomic and functional beta diversities between Glorioso and Juan de Nova were not different from the null expectation (P value = 0.895 and 0.63, respectively). The decomposition of the beta diversity indicated that the functional beta diversity between Glorioso and Juan de Nova also tended to be determined by turnover (95%). However, the nestedness-resultant component remained important between Europa and Glorioso (0.18) and between Europa and Juan de Nova (0.19), but it was negligible between Glorioso and Juan de Nova (0.07). The ordination plot, used for the visualization of multivariate dispersion in community composition, clearly demonstrates the difference in composition among reefs (see Fig. 3).

For the taxonomic beta diversity, the ordination plot produced three distinct groups that mainly separated sites from the three reefs (see Fig. 3). The ordination plot revealed a difference in taxonomic structure between Europa and the two other reefs (see barycentre locations on Fig. 3). For functional beta diversity, the ordination plot did not produce clearly separated groups among reefs, illustrating the low functional beta diversity among reefs, particularly between Glorioso and Juan de Nova (Fig. 3). Functional beta diversity between Europa/Juan de Nova and Europa/Glorioso was 0.33 and 0.39, respectively, and 0.19 for Juan de Nova/Glorioso. The main differences in functional diversity among reefs appear to be due to differences in species mean height and fixation strength (see Table 2, Fig. 4). More generally, community-level weighted means of trait values were quite similar among reefs, explaining the lower value of functional beta diversity compared to taxonomic beta diversity (see Fig. 4, Table 2). This result was also confirmed by the shape

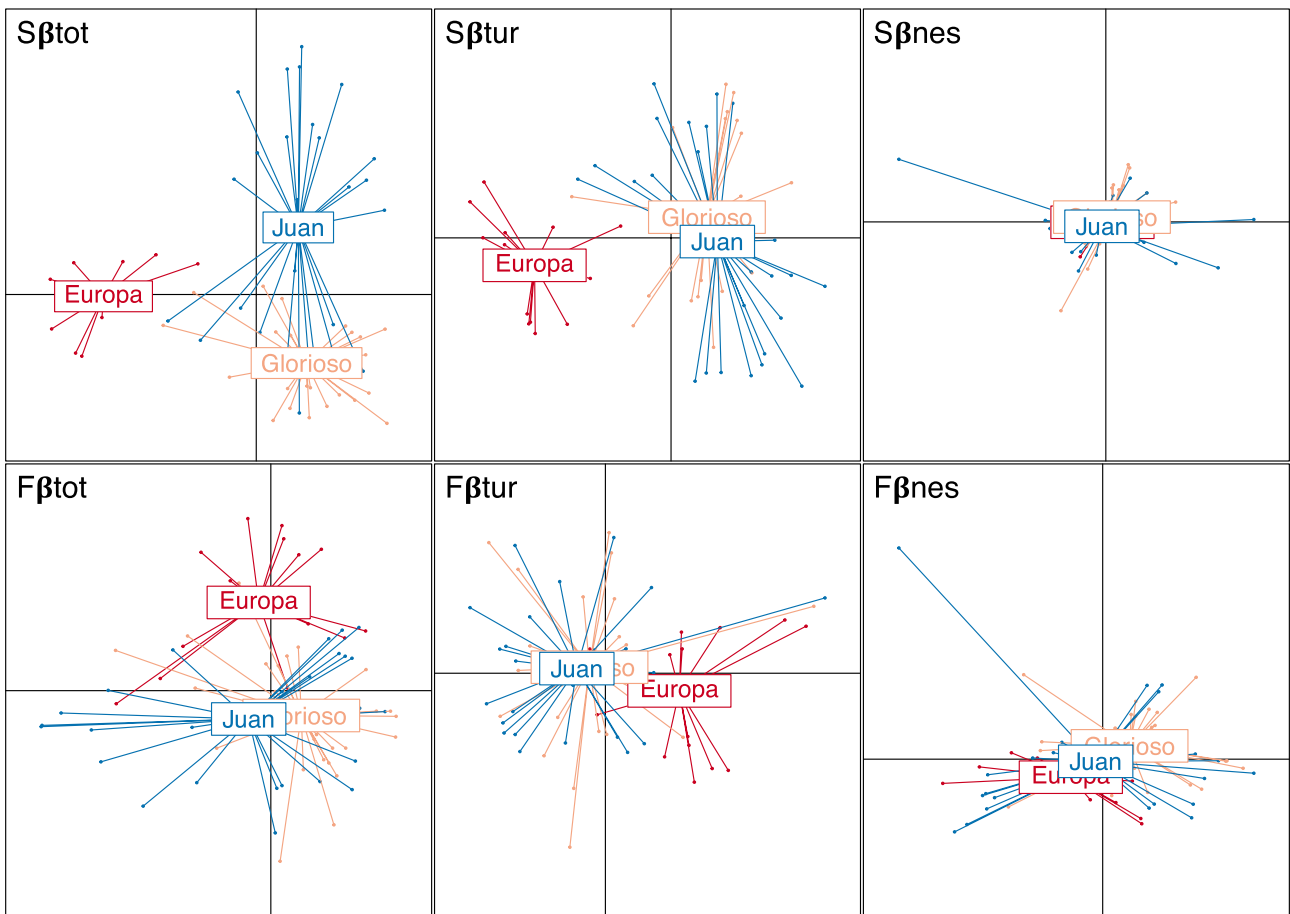


Fig. 3 Illustration of taxonomic (top row) and functional (bottom row) dissimilarity and their partitioning component between each site using a PCoA. $S\beta_{tot}$: taxonomic beta diversity, $S\beta_{tur}$: taxonomic turnover, $S\beta_{nes}$: taxonomic nestedness-resultant, $F\beta_{tot}$: functional

beta diversity, $S\beta_{tur}$: functional turnover, $S\beta_{nes}$: functional nestedness-resultant. Color code: Europa is orange, Glorioso is blue, and Juan de Nova is pink

Table 2 Community-weighted means (the most common values) of functional traits at each reef

	Europa	Glorioso	Juan de Nova
Growth	Fast	Fast	Fast
Mean height	Small	Large	Medium
Longevity	Perennial	Perennial	Perennial
Primary productivity	2	2	2
Calcification	No	No	No
Substratum	Hard substratum	Hard substratum	Hard substratum
Fixation strength	Medium	Medium	High
Interaction	2	1	1
Ability to proliferate	No	No	No
Repellent molecules	Yes	Yes	Yes

similarity in functional spaces of the three reefs and position of species within the functional space (see Fig. 5, Fig. S2).

At the scale of sites (within reefs), the overall taxonomic and functional beta diversity ranged from 0.30 to 1 (0.89 ± 0.08) and from 0.35 to 1 (0.64 ± 0.17), respectively (Fig. 2). On average, the taxonomic beta diversity among sites did not differ from random expectation (mean P value = 0.43 ± 0.35 , 0.45 ± 0.36 , and 0.45 ± 0.39 , for Europa, Glorioso, and Juan de Nova, respectively). Similarly, the functional beta diversity did not differ from random expectation (mean P value = 0.52 ± 0.28 , 0.27 ± 0.26 , and 0.34 ± 0.26 , respectively).

However, results were highly variable (strong standard deviation) with P value ranging from 0.001 to 0.999 for both beta diversity facets among sites. The overall taxonomic and functional beta diversity among sites for the three reefs was mainly determined by turnover, reaching in average 96% and 67%, respectively.

For assemblages among sites, the taxonomic and functional beta diversities were explained by the three variables: geomorphology, depth and swell exposure (see Table 3, Table S2). The PERMANOVA results showed that swell exposure and geomorphology best explained the taxonomic beta diversity ($0.11 < R^2 < 0.15$ and $0.09 < R^2 < 0.15$, respectively) and the functional beta diversity ($0.11 < R^2 < 0.16$ and $0.09 < R^2 < 0.19$, respectively; see Table 3). Depth, despite significant P value, poorly explained the functional differences in assemblages ($0.03 < R^2 < 0.1$) (Table 3). Due to its very low value, the nestedness-resultant component was very poorly explained by environmental variables (see Table S3).

Discussion

The floras of the three islands were mostly a subset of the regional diversity, representing 23.5% of the species richness of the Mozambique Channel (Mattoo et al. 2016), although they appeared individually quite contrasted. Relatively few

species were shared between Europa and Juan de Nova (41 spp.) and Europa and Glorioso (50 spp.), whereas Juan de Nova and Glorioso appeared more similar (78 spp. in common) (Mattoo et al. 2016). Each reef has its own dynamics, due to their different geographical position in the Mozambique Channel, and regional biogeographic affinities (see discussion in Mattio et al. 2016). The unique geological history of each reef has also shaped contrasting geomorphologies (Jorry et al. 2016). All of these factors would be expected to drive distinct patterns of species communities and functional traits portfolio for each reef. Our results revealed at least two scenarios which speak against this assumption.

First, a low functional beta diversity was observed between Glorioso and Juan de Nova despite the presence of different sets of species between the three reefs. However, when comparing the beta diversities of the two reefs against null models, our results did not provide the evidence of functional trait-based community assemblies. In other words, the observed beta diversity was indistinguishable from a random assignment of species and functional traits. The low functional beta diversity may suggest a functional convergence, which could be the result of similar environmental conditions. The two reefs are a part of the same ecoregion, where biogeographic forces are relatively similar (Quérel et al. 2016). Although these two reefs have different geological histories, they have relatively similar habitats and environmental conditions, which could explain that they host macroalgal communities with similar functional diversities. Overall, this finding beta diversity finding supports the idea that, despite distinct species composition, macroalgal communities can provide similar functional portfolio and, therefore, similar ecological functions (see Guillemot et al. 2011 for similar results on fish communities, Fig. 5).

Second, the reef of Europa, which is geomorphologically and geologically different to the two other reefs (Quérel et al. 2016), and harbors specific habitats such as mangroves, was expected to show distinct taxonomic and, to a lower extent, functional composition (Poupin et al. 2013). Our results

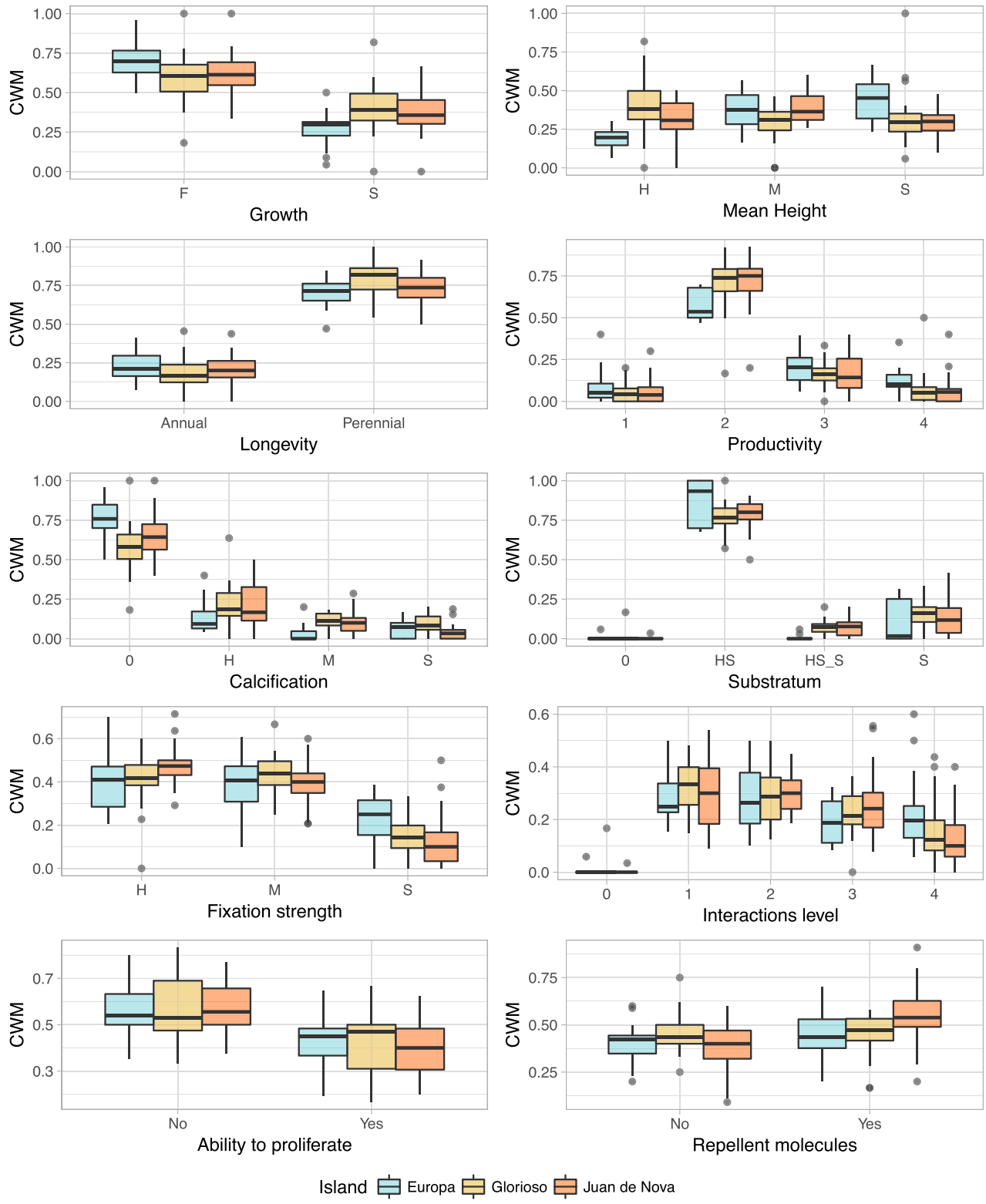


Fig. 4 Community-weighted means of functional trait among the three reefs (Europa, Glorioso, and Juan de Nova). Boxplots represent the distribution of the CWM value for each modality of each functional trait. For codes of the different modalities, see Table 1

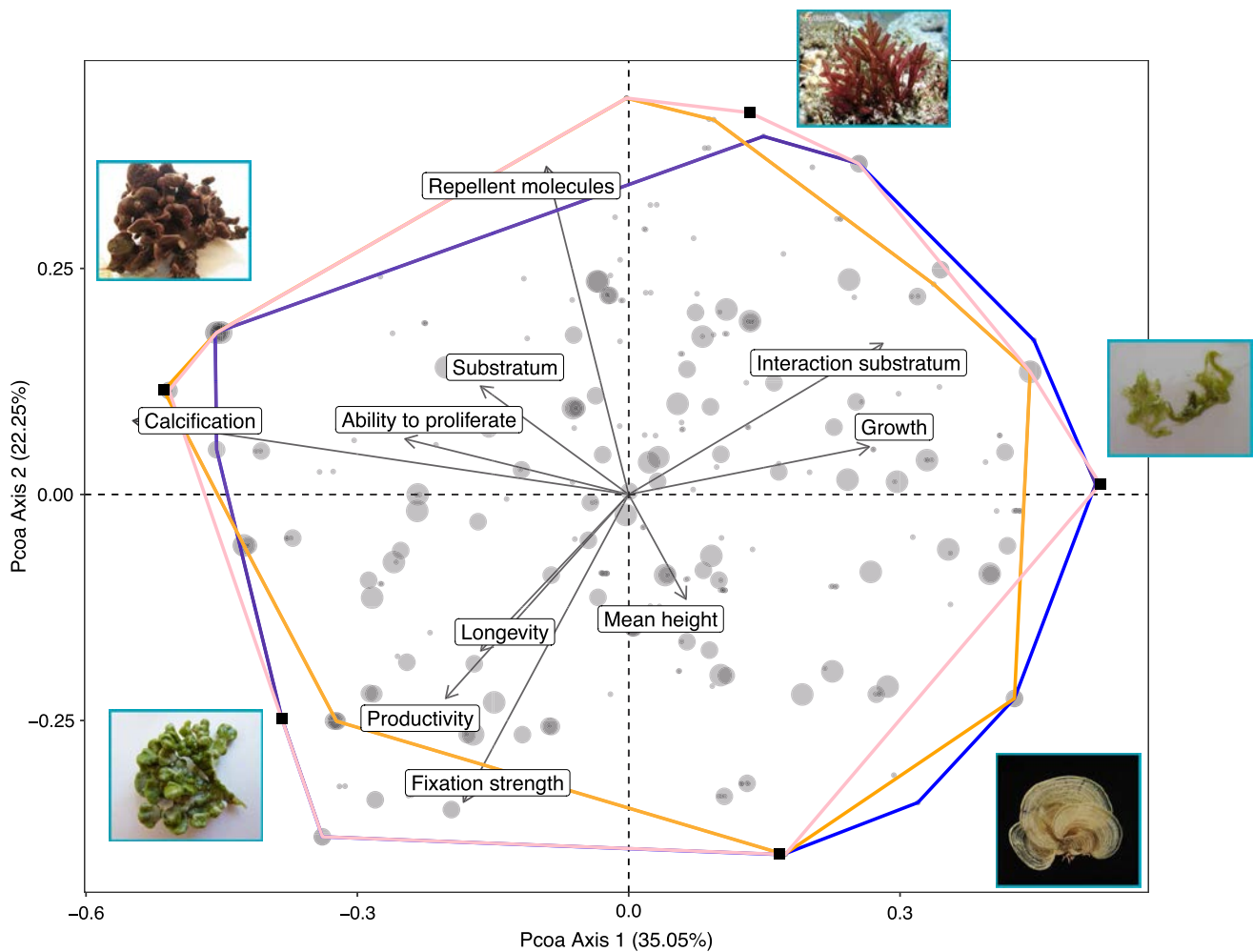


Fig. 5 Functional space and distribution of species inside the functional space of Europa, Glorioso and Juan de Nova (orange, blue, and pink, respectively). Circles represent species and are proportional to their respective occurrence at the three reefs. Large circle = species has been collected at the three reefs, medium circle: species has been collected at two reefs, and small circle: species has been collected at

one reef only. From the bottom in clockwise direction, the black dots for *Champia compressa*, *Corallinales* sp., *Halimaeda melanesica*, *Padina* sp., and *Cladophora* sp3 mark vertices species. When some species have the same functional trait, the corresponding dot has been moved slightly for visual purposes (i.e., randomly jittered)

confirmed this assumption with the values of taxonomic and functional beta diversities higher than expected for a null model. Hence, the singularity of environmental conditions and habitats at Europa is likely the driver of its distinct taxonomic composition and to a lesser extent, functional trait diversity.

Most seaweeds are poor dispersers, because their spores and zygotes are typically short-lived and negatively buoyant (Kinlan and Gaines 2003). Then, many seaweed species have restricted geographic ranges and molecular data indicate that several allegedly widely distributed species in fact represent cryptic species with narrow distributions (e.g., Zuccarello and West 2003; Saunders 2005; Gabriel et al. 2017). This limited dispersal could explain the high taxonomic beta diversity observed among the three reefs. Despite singularity

of their environmental variables (particularly Europa), the three reefs share similar climate conditions that could lead to a convergence in functional traits explaining the low functional beta diversity and similar CWM.

At small spatial scales, macroalgae species and functional beta diversity were high among sites mainly due to a strong turnover. In average, both beta diversities did not differ from the null expectation. However, the *P* value was extremely variable (from 0.001 to 0.999) advocating for a complex and multiple processes combining effect of the environmental gradient, limiting similarity and stochastic effects on the structure of macroalgal communities. This means that environmental variables, competition, and stochasticity may be ruling the beta diversity patterns. This hypothesis was confirmed by the results of the

Table 3 Relationships between environmental variables (geomorphology, depth, and swell exposure) and taxonomic and functional beta diversity of macroalgae

Beta	Reefs	Variables	df	SumsSqs	F	R ²	P value
Sβtot	Europa	Swell exposure	2	0.895	1.322	0.152	0.039
		Depth	1	0.723	2.134	0.123	0.002
		Geomorphology	2	0.888	1.312	0.151	0.022
	Glorioso	Swell exposure	2	0.993	1.598	0.113	0.003
		Depth	1	0.812	2.615	0.092	0.001
		Geomorphology	3	1.099	1.179	0.125	0.108
	Juan de Nova	Swell exposure	2	1.261	2.030	0.132	0.001
		Depth	1	0.934	3.005	0.098	0.001
		Geomorphology	2	0.829	1.335	0.087	0.051
Fβtot	Europa	Swell exposure	2	0.821	0.821	0.152	0.114
		Depth	1	0.353	0.353	0.110	0.018
		Geomorphology	2	0.663	0.663	0.182	0.019
	Glorioso	Swell exposure	2	0.666	1.452	0.117	0.016
		Depth	1	0.436	1.901	0.068	0.027
		Geomorphology	3	1.067	1.550	0.186	0.040
	Juan de Nova	Swell exposure	2	0.746	1.232	0.17	0.014
		Depth	1	0.470	1.554	0.056	0.111
		Geomorphology	2	0.753	1.244	0.031	0.989

Model summaries and parameter estimates for the permutational multivariate analysis of variance (PERMANOVA)

Parameters are as follows: degrees of freedom (df), sums of squares (SumsSqs), and pseudo-coefficient of determination for GLM (R^2); the significance of the pseudo F-Model was tested using a permutation test (9999 permutations); significant results (P value < 0.05) are indicated in bold

PERMANOVA analysis which highlighted the influence of environmental variables on taxonomic and functional beta diversities. However, an important proportion of the beta diversities were not fully explained by the environmental variables alone. Several others potential factors could explain this result. First, the sampling strategy of the initial project was designed to maximize records of diversity (species inventories) with low replication within similar habitats (Mattio et al. 2016). Second and more importantly, a number of environmental variables were not considered in this study, such as biotic (coral cover, biomass of herbivorous fishes, etc.) and abiotic (nutrients and water movement) variables, which have been shown to influence the structure of macroalgal communities in the other studies (Burkpile and Hay 2010; De'ath and Fabricius 2010; Keith et al. 2014). These variables were not recorded systematically in the initial study design (Mattio et al. 2016) and could not be used in the present study. In addition, small-scale processes (competition and herbivory) were difficult to assess. Functional traits, such as the capacity to produce repellent molecules, could be a minor contributor to explain the variability among sites but could possibly explain the distribution of macroalgae at very small scale within sites. Competition is a key process determining the composition and structural changes of benthic communities in coral reefs, particularly interactions between corals and macroalgae (McCook et al. 2001). Negative effects of

algae on coral health occur at very small scale by direct physical effects such as shading or smothering (Jompa and McCook 2003), and by chemically and microbially mediated mechanisms (Thurber et al. 2012). Future studies should increase the sampling effort in each habitat, measure a larger range of environmental variables, and extend the study to other benthic species. Revealing functional traits that influence most interactions among macroalgae and other reef species could bridge the gap in knowledge between small-scale processes and macro-ecology.

In addition, future work should investigate the influence of season on taxonomic and functional beta diversity. Environmental variability (Segar et al. 2013) may lead to changes in the onset of a function; for example, the supply of inorganic nutrients may alter or enhance productivity (Wenger et al. 2015). Finally, our study does not consider the species abundance and/or their biomass, but only used the presence-absence data. There is strong evidence that dominant species/functional entities have a significant effect on ecosystem functioning (Gagic et al. 2015). Abundance and biomass data would allow to weigh the contribution of each species (Grime 1998; Villéger et al. 2008) to better assess their respective responses to forcing variables and/or their importance for ecosystem functioning. However, considering our first objectives, which were fairly descriptive, this first analysis based on the presence-absence data provides a base for further investigation.

By providing insights into the functional diversity of macroalgal communities, our work provides a baseline of the natural distribution and function of macroalgae in isolated coral reef ecosystems of the Mozambique Channel. Fundamental knowledge on species variability and functional community composition is essential for adequate management of the coral reef ecosystem of the Îles Éparses. The high dissimilarity in species composition and to a lesser extent in functional composition among reefs, and the dominance of turnover within reefs and among reefs, calls for the conservation of a large number of different sites at the three reefs (i.e., a single reef cannot replace a global protection of the three reefs). This supports the conservation strategy already established in the Îles Éparses which includes all regional marine diversity (Chabanet et al. 2016).

Finally, understanding the dynamics of communities in a changing world critically relies upon the robust quantification of functional differences among species (Madin et al. 2016). We argue that progress in macroalgal ecology research is hindered by the limited number of species for which trait data are available compared to terrestrial flora (Buzzard et al. 2015) or other taxonomic groups in coral reefs (Parravicini et al. 2014). At the moment, no significant database with uniform terminology exists for macroalgae. Our work is a first step toward using functional diversity in macroalgal ecology; functional traits are a proxy of the “real” functions of species and information is still missing for some species. More knowledge about the phenotypical and physiological variations in life-history traits such as productivity, calcification, and production of molecules will further our understanding of the dynamics of these assemblages and their function in the coral reef ecosystem. For instance, information about reproduction could be an essential trait to understand functional biogeography of macroalgae, but information about this trait was too scarce to be used in this study. Within the European Marine Observation Data Network (EMODnet) Biology project (www.emodnet-biology.eu), a trait matrix is upcoming for European algal diversity. Traditionally, abundance of opportunistic macroalgae and species shift in floristic composition has been used successfully as descriptors of human-induced eutrophication (Blanfuné et al. 2017). Future studies should explore linkages between the disturbance and functional composition of macroalgal communities, as it may be more predictive than taxonomic indicators (see Teresa and Casatti 2017, on fish).

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Author contributions Authors whose names appear on the submission have contributed sufficiently to the scientific work and, therefore, share collective responsibility and accountability for the results.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Human and animal rights statement This article does not contain any studies with human participants or animals performed by any of the authors. All necessary permits for sampling and observational fields have been obtained by the authors from the competent authorities (TAAF) and are mentioned in the acknowledgments. We took care not to disturb wildlife or the surrounding environment more than necessary to gather the samples.

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