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Multi-scale drivers of community diversity and composition across tidal heights: an example on temperate seaweed communities

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Summary

1. Despite recent advances in understanding community assembly processes, appreciating how these processes vary across multiple spatial scales and environmental gradients remains a crucial issue in ecology.

2. This study aimed to disentangle the drivers of diversity and composition of seaweed communities through a gradient of spatial scales based on a hierarchical sampling design consisting of 19 sites distributed in four sectors along the Brittany coastline. Using randomised community matrices and Moran's eigenvector maps (MEMs), we compared (i) the relative importance of deterministic and stochastic processes, (ii) the environmental correlates of community composition, and (iii) the scale of variation in community composition for seaweed communities located at two different tidal heights.

3. Processes shaping community patterns are expected to vary along a gradient of tidal heights. Therefore, we specifically examined the following hypotheses: the contribution of deterministic over stochastic processes as well as the relative importance of environmental filtering over biotic interactions should be enhanced for seaweed communities of the infralittoral fringe compared to subtidal ones, whereas dispersal of propagules in the water column should be more restricted resulting in finer scale variation in community composition for seaweed communities of the infralittoral fringe compared to subtidal communities.

4. Seaweed communities were largely shaped by deterministic processes, although the relative importance of deterministic processes was greater for communities of the infralittoral fringe than for subtidal communities. Sea surface temperature and geophysical variables were correlates of community composition at the two tidal heights; additionally, waves and current were correlated with the composition of the communities of the infralittoral fringe while kelp density was correlated with the composition of subtidal communities. Variation in community composition was observed at a finer scale for infralittoral fringe than for subtidal communities.

5. *Synthesis.* Our results suggest that the relative importance of deterministic and stochastic processes in structuring seaweed communities varies across tidal heights. Furthermore, the Moran's eigenvector maps framework highlights that the nature of environmental correlates and the spatial scale at which they were good correlates of community composition also vary across tidal heights and may therefore be useful to broaden our understanding of community assembly across vertical gradients.

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Introduction

Understanding how species assemble into communities is a key and highly debated issue in ecology. The structure of communities has been traditionally explained as the result of deterministic processes where species persistence in its environment is determined by abiotic conditions and biotic interactions (Hutchinson 1957; Grime 1973; Tilman 1982). In 2001, Hubbell proposed an alternative view: the unified theory of biodiversity and biogeography which considers the structure of communities as the fruit of stochastic processes only (Hubbell 2001). Over the last 15 years, important efforts have been made to disentangle the relative contribution of deterministic and stochastic processes in shaping community structure, including the proposition of a theoretical framework (Leibold *et al.* 2004; Logue *et al.* 2011). It is now widely recognised that both deterministic (i.e. environmental filtering and biotic interactions) and stochastic processes (i.e. ecological drift and limited dispersal) influence community structure (Leibold & McPeek 2006), however, there is no consensus regarding the relative importance of these two kinds of processes which seem to differ both among different environmental conditions (Chase 2007; Chase & Myers 2011) and across spatial scales (Cottenie 2005; Chase & Myers 2011; Logue *et al.* 2011).

The consideration of multiple spatial scales to better understand patterns of biodiversity and processes driving them has therefore become a cornerstone of modern ecology. Indeed, communities are organised at multiple scales and form a network of communities that are connected by dispersal of multiple potentially interacting species called metacommunities (see Leibold *et al.* 2004 for review). Connectivity among communities occur at various rates, depending on both species dispersal abilities and landscape features, and affect the structure of metacommunities in interaction with ecological drift, environmental filtering and biotic interactions. Yet, our knowledge regarding how biodiversity is structured across spatial scales varies greatly among ecosystems: most empirical support comes from research on terrestrial ecosystems, in which dispersal distances are much easier to estimate than in marine ecosystems. In the absence of robust dispersal estimates and considering the fluid characteristics of the ocean, it has long been considered that dispersal rates were greater in the marine realm compared to terrestrial environments (Cowen 2000). However, the recent methodological advances in the study of dispersal pathways and connectivity among marine populations have greatly improved estimates of marine dispersal and challenge the simplicity of this long-standing paradigm. As such, in their review of propagule dispersal in marine and terrestrial environments, Kinlan & Gaines (2003) have shown that marine organisms displayed a huge variety in their mean dispersal distance ranging from a few metres to nearly 1000 km.

In cold to temperate waters, rocky subtidal assemblages are dominated by kelps, brown seaweeds which form underwater forests and are of major ecological importance since they provide habitat, food and protection to a myriad of other marine organisms (Dayton 1985; Steneck *et al.* 2002). These kelp forests are one of the most diverse and productive ecosystems world-wide (Mann 1973). Biodiversity patterns of kelp-dominated communities have been described mostly at local scales in different places of the world (e.g. Hawkins & Harkin 1985; Leliaert *et al.* 2000; Christie *et al.* 2003; Graham 2004; Pehlke & Bartsch 2008; Leclerc *et al.* 2015), more rarely at regional scales (Wernberg, Kendrick & Phillips 2003; Derrien-Courtel, Le Gal & Grall 2013; Robuchon *et al.* 2015) but to date, only Smale, Kendrick & Wernberg (2011) looked at these patterns across multiple spatial scales. In their study of the subtidal flora of the south-western Australia coastline, they showed that diversity and turnover of communities varied considerably at all spatial scales, although small-scale variability contributed most to total variation. This important small-scale variability, a common pattern in rocky shore communities (Fraschetti, Terlizzi & Benedetti-Cecchi 2005), was mainly attributed to the action of waves and habitat heterogeneity while regional scale variability was attributed to climatic factors as most species had cool-water affinities (Smale, Kendrick & Wernberg 2011). Despite providing great insights in the understanding of multi-scale variability in kelp-dominated communities, the study of Smale, Kendrick & Wernberg (2011) did not explicitly address the question of what are the underlying processes that explained the biodiversity patterns they documented. Addressing the relative contribution of deterministic and stochastic processes driving biodiversity patterns of kelp-dominated communities across multiple spatial scales remains an open issue.

In recent years, methods to analyse spatial ecological data across different scales have been improved, notably with the emergence of a set of methods now called Moran's eigenvector maps (MEMs; Dray, Legendre & Peres-Neto 2006). These methods can model structures at scales ranging from the broadest down to the finest on the basis of a weighted matrix representing the degree of connection between sampling sites, where the weighted matrix can take several forms from the simplest (a binary matrix: sites are connected or not) to the most geographically realistic (a matrix of geographic distances among sites). A principal coordinates analysis (PCoA) is then performed on the truncated weighted matrix and the resulting eigenvectors that model spatial correlation are used as spatial explanatory variables in canonical ordination (Borcard, Gillet & Legendre 2011). Therefore, the MEMs framework is a way to evaluate the importance of measured explanatory variables in driving community patterns through a gradient of spatial scales as well as to identify significant residual spatial patterns that could arise from the omission of important unmeasured explanatory variables or processes (Dray *et al.* 2012).

In this study, our objective was to disentangle drivers of community diversity and composition across multiple spatial scales for kelp-dominated seaweed communities along c. 500 km of the Brittany coastline (France). This region harbours a hot spot of seaweed diversity (Kerswell 2006; Keith, Kerswell & Connolly 2014) and forms along the European Atlantic coastline a transition zone between two biogeographic provinces, the warm temperate Lusitanian province in the south and the cold temperate Northern European Seas province in the north (Spalding *et al.* 2007). We addressed this question in seaweed communities located at two different tidal heights: (i) *Laminaria digitata* understorey communities, spanning the lower intertidal (i.e. the infralittoral fringe), and upper subtidal zones and (ii) *Laminaria hyperborea* communities, found in the subtidal zone (i.e. the infralittoral zone). Note that, even if *L. digitata* understorey communities are located both in the infralittoral fringe and the upper subtidal zone, they will be referred hereafter as infralittoral fringe communities to facilitate the reading. Based upon these contrasted tidal heights, we can formulate three hypotheses regarding the differences expected between infralittoral fringe communities and subtidal ones in terms of relative importance of deterministic processes, environmental drivers of community composition and propagule dispersal distances (Fig. 1). First, some recent works have suggested that the relative importance of deterministic processes in structuring communities was greater in disturbed compared to undisturbed environment (Chase 2007; Chase & Myers 2011). The intertidal environment experiences frequent changes between immersion and emersion and is exposed to waves; hence it is more disturbed than the subtidal one which is always immersed (Raffaelli & Hawkins 1996). We can, therefore, hypothesise that the relative importance of deterministic processes in structuring communities is greater in infralittoral fringe communities than in subtidal ones. Second, the relative importance of environmental filters over biotic interactions in structuring littoral communities is known to increase with tidal height (Raffaelli & Hawkins 1996). Therefore, the relative importance of abiotic over biotic variables in driving community composition is expected to be greater in infralittoral fringe communities compared to subtidal ones. Finally, third, infralittoral fringe communities are located higher on the vertical gradient of tidal heights than subtidal communities. Consequently, dispersal distances should be lower in these communities because they are less often immersed (which limits the dispersal of propagules in the water column) but most importantly they experience osmotic and thermic stresses during periods of emersion (which stimulate the simultaneous release of propagules at low tides and thus short-distance dispersal, Norton 1992). Such differences in terms of propagule dispersal between the infralittoral fringe and the subtidal zone have recently been evidenced by comparing genetic connectivity of *L. digitata* and *L. hyperborea* populations (Robuchon *et al.* 2014). Therefore, variation in community composition should be observed at a finer spatial scale in infralittoral fringe communities compared to subtidal ones.

Towards our objective, we conducted an extensive and quantitative survey of seaweed communities using a nested sampling design, characterised the variation in diversity indices and their deviations from null models at the different levels of our sampling hierarchy and investigated how environmental variables fitted community composition at multiple spatial scales using the MEMs framework.

Materials and methods

STUDY AREA AND DATA SOURCES

To determine the drivers of seaweeds' community structure across spatial scales, we compiled data on floristic composition and environmental variables across 19 sites distributed in four sectors of Brittany (France, Fig. 2). These sectors were chosen because they display distinct features which characterised the environmental heterogeneity of the Brittany coastline: St Malo Bay shows a more irregular topography and is characterised by the presence of cyclonic and anticyclonic gyres that increase the water mass residence times and may affect propagule dispersal (Salomon & Breton 1993), water bodies of Southern Brittany are stratified (Le Fèvre 1987) and between these two regions, Iroise Sea and Morlaix Bay form a cold and resilient water pocket (Gallon *et al.* 2014). Floristic composition was assessed during a survey of seaweed diversity conducted in winter 2011 by scuba diving and targeting the flora living beneath the canopy of *L. digitata* and *L. hyperborea*, which differ by their distributions along the tidal zone: *L. digitata* occupies the infralittoral fringe, between +1 and −1 m depth whereas *L. hyperborea* occupies the infralittoral zone between −1 and −30 m (reviewed by Robuchon *et al.* 2014). This difference in vertical distribution implies that *L. digitata* populations and associated understorey communities are sometimes emerged (83 h over the year 2011 based on the SHOM data - http://www.shom.fr/ - for the city of Roscoff, in Morlaix Bay), whereas *L. hyperborea* populations and associated understorey communities are always underwater. At each site, six quadrats of 0·10 m^2 were randomly placed among the kelps holdfasts at a few metres of distance (three among *L. digitata* and three among *L. hyperborea*) and sampled for all macroscopic specimens of seaweeds (except crustose seaweeds) present in these quadrats. Then, specimens were sorted by morphotype and identified using the floristic keys and field guides available for the region (Dixon & Irvine 1977; Irvine 1983; Fletcher 1987; Burrows 1991; Maggs & Hommersand 1993; Irvine, Chamberlain & Maggs 1994; Brodie & Irvine 2003; Cabioc'h *et al.* 2006). The number of individuals per morphotype within each quadrat was counted, allowing generating one quadrat-by-species and one site-by-species abundance matrices.

We also built a site-by-environment matrix resulting from the compilation of 32 environmental variables (Table 1) related to the density of *Laminaria* individuals (measured during the floristic survey), geophysical and bioclimatic characteristics (extracted from MARSPEC layers, Sbrocco & Barber 2013) and sea-states characteristics (calculated from the HOMERE database, Boudière *et al.* 2013).

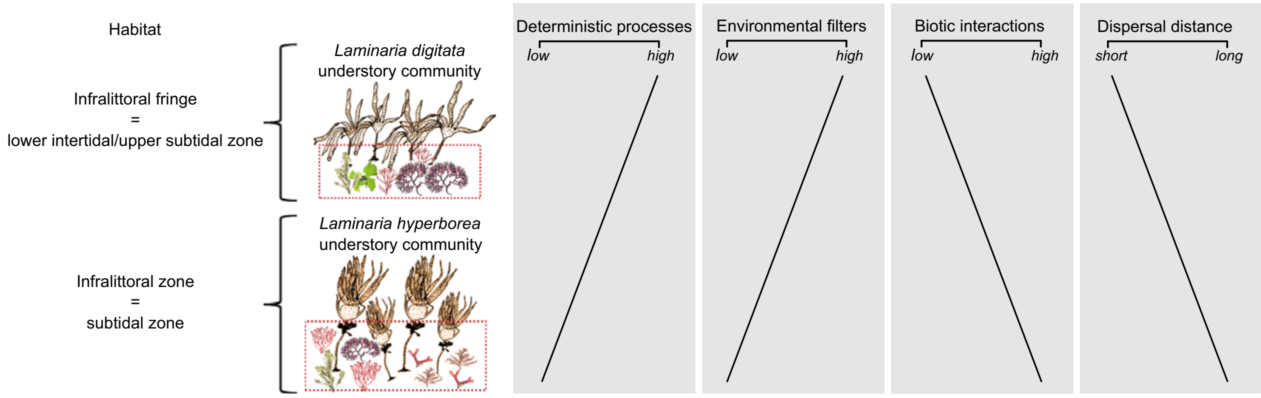

Fig. 1. Diagram showing the different hypotheses of our study regarding the relative importance of deterministic processes, environmental filters, biotic interactions and dispersal distance in structuring seaweed communities at two tidal heights.

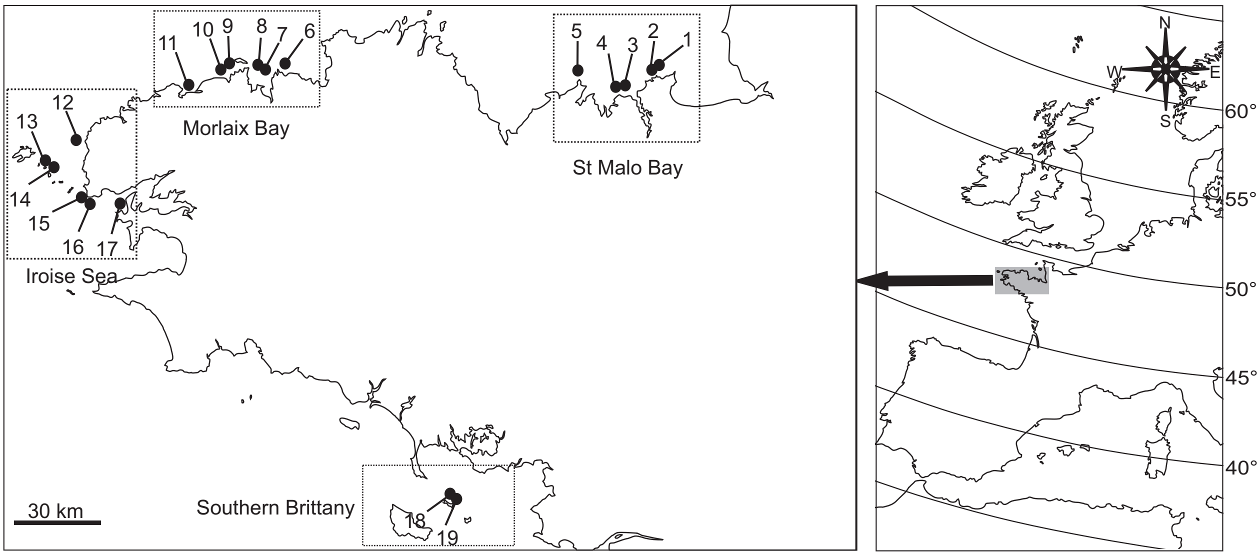

Fig. 2. Map showing the 19 sampling sites distributed in the four sectors along the Brittany coastline, France. Sites are: Guimereux (1), La Bigne (2), Nerput (3), Le Moulin (4), Les Amas du Cap (5), Primel (6), Duons Est (7), Duons Ouest (8), Santec 2 (9), Santec 1 (10), Les Amiettes (11), Les Linious (12), Men Vriant (13), Klosenn Malaga (14), Les Rospects (15), St Mathieu (16), Pointe du Grand Gouin (17), Houat 2 (18) and Houat 1 (19). For site coordinates, see Appendix S1, Supporting Information.

HIERARCHICAL ANALYSES OF DIVERSITY INDICES

Species richness (SR) and Shannon diversity index based on $\log_e$ (H′, Shannon 1948) were calculated for the infralittoral fringe communities and the subtidal communities at three spatial scales: sector (4 levels), site (19 levels) and quadrat (57 levels). Variability in SR and H′ was examined at the different spatial scales with nested ANOVA conducted with the R package BiodiversityR (Kindt & Coe 2005). The design was fully hierarchical; sectors were fixed while nested factors were treated as random. As neither SR nor H′ fit the assumptions of normality and homogeneity of variance, a dissimilarity matrix based on Bray–Curtis coefficients (Bray & Curtis 1957) derived from untransformed SR and H′ (using a dummy variable equal to 1) was generated for the analyses, which used 999 permutations.

To examine if observed SR and H′ at the three spatial scales of sampling hierarchy differed from results expected under a null model, we performed an additive diversity partitioning following Crist *et al.* (2003) where mean values of α diversity at lower levels of a sampling hierarchy are compared to the total diversity in the entire dataset, that is, γ diversity. The expected diversity components were calculated 999 times by individual-based randomisation of the community data matrix using the R package vegan (Oksanen *et al.* 2015).

MULTIVARIATE SPATIAL ANALYSES

To analyse spatial structures of seaweed communities across multiple spatial scales, we used the approach proposed by Dray *et al.* (2012). It consists of examining how the spatial pattern of beta diversity changes when considering the initial site-by-species abundance matrix (i.e. the community matrix), its approximation by environmental variables (i.e. the fitted matrix) and its residual counterpart (i.e. the residual matrix) on the one hand (McIntire & Fajardo 2009) and to estimate and test at which spatial scale these beta diversity changes occur using MEMs (Dray, Legendre & Peres-Neto 2006) on the other hand.

We carried out this approach independently for infralittoral fringe communities and for subtidal communities. To that purpose, we

Table 1. Characteristics of the environmental variables used in this study

Name (abbreviation)	Description (units)	Type (resolution)	Source
Density of *Laminaria digitata* (Ld.density)*	Density of *L. digitata* individuals [semi-quantitative measure ranging from 1 (low density) to 4 (high density)]	*In situ* measure	This study
Density of *Laminaria hyperborea* (Lh.density)†	Density of *L. hyperborea* individuals [semi-quantitative measure ranging from 1 (low density) to 4 (high density)]	*In situ* measure	This study
Bathymetry (bathy)	Depth of the seafloor (m)	Remotely sensed measure (30 arc-second)	MARSPEC‡
East/West aspect (ew.aspect)*,†	Horizontal orientation of the seafloor on the East/West gradient (radians)	Derived from remotely sensed bathymetry (30 arc-second)	MARSPEC‡
North/South aspect (ns.aspect)*,†	Horizontal orientation of the seafloor on the North/South gradient (radians)	Derived from remotely sensed bathymetry (30 arc-second)	MARSPEC‡
Plan curvature (pl.curv)*,†	Terrain curvature in the direction perpendicular to the maximum slope (none)	Derived from remotely sensed bathymetry (30 arc-second)	MARSPEC‡
Profile curvature (pr.curv)	Terrain curvature in the direction parallel to the maximum slope (none)	Derived from remotely sensed bathymetry (30 arc-second)	MARSPEC‡
Distance to shore (shore.dist)*,†	Distance to shore (km)	Derived from remotely sensed shoreline (30 arc-second)	MARSPEC‡
Bathymetric slope (slope)*,†	Slope of the seafloor (°)	Derived from remotely sensed bathymetry (30 arc-second)	MARSPEC‡
Concavity (concav)	Slope of the bathymetric slope (°)	Derived from remotely sensed bathymetry (30 arc-second)	MARSPEC‡
Mean annual SSS (sss.mean)	Mean sea surface salinity averaged over the period 1955–2006 (psu)	Derived from *in situ* measures (30 arc-second)	MARSPEC‡
Minimum monthly SSS (sss.min)	Salinity of the least salty month averaged over the period 1955–2006 (psu)	Derived from *in situ* measures (30 arc-second)	MARSPEC‡
Maximum monthly SSS (sss.max)	Salinity of the saltiest month averaged over the period 1955–2006 (psu)	Derived from *in situ* measures (30 arc-second)	MARSPEC‡
Annual range in SSS (sss.range)	Annual range in sea surface salinity averaged over the period 1955–2006 (psu)	Derived from *in situ* measures (30 arc-second)	MARSPEC‡
Annual variance in SSS (sss.var)	Annual variance in sea surface salinity averaged over the period 1955–2006 (psu)	Derived from *in situ* measures (30 arc-second)	MARSPEC‡
Mean annual SST (sst.mean)*,†	Mean sea surface temperature averaged over the period 1955–2006 (°C)	Derived from remotely sensed measures (30 arc-second)	MARSPEC‡
Minimum monthly SST (sst.min)	Temperature of the coldest month averaged over the period 1955–2006 (°C)	Derived from remotely sensed measures (30 arc-second)	MARSPEC‡
Maximum monthly SST (sst.max)	Temperature of the warmest month averaged over the period 1955–2006 (°C)	Derived from remotely sensed measures (30 arc-second)	MARSPEC‡
Annual range in SST (sst.range)*,†	Annual range in sea surface temperature averaged over the period 1955–2006 (°C)	Derived from remotely sensed measures (30 arc-second)	MARSPEC‡
Annual variance in SST (sst.var)	Annual variance in sea surface temperature averaged over the period 1955–2006 (°C)	Derived from remotely sensed measures (30 arc-second)	MARSPEC‡
Mean annual CGE (cge.mean)*	Mean wave energy flux averaged over the period 1994–2012 (kW m^{-1})	Derived from model outputs in HOMERE database§ (value from the nearest node)	This study
Minimum monthly CGE (cge.min)	Wave energy flux of the energy-calmest month averaged over the period 1994–2012 (kW m^{-1})	Derived from model outputs in HOMERE database§ (value from the nearest node)	This study
Maximum monthly CGE (cge.max)†	Wave energy flux of the energy-most agitated month averaged over the period 1994–2012 (kW m^{-1})	Derived from model outputs in HOMERE database§ (value from the nearest node)	This study
Annual range in CGE (cge.range)	Annual range in wave energy flux averaged over the period 1994–2012 (kW m^{-1})	Derived from model outputs in HOMERE database§ (value from the nearest node)	This study
Mean annual number of CGE extreme measures (cge.next.mean)	Mean number of measures in wave energy flux exceeding 14 kW m^{-1} averaged over the period 1994–2012 (none)	Derived from model outputs in HOMERE database§ (value from the nearest node)	This study

(continued)

Table 1. (continued)

Name (abbreviation)	Description (units)	Type (resolution)	Source
Number of CGE extreme measures within the 3 months preceding the floristic survey (cge.next.3 months)	Number of measures in wave energy flux exceeding 14 kW m^{-1} within the 3 months preceding the floristic survey (none)	Derived from model outputs in HOMERE database[§] (value from the nearest node)	This study
Mean annual CUR (cur.mean)	Mean sea water velocity averaged over the period 1994–2012 (m s^{-1})	Derived from model outputs in HOMERE database[§] (value from the nearest node)	This study
Minimum monthly CUR (cur.min)[*,†]	Sea water velocity of the current-calmest month averaged over the period 1994–2012 (m s^{-1})	Derived from model outputs in HOMERE database[§] (value from the nearest node)	This study
Maximum monthly CUR (cur.max)	Sea water velocity of the current-most agitated month averaged over the period 1994–2012 (m s^{-1})	Derived from model outputs in HOMERE database[§] (value from the nearest node)	This study
Annual range in CUR (cur.range)	Annual range in sea water velocity averaged over the period 1994–2012 (m s^{-1})	Derived from model outputs in HOMERE database[§] (value from the nearest node)	This study
Mean annual number of extreme CUR measures (cur.next.mean)	Mean number of measures in sea water velocity exceeding 0·15 m s^{-1} averaged over the period 1994–2012 (none)	Derived from model outputs in HOMERE database[§] (value from the nearest node)	This study
Number of CUR extreme measures within the 3 months preceding the floristic survey (cur.next.3 months)	Number of measures in sea water velocity exceeding 0·15 m s^{-1} within the 3 months preceding the floristic survey (none)	Derived from model outputs in HOMERE database[§] (value from the nearest node)	This study

*Variable retained in E_Ld.
[†]Variable retained in E_Lh.
[‡]Sbrocco & Barber (2013).
[§]Boudière *et al.* (2013).

considered two initial site-by-species abundance matrices, one for infralittoral fringe communities and one for subtidal communities as well as the two corresponding site-by-environment matrices containing explanatory environmental variables (i.e. the environmental matrices). The environmental matrices were generated by testing correlations among all variables listed in Table 1 and removing variables driving absolute values of pairwise correlations superior to 0·75 using the R package caret (Kuhn 2015). The community matrices were transformed using the Hellinger transformation to put emphasis on abundant species as recommended by Rao (1995). Then, we performed a principal component analysis (PCA) to identify the main patterns in community data.

Redundancy analysis (RDA) was conducted to reveal the main structures in community data explained by environmental variables (i.e. analysis of the two fitted matrices) using a forward selection procedure to retain informative environmental variables only, whereas partial residual analysis (PRA) was performed to identify the structures in community data not explained by environmental variables (i.e. analysis of the two residual matrices). To generate the spatial explanatory variables, we conducted a classical distance-based MEMs approach (formally called Principal Coordinates of Neighbour Matrices) following guidelines in Borcard, Gillet & Legendre (2011): (i) we computed a matrix of geographic distances among sites using the shortest path by the sea, (ii) we truncated the matrix using a distance threshold equal to the maximum distance between two consecutive sites across the coastline, (iii) we performed a PCoA on the truncated distance matrix and (iv) we retained 18 eigenvectors that model spatial correlation as spatial explanatory variables. Scalograms were computed for the community, the fitted and the residual matrices by projecting the sites scores on the first two axes of the different analyses (PCA, RDA and PRA respectively) onto the spatial basis formed by the 18 MEMs, therefore representing a partitioning of the respective variances across multiple spatial scales ranked from the broadest to the finest. They are represented in a smoothed version (as in Munoz 2009) with six spatial components formed by groups of three successive MEMs, which is a way to avoid undesired sampling artefacts at fine scales (aliasing effects, Platt & Denman 1975). The individual R^2 values that form the scalograms and correspond to the amount of variation explained by a given scale are expected to be uniformly distributed in the absence of spatial structure (Ollier, Couteron & Chessel 2006). To uncover significant spatial structure, we therefore tested if the maximum observed R^2 was significantly larger than values obtained in the absence of spatial structure using a permutation procedure with 999 repetitions.

All analyses were carried out in R (R Core Team 2015) and based on the script provided in Dray *et al.* (2012) and adapted to our data.

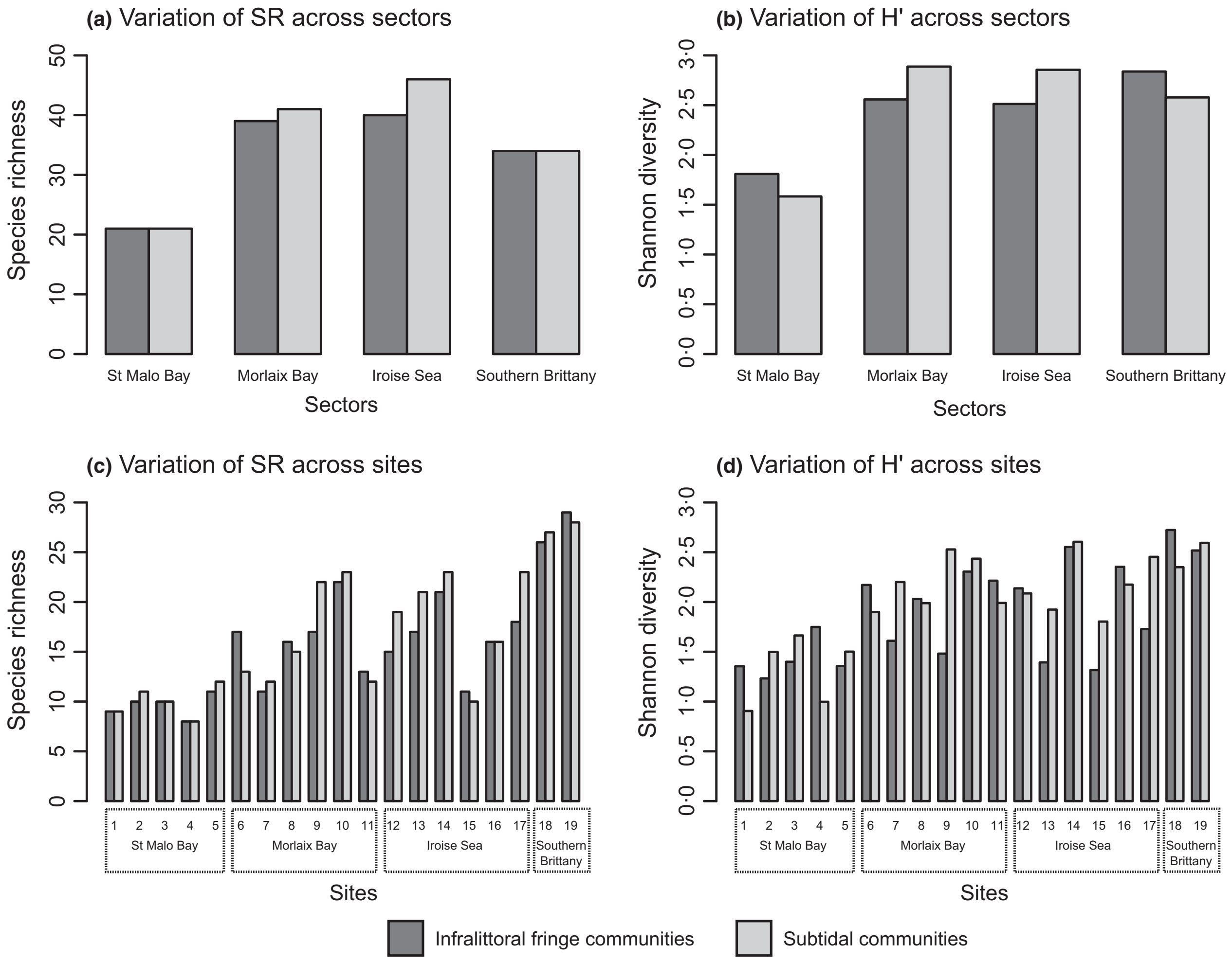

Fig. 3. Comparison of species diversity estimates between infralittoral fringe communities and subtidal communities across space. (a) Species richness (SR) by sector, (b) Shannon diversity (H′) by sector, (c) SR by site and (d) H′ by site. For site names, see Fig. 2.

Results

In total, 5292 specimens corresponding to 69 species were identified from the 57 quadrat samples of the infralittoral fringe communities and 5179 specimens corresponding to 68 species were identified from the 57 quadrat samples of the subtidal communities. For both infralittoral fringe and subtidal communities, red seaweeds constituted the most abundant and the most diverse seaweed lineage (respectively 94% and 92% of total abundance/78% and 76% of total SR), followed by brown seaweeds (respectively 3·9% and 7·2% of total abundance/14% and 18% of total SR) and green seaweeds (respectively 0·2% and 0·1% of total abundance/5·8% and 4·4% of total SR).

At the scale of sector and for both infralittoral fringe and subtidal communities, SR was minimum in St Malo Bay and maximum in Iroise Sea (equally maximum in Morlaix Bay for infralittoral fringe communities, Fig. 3a). Shannon diversity (H′) was also minimum in St Malo Bay for both infralittoral fringe and subtidal communities; however, it reached its maximum in Southern Brittany for infralittoral fringe communities and in Morlaix Bay for subtidal communities (Fig. 3b). At the scale of site and for both communities, SR encountered its minimum in site 4 (a site in St Malo Bay) and its maximum in site 19 (a site in Southern Brittany), and could be markedly variable among sites within the same sector as reported in Morlaix Bay and Iroise Sea (Fig. 3c). Finally, H′ was minimum in sites of St Malo Bay and very variable both among sites and between kelp communities (Fig. 3d). For both infralittoral fringe and subtidal communities, nested ANOVA indicated that both SR and H′ were considerably and significantly variable at all spatial scales (Table 2). In all cases, the examination of variance components suggested that the relative importance of fine-scale variability (i.e. site and residuals) outweighed that of broad-scale variability (i.e. sector), although the relative importance of broad-scale variability was higher for SR than for H′.

Results of additive diversity partitioning indicated that in almost all cases, observed SR and H′ were significantly different from expectations under a null model for α and β diversities and at the three levels of sampling hierarchy (quadrat, site and sector) (Table 3). Specifically, α diversity was always lower than expected. The only exception was found for β diversity in subtidal communities for which among-sites differences in terms of SR did not differ from null expectations.

Regarding the computation of the environmental matrices, 10 out of 32 environmental variables were retained for the

Table 2. Results of nested ANOVA for factor ‘site’ nested in factor ‘sector’ based on Bray–Curtis dissimilarity coefficients derived from untransformed species richness (SR) and Shannon diversity (H′) using a dummy variable equal to 1; all tests used 999 permutations

	d.f.	SS	*F*	*P*	Var. comp (%)
(a) SR, Infralittoral fringe communities					
Sector	3	0·942	9·64	0·001	44·9
Sector:Site	15	0·489	1·85	0·040	23·3
Residuals	38	0·669	0·02		31·9
(b) H′, Infralittoral fringe communities					
Sector	3	0·198	5·82	0·004	36·5
Sector:Site	15	0·170	2·45	0·009	31·3
Residuals	38	0·175	<0·01		32·2
(c) SR, Subtidal communities					
Sector	3	0·778	6·37	0·006	40·9
Sector:Site	15	0·611	3·02	0·005	32·1
Residuals	38	0·512	0·01		26·9
(d) H′, Subtidal communities					
Sector	3	0·196	6·16	0·006	36·4
Sector:Site	15	0·159	2·20	0·030	29·6
Residuals	38	0·183	<0·01		34·0

d.f., degrees of freedom; SS, sum of squares; *F*, *F*-ratio; *P*, *P*-value estimating the significance of *F*-ratios; Var.comp, estimated relative contribution to total variance.

Table 3. Results of additive diversity partitioning from untransformed species richness (SR) and Shannon diversity (H′) comparing simulated statistics under a null model to observed statistics of α and β diversity at three levels of sampling hierarchy (‘quadrat’, ‘site’ and ‘sector’) as well as γ diversity of the entire dataset; all tests used 999 simulations

	Observed statistic	SES	Mean simulated statistic	*P*
(a) SR, Infralittoral fringe communities				
α. quadrat	9·05	−72·30	25·02	0·001
α. site	15·63	−56·61	37·53	0·001
α. sector	33·5	−31·58	52·55	0·001
γ	61·00	0·00	61·00	1·000
β. quadrat	6·58	−16·16	12·49	0·001
β. site	17·87	4·36	15·07	0·015
β. sector	27·50	31·58	8·50	0·001
(b) H′, Infralittoral fringe communities				
α. quadrat	1·55	−91·00	2·66	0·001
α. site	1·88	−89·98	2·90	0·001
α. sector	2·43	−155·69	3·02	0·001
γ	3·03	0·00	3·03	1·000
β. quadrat	0·33	7·89	0·24	0·001
β. site	0·55	38·71	0·11	0·001
β. sector	0·61	155·69	0·02	0·001
(c) SR, Subtidal communities				
α. quadrat	9·81	−63·83	22·36	0·001
α. site	16·53	−47·11	35·10	0·001
α. sector	35·50	−27·12	53·10	0·001
γ	62·00	0·00	62·00	1·000
β. quadrat	6·72	−16·67	13·42	0·001
β. site	18·97	1·34	19·32	0·171
β. sector	26·50	27·12	10·25	0·001
(d) H′, Subtidal communities				
α. quadrat	1·64	−76·16	2·57	0·001
α. site	1·98	−74·74	2·79	0·001
α. sector	2·48	−130·93	2·90	0·001
γ	2·92	0·00	2·92	1·000
β. quadrat	0·34	12·74	0·22	0·001
β. site	0·50	33·42	0·11	0·001
β. sector	0·44	130·93	0·02	0·001

SES, standardised effect sizes of the observed statistic quantifying the size of the difference between expected and observed values; *P*, *P*-value of the statistic based on simulations.

infralittoral fringe as well as for the subtidal zone of which eight are common to the two matrices (Table 1). After a forward selection procedure to retain environmental variables which best explained the variations of the community matrices, 4 out of the 10 previously retained environmental variables were selected for explaining the infralittoral fringe community matrix (i.e. bathymetry, maximum monthly sea surface temperature, maximum monthly wave energy flux and mean annual sea water velocity) and four out of the eight previously retained environmental variables were selected for explaining the subtidal community matrix (i.e. density of *L. hyperborea*, distance to shore, bathymetric slope, annual range in sea surface temperature).

The environmental variables explained a significant proportion of the variation of both the infralittoral fringe community matrix ($R^2 = 0{\cdot}457$, $P = 0{\cdot}001$) and the subtidal community matrix ($R^2 = 0{\cdot}461$, $P = 0{\cdot}001$). The fitted matrix of the infralittoral fringe exhibited two prominent axes representing a total of 83·9% of the total variance, correlating mainly with maximum monthly sea surface temperature ($r = -0{\cdot}79$ for the first axis and $-0{\cdot}58$ on the second axis) and bathymetry ($r = -0{\cdot}29$ for the first axis and $-0{\cdot}52$ on the second axis). Representing a total of 78·0% of the total variance, the first two axes of the subtidal fitted matrix correlated mainly with density of *L. hyperborea* ($r = -0{\cdot}60$ for the first axis and $-0{\cdot}78$ on the second axis) and annual range in sea surface temperature ($r = -0{\cdot}83$ for the first axis and 0·29 on the second axis).

Figures 4–6 show ordination of sites and the associated scalograms of the main ordination axes for the community matrices (Fig. 4), the fitted matrices (Fig. 5) and the residual matrices (Fig. 6). The scalograms for the first two axes exhibited distinct shapes for the infralittoral fringe community matrix and the subtidal community matrix, with variance accumulation in both broad- (axes 1 and 2) and fine-scale (axis 1 only) components for the infralittoral fringe community matrix (Fig. 4a) and accumulation in broad-scale components only for the subtidal community matrix (Fig. 4b). Indeed, the first axis of the infralittoral fringe community matrix exhibited a fine-scale non-random spatial pattern ($R^2_{\text{Max}} = 0{\cdot}53$, $P = 0{\cdot}008$) and an important but nonsignificant broad-scale component ($R^2_{\text{Max}} = 0{\cdot}38$, $P = 0{\cdot}073$) while its second axis showed a broad-scale non-random spatial pattern ($R^2_{\text{Max}} = 0{\cdot}47$, $P = 0{\cdot}007$). In contrast, the main axis of the subtidal community matrix exhibited significantly skewed distributions towards the broad-scale components solely (axis 1: $R^2_{\text{Max}} = 0{\cdot}79$, $P = 0{\cdot}001$; axis 2: $R^2_{\text{Max}} = 0{\cdot}44$, $P = 0{\cdot}023$). These results regarding community matrices signify that community variability is important at both broad and fine scales for infralittoral fringe communities and at broad-scale only for subtidal communities.

Regarding the fitted matrices (Fig. 5), scalograms of the first two axes displayed a broad-scale non-random spatial pattern for both the subtidal fitted matrix (axis 1: $R^2_{\text{Max}} = 0{\cdot}47$, $P = 0{\cdot}011$; axis 2: $R^2_{\text{Max}} = 0{\cdot}68$, $P = 0{\cdot}004$) and the infralittoral fringe fitted matrix (axis 1: $R^2_{\text{Max}} = 0{\cdot}76$, $P = 0{\cdot}001$; axis 2: $R^2_{\text{Max}} = 0{\cdot}37$, $P = 0{\cdot}048$). In addition, the first axis of the infralittoral fringe fitted matrix showed a fine-scale non-random spatial pattern ($R^2_{\text{Max}} = 0{\cdot}47$, $P = 0{\cdot}013$) while the second axis of the subtidal fitted matrix exhibited an important but nonsignificant medium-scale component ($R^2_{\text{Max}} = 0{\cdot}32$, $P = 0{\cdot}109$). These results regarding fitted matrices are similar to those observed for the community matrices and indicate that environmental variables well explain community variability at broad spatial scales for both infralittoral fringe and subtidal communities, and, additionally, at fine-scale for infralittoral fringe communities.

Finally, the scalograms for the first two axes of the residual matrices exhibited distinct patterns for the infralittoral fringe-fitted matrix (Fig. 6a), showing variation accumulated mainly and significantly in broad-scale components (axis 1: $R^2_{\text{Max}} = 0{\cdot}37$, $P = 0{\cdot}046$; axis 2: $R^2_{\text{Max}} = 0{\cdot}52$, $P = 0{\cdot}005$), and the subtidal-fitted matrix (Fig. 6b), displaying variation accumulated in medium-scale components (and only significantly for axis 1: $R^2_{\text{Max}} = 0{\cdot}41$, $P = 0{\cdot}043$). Regarding infralittoral fringe communities, this indicates that a significant broad-scale spatial pattern remained in the data after the effects attributable to the measured environmental variables (mainly a combination of maximum temperature and bathymetry) were partialled out. Regarding subtidal communities, this reveals that a significant medium-scale spatial pattern remained in the data after the broad-scale effects related to the measured environmental variables (mainly temperature range and kelp density) were removed.

Discussion

In marine ecology, the variation in community patterns along the vertical gradient of tidal heights is a long-standing issue (Raffaelli & Hawkins 1996) while its examination along a gradient of multiple spatial scales is more recent and still scarce in major coastal ecosystems such as kelp forests (but see Smale, Kendrick & Wernberg 2011). In this study of kelp-dominated seaweed communities, we sought to understand how the relative roles of stochastic (i.e. ecological drift and limited dispersal) and deterministic (i.e. environmental filtering and biotic interactions) processes in structuring communities vary both along the vertical gradient of tidal heights and across multiple spatial scales. Specifically, we highlight the crucial role of deterministic processes in shaping these communities, we identify environmental correlates of community composition and we show that the scale of variation in community composition differs across tidal heights.

RELATIVE IMPORTANCE OF DETERMINISTIC PROCESSES IN STRUCTURING COMMUNITIES

Our results show that variability in α and β species diversity differed from expectations under a null model at all spatial scales for infralittoral fringe communities, indicating that they are largely shaped by deterministic processes at all scales from the finest (the quadrats, separated by a few metres) to the broadest (the sectors, separated by more than 60 km). The same pattern was observed for subtidal

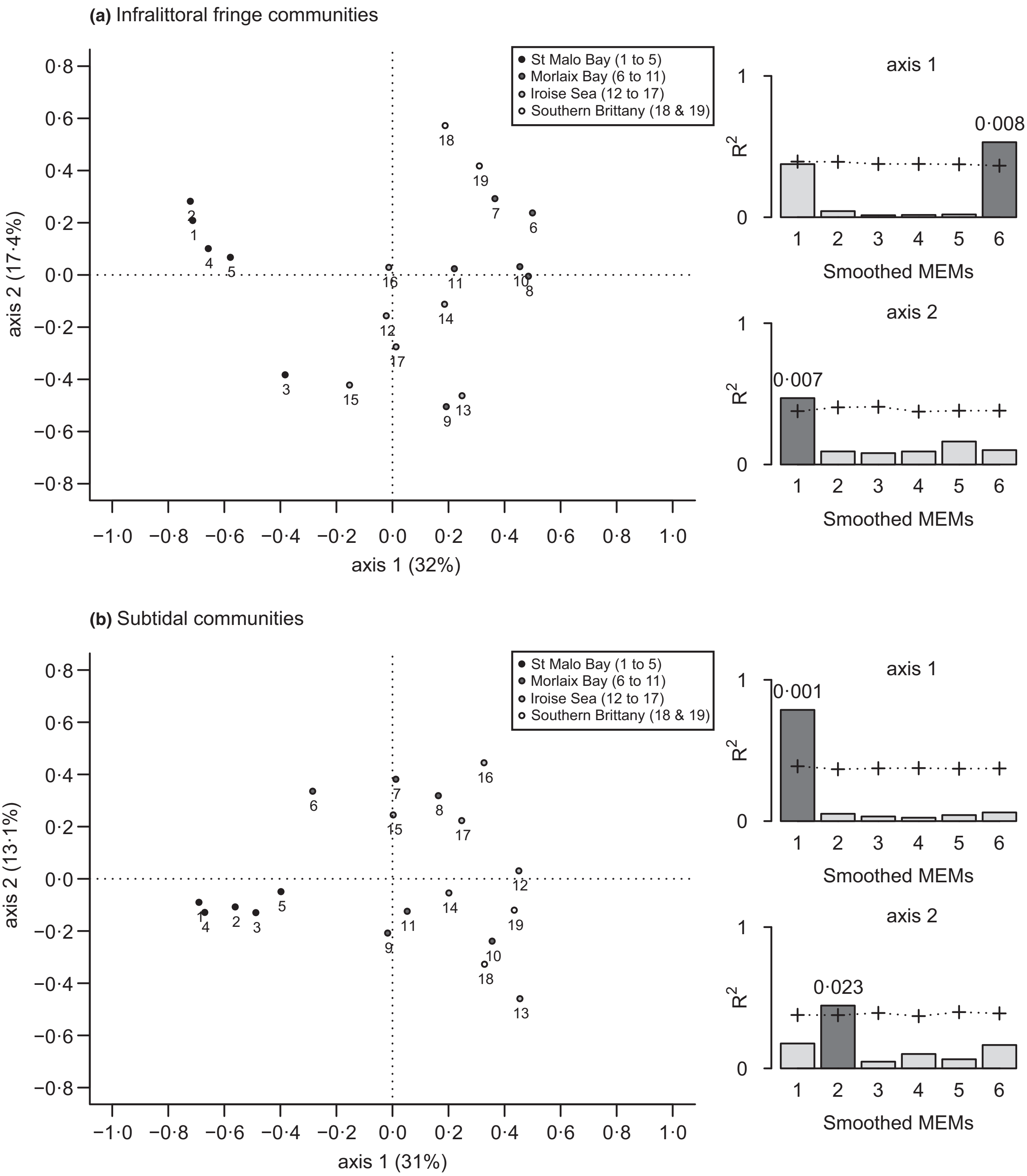

Fig. 4. Plots of site scores on the first two axes of the principal components analyses of site-by-species abundance matrices (a) for infralittoral fringe communities and (b) for subtidal communities. For each score, a smoothed scalogram [the 18 Moran's eigenvector maps (MEMs) are assembled in 6 groups] indicates the portion of variance (R^2) explained by each spatial scale ranked from the broadest to the finest. For each scalogram, the scale corresponding to the highest R^2 (in dark grey) is tested using 999 permutations of the observed values (*P*-values are given). The 95% confidence limit is also represented by the line of plus signs.

communities, except for the variability in β SR which did not differ from null expectations at the intermediate scale of sites (separated by more than 300 m), suggesting that variability in SR between sites can be explained by the action of stochastic processes only. Therefore, the relative importance of deterministic processes in structuring communities appears to be slightly greater in infralittoral fringe communities than in subtidal ones. Such differences might be related to the fact that infralittoral fringe communities inhabit a more disturbed environment than subtidal communities: the prevalence of deterministic processes in disturbed environments has been advocated to explain

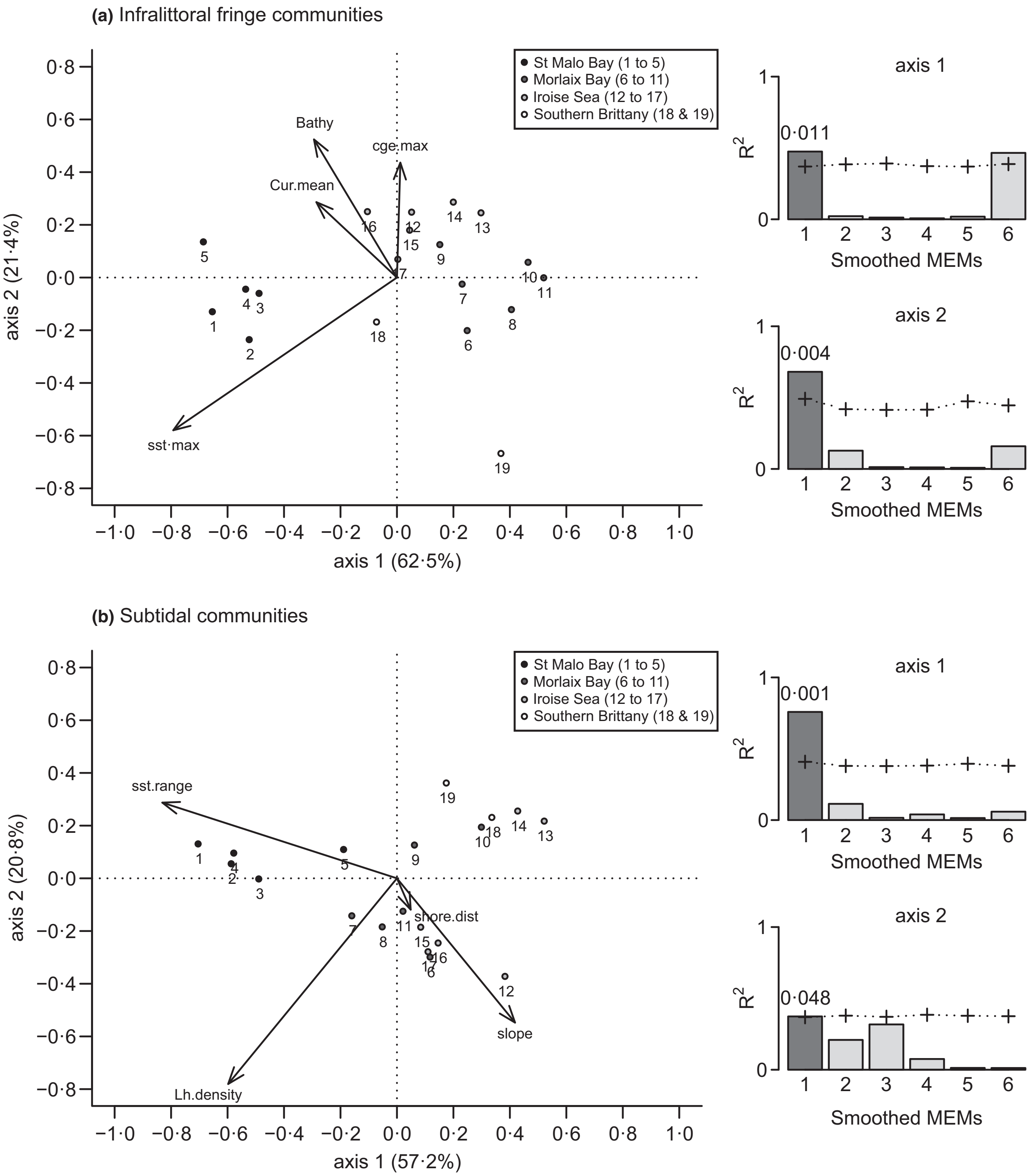

Fig. 5. Plots of site scores on the first two axes of the redundancy analyses using the site-by-environment matrices as predictors (a) for infralittoral fringe communities and (b) for subtidal communities. For each score, a smoothed scalogram [the 18 Moran's eigenvector maps (MEMs) are assembled in 6 groups] indicates the portion of variance (R^2) explained by each spatial scale ranked from the broadest to the finest. For each scalogram, the scale corresponding to the highest R^2 (in dark grey) is tested using 999 permutations of the observed values (*P*-values are given). The 95% confidence limit is also represented by the line of plus signs.

variation in community patterns along a gradient of disturbance in a variety of other organisms (i.e. small freshwater ponds: Chase 2007 and plants: Myers & Harms 2011). Nevertheless, it does not imply that deterministic processes do not structure subtidal communities. In particular, α diversity was lower than expected for the three spatial scales and the two diversity metrics examined. These results suggest that distribution of kelp understorey seaweeds is far from random and may be the result of species-specific factors such as biogeographic history and dispersal ability as well as deterministic processes of environmental filtering and/or biotic interactions.

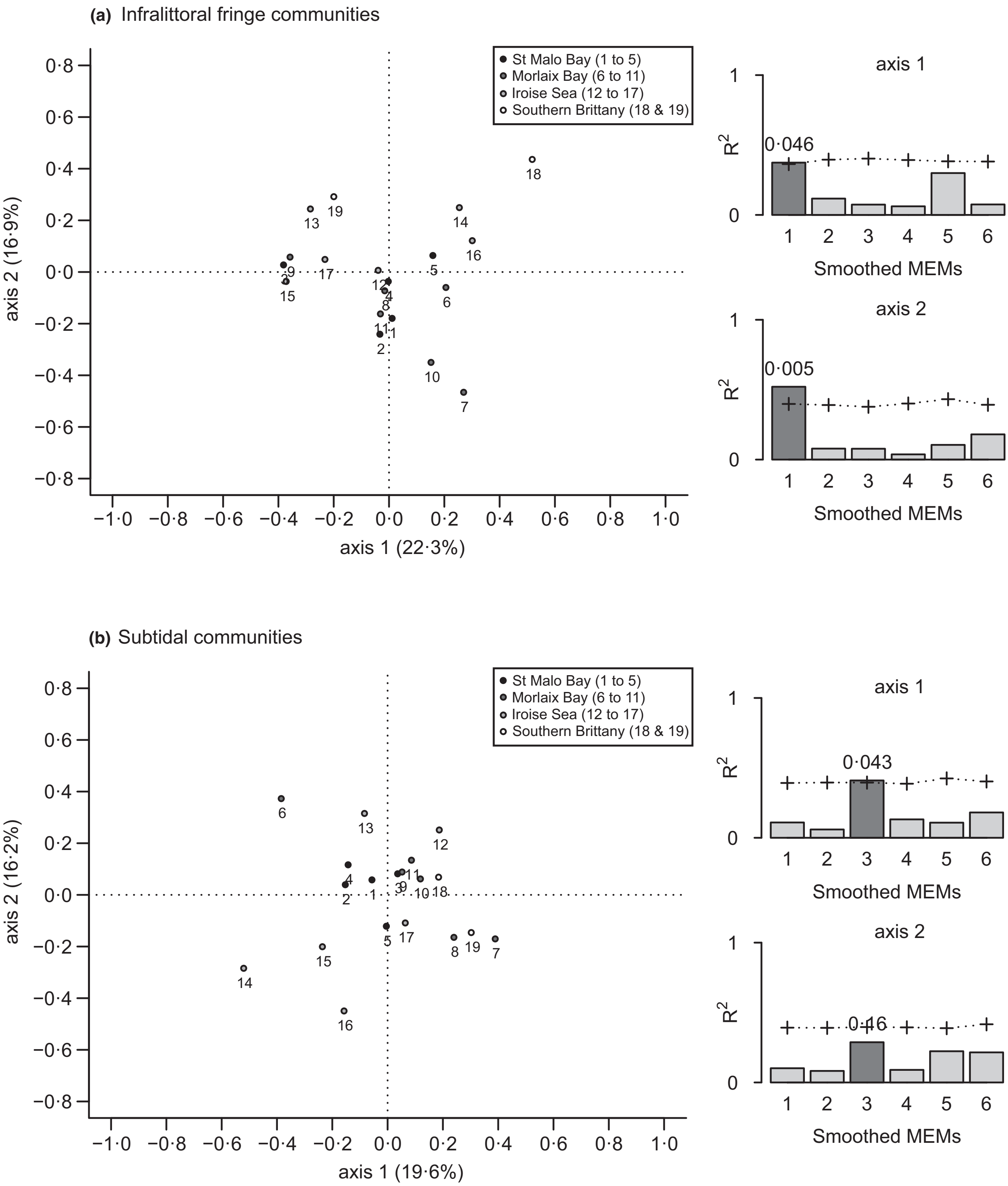

Fig. 6. Plots of site scores on the first two axes of the partial principal component analysis using the site-by-environment matrices as co-variables (a) for infralittoral fringe communities and (b) for subtidal communities. For each score, a smoothed scalogram [the 18 Moran's eigenvector maps (MEMs) are assembled in 6 groups] indicates the portion of variance (R^2) explained by each spatial scale ranked from the broadest to the finest. For each scalogram, the scale corresponding to the highest R^2 (in dark grey) is tested using 999 permutations of the observed values (*P*-values are given). The 95% confidence limit is also represented by the line of plus signs.

ENVIRONMENTAL CORRELATES OF COMMUNITY COMPOSITION

The relative importance of abiotic over biotic variables in driving community composition established from the list of variables retained in our analysis was slightly greater in infralittoral fringe communities compared to subtidal ones: four abiotic variables correlated with composition of infralittoral fringe communities, whereas a combination of one biotic and three abiotic variables correlated with composition of subtidal communities. Community composition was correlated with variables related to sea surface temperature for both infralittoral fringe and subtidal communities. This finding is consistent with previous studies on kelp forests showing that distribution of understorey red seaweeds was mainly driven by annual amplitude in sea surface temperature (Gallon *et al.* 2014) and that large-scale community variation was related to the differences in species temperature affinities (Smale, Kendrick & Wernberg 2011; Derrien-Courtel, Le Gal & Grall 2013). In agreement with recent reports documenting the sensitivity of kelp species (e.g. Pehlke & Bartsch 2008; Oppliger *et al.* 2014) and associated communities (e.g. Gallon *et al.* 2014; Wernberg *et al.* 2016) to rising temperatures, our study therefore suggests that kelp forests would be largely affected by climate change.

Geophysical variables were also correlated with community composition and more specifically bathymetry for infralittoral communities and slope for subtidal ones. These results are not surprising since bathymetry and slope might capture the action of other factors (not included in our study) important for the settlement and growth of sessile organisms. For example, light availability decreases with bathymetry and sediment burying decreases with slope and these two factors have been previously described as influencing the composition of rocky subtidal communities (e.g. Miller & Etter 2008).

Moreover, some variables were correlates of composition for infralittoral fringe communities but not for subtidal ones, and *vice versa*. As such, current and wave energy explained variation in composition for infralittoral fringe communities but not for subtidal ones, a finding which is logical since infralittoral fringe communities are located closer to the sea surface and are therefore more prone to be affected by the action of currents and waves than subtidal communities. A strong hydrodynamism can affect kelp-dominated communities either directly through dislodgement of individual kelps (Wernberg & Connell 2008) or indirectly by modulating herbivores' abundances (Vanderklift, Lavery & Waddington 2009). Furthermore, kelp density explained variation in composition for subtidal communities but not for infralittoral fringe communities. This outcome might reflect an interaction between *L. hyperborea* canopy and its understorey community. Such canopy-understorey interaction can be either competitive or facilitative. Specifically, canopy formers may competitively exclude understorey species by shading their environment and scouring recruits or juveniles or facilitate the recruitment and existence of other species by mitigating physical stress such as hydrodynamic forces (e.g. Kain 1979; Wernberg, Kendrick & Toohey 2005; Bennett & Wernberg 2014). As we recorded lower species diversity in sites characterised by a high kelp density, the canopy–understorey interactions we detected in subtidal communities are likely dominated by competition.

Our results revealed that the measured environmental variables were good correlates of community composition at both broad and fine scale for infralittoral fringe communities, and at broad scale only for subtidal communities; however, significant spatial patterns remained in the data after the effects attributable to the measured environmental variables were partialled out. These remaining significant spatial patterns could be attributed either to unmeasured environmental variables (see the paragraph 'Study limitations and future directions') and/or to stochastic processes such as ecological drift and limited dispersal.

MULTI-SCALE VARIATION IN COMMUNITY COMPOSITION

We found that variation in community composition was concentrated at both fine and broad spatial scales in infralittoral fringe communities, and only at broad spatial scales in subtidal ones. Expected lower dispersal distances in infralittoral fringe than in subtidal communities may contribute to this difference, promoting finer scale variation in community composition in the infralittoral fringe. In accordance to this hypothesis, some studies have shown that genetic connectivity among populations decreased with tidal height for different organisms of rocky shores (e.g. Engel, Destombe & Valero 2004; Kelly & Palumbi 2010; Valero *et al.* 2011), including the two kelps *L. digitata* and *L. hyperborea* (Robuchon *et al.* 2014). Alternatively, our results also indicate that environmental variables were good correlates of community composition at fine scale for infralittoral fringe communities. Thus, fine-scale variability in the composition of infralittoral fringe communities may also be the result of environmental filters acting at a fine scale.

STUDY LIMITATIONS AND FUTURE DIRECTIONS

Our study permitted the identification of environmental correlates of community composition for infralittoral fringe and subtidal communities. Although this work could be refined regarding the identification of variables driving community patterns, our approach allowed us to test the correlation between observed community patterns and a set of environmental variables possibly affecting these patterns. Additional experimental approaches are needed to assess causal relationships among the environmental correlates we identified and community composition. Furthermore, some potentially important variables were not included in our framework: despite being important drivers of seaweed community structure, sea turbidity, nutrient availability and herbivores' abundances were not included because data were not available at a spatial resolution fine enough for our study. Nonetheless, other studies on these omitted variables at a coarser spatial resolution indicate strong differences among regions that might contribute to regional differences in community structure; for instance, sea turbidity is higher in St Malo Bay than in the other three regions (Gohin 2011). This limitation was partially overcome because the geophysical and hydrodynamic variables that we included in our study may influence these omitted variables. Nonetheless, future work investigating environmental drivers of kelp-dominated seaweed communities should include all pertinent variables at the appropriate scale, maybe by doing direct *in situ* measurements when remote sensing data are not available.

Although our outcomes are coherent with individual processes known to vary across a gradient of tidal heights, our study did not permit to identify how these local processes act together to form the patterns we observed, neither to fully understand the interplay between these local processes and biogeographic history of species. A study including all tidal heights from the high intertidal to the subtidal and covering entire biogeographical regions would be very helpful to further characterise how ecological drift, environmental filtering, competition, facilitation and dispersal interact with the biogeographical history of species to shape community patterns along the whole gradient of tidal heights. Yet, even on a set of two neighbour tidal heights, the MEMs framework permitted us to highlight that the nature of environmental correlates and the spatial scale at which they were good correlates of community composition vary across tidal heights. Therefore, this framework seems promising to broaden our understanding of community assembly across other vertical gradients, both in the sea and on land.

Author's contributions

M.R., M.V. and L.L. conceived the ideas and designed methodology; M.R. and L.L. collected the data; M.R. analysed the data; E.T. critically interpreted the first results and contributed to reorient the analyses; M.R. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

Data deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.3s96n (Robuchon *et al.* 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Taxonomic and geographic information on seaweed specimens collected for the study.

Appendix S2. Matrix of pairwise geographic distances among the sites of the study.

Appendix S3. Site-by-environment matrix containing explanatory environmental variables for infralittoral fringe communities.

Appendix S4. Site-by-environment matrix containing explanatory environmental variables for subtidal communities.

Appendix S5. R script to reproduce the analyses using data of Appendices S1–S4, Supporting Information.