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

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18 Running title: Multi-scale community variation in Brittany kelp forests

19 **Summary**

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

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

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

39 4. Seaweed communities were largely shaped by deterministic processes, although
40 the relative importance of deterministic processes was greater for communities of the
41 infralittoral fringe than for subtidal communities. Sea surface temperature and
42 geophysical variables were correlates of community composition at the two tidal

43 heights; additionally, waves and current were correlated with the composition of the
44 communities of the infralittoral fringe while kelp density was correlated with the
45 composition of subtidal communities. Variation in community composition was
46 observed at a finer scale for infralittoral fringe than for subtidal communities.

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

53 **Key-words**

54 Brittany, community composition, determinants of plant community diversity and
55 structure, deterministic and stochastic processes, environmental filtering, kelp,
56 Moran's eigenvector map, multiple spatial scales, seaweed communities, tidal height

57 **Introduction**

58 Understanding how species assemble into communities is a key and highly debated
59 issue in ecology. The structure of communities has been traditionally explained as
60 the result of deterministic processes where species persistence in its environment is
61 determined by abiotic conditions and biotic interactions (Hutchinson 1957; Grime
62 1973; Tilman 1982). In 2001, Hubbell proposed an alternative view: the unified theory
63 of biodiversity and biogeography which considers the structure of communities as the
64 fruit of stochastic processes only (Hubbell 2001). Over the last fifteen years,
65 important efforts have been made to disentangle the relative contribution of
66 deterministic and stochastic processes in shaping community structure, including the
67 proposition of a theoretical framework (Leibold *et al.* 2004; Logue *et al.* 2011). It is
68 now widely recognised that both deterministic (i.e. environmental filtering and biotic
69 interactions) and stochastic processes (i.e. ecological drift and limited dispersal)
70 influence community structure (Leibold & McPeck 2006), however, there is no
71 consensus regarding the relative importance of these two kinds of processes which
72 seem to differ both among different environmental conditions (Chase 2007; Chase &
73 Myers 2011) and across spatial scales (Cottenie 2005; Chase & Myers 2011; Logue
74 *et al.* 2011).

75 The consideration of multiple spatial scales to better understand patterns of
76 biodiversity and processes driving them has therefore become a cornerstone of
77 modern ecology. Indeed, communities are organised at multiple scales and form a
78 network of communities that are connected by dispersal of multiple potentially
79 interacting species called metacommunities (see Leibold *et al.* 2004 for review).
80 Connectivity among communities occur at various rates, depending on both species
81 dispersal abilities and landscape features, and affect the structure of

82 metacommunities in interaction with ecological drift, environmental filtering and biotic
83 interactions. Yet, our knowledge regarding how biodiversity is structured across
84 spatial scales varies greatly among ecosystems: most empirical support comes from
85 research on terrestrial ecosystems, in which dispersal distances are much easier to
86 estimate than in marine ecosystems. In the absence of robust dispersal estimates
87 and considering the fluid characteristics of the ocean, it has long been considered
88 that dispersal rates were greater in the marine realm compared to terrestrial
89 environments (Cowen 2000). However, the recent methodological advances in the
90 study of dispersal pathways and connectivity among marine populations have greatly
91 improved estimates of marine dispersal and challenge the simplicity of this long-
92 standing paradigm. As such, in their review of propagule dispersal in marine and
93 terrestrial environments, Kinlan and Gaines (2003) have shown that marine
94 organisms displayed a huge variety in their mean dispersal distance ranging from a
95 few meters to nearly 1000 kilometres.

96 In cold to temperate waters, rocky subtidal assemblages are dominated by
97 kelps, brown seaweeds which form underwater forests and are of major ecological
98 importance since they provide habitat, food and protection to a myriad of other
99 marine organisms (Dayton 1985; Steneck *et al.* 2002). These kelp forests are one of
100 the most diverse and productive ecosystems worldwide (Mann 1973). Biodiversity
101 patterns of kelp-dominated communities have been described mostly at local scales
102 in different places of the world (e.g. Hawkins & Harkin 1985; Leliaert *et al.* 2000;
103 Christie *et al.* 2003; Graham 2004; Pehlke & Bartsch 2008; Leclerc *et al.* 2015), more
104 rarely at regional scales (Wernberg, Kendrick & Phillips 2003; Derrien-Courtel, Le Gal
105 & Grall 2013; Robuchon *et al.* 2015) but to date, only Smale, Kendrick and Wernberg
106 (2011) looked at these patterns across multiple spatial scales. In their study of the

107 subtidal flora of the south-western Australia coastline, they showed that diversity and
108 turnover of communities varied considerably at all spatial scales, although small
109 scale variability contributed most to total variation. This important small scale
110 variability, a common pattern in rocky shores communities (Fraschetti, Terlizzi &
111 Benedetti-Cecchi 2005), was mainly attributed to the action of waves and habitat
112 heterogeneity while regional scale variability was attributed to climatic factors as most
113 species had cool-water affinities (Smale, Kendrick & Wernberg 2011). Despite
114 providing great insights in the understanding of multi-scale variability of kelp-
115 dominated communities, the study of Smale, Kendrick and Wernberg (2011) did not
116 explicitly address the question of what are the underlying processes that explained
117 the biodiversity patterns they documented. Addressing the relative contribution of
118 deterministic and stochastic processes driving biodiversity patterns of kelp-dominated
119 communities across multiple spatial scales remains an open issue.

120 In recent years, methods to analyse spatial ecological data across different
121 scales have been improved, notably with the emergence of a set of methods now
122 called MEMs (Moran's eigenvector maps, Dray, Legendre & Peres-Neto 2006).
123 These methods can model structures at scales ranging from the broadest down to
124 the finest on the basis of a weighted matrix representing the degree of connection
125 between sampling sites, where the weighted matrix can take several forms from the
126 simplest (a binary matrix: sites are connected or not) to the most geographically
127 realistic (a matrix of geographic distances among sites). A principal coordinates
128 analysis (PCoA) is then performed on the truncated weighted matrix and the resulting
129 eigenvectors that model spatial correlation are used as spatial explanatory variables
130 in canonical ordination (Borcard, Gillet & Legendre 2011). Therefore, the MEMs
131 framework is a way to evaluate the importance of measured explanatory variables in

132 driving community patterns through a gradient of spatial scales as well as to identify
133 significant residual spatial patterns that could arise from the omission of important
134 unmeasured explanatory variables or processes (Dray *et al.* 2012).

135 In this study, our objective was to disentangle drivers of community diversity
136 and composition across multiple spatial scales for kelp-dominated seaweed
137 communities along ca 500 km of the Brittany coastline (France). This region harbours
138 a hot spot of seaweed diversity (Kerswell 2006; Keith, Kerswell & Connolly 2014)
139 and, forms along the European Atlantic coastline a transition zone between two
140 biogeographic provinces, the warm temperate Lusitanian province in the south and
141 the cold temperate Northern European Seas province in the north (Spalding *et al.*
142 2007). We addressed this question in seaweed communities located at two different
143 tidal heights: i) *Laminaria digitata* understory communities, spanning the lower
144 intertidal (i.e. the infralittoral fringe) and upper subtidal zones and ii) *Laminaria*
145 *hyperborea* communities, found in the subtidal zone (i.e. the infralittoral zone). Note
146 that, even if *L. digitata* understory communities are located both in the infralittoral
147 fringe and the upper subtidal zone, they will be referred hereafter as infralittoral fringe
148 communities to facilitate the reading. Based upon these contrasted tidal heights, we
149 can formulate three hypotheses regarding the differences expected between
150 infralittoral fringe communities and subtidal ones in terms of relative importance of
151 deterministic processes, environmental drivers of community composition and
152 propagule dispersal distances (Fig. 1). First, some recent works have suggested that
153 the relative importance of deterministic processes in structuring communities was
154 greater in disturbed compared to undisturbed environment (Chase 2007; Chase &
155 Myers 2011). The intertidal environment experiences frequent changes between
156 immersion and emersion and is exposed to waves; hence it is more disturbed than

157 the subtidal one which is always emerged (Raffaelli & Hawkins 1996). We can
158 therefore hypothesise that the relative importance of deterministic processes in
159 structuring communities is greater in infralittoral fringe communities than in subtidal
160 ones. Second, the relative importance of environmental filters over biotic interactions
161 in structuring littoral communities is known to increase with tidal height (Raffaelli &
162 Hawkins 1996). Therefore, the relative importance of abiotic over biotic variables in
163 driving community composition is expected to be greater (resp. lesser) in infralittoral
164 fringe communities compared to subtidal ones. Finally, third, infralittoral fringe
165 communities are located higher on the vertical gradient of tidal heights than subtidal
166 communities. Consequently, dispersal distances should be lower in these
167 communities because they are less often immersed (which limits the dispersal of
168 propagules in the water column) but most importantly they experience osmotic and
169 thermic stresses during periods of emersion (which stimulate the simultaneous
170 release of propagules at low tides and thus short-distance dispersal, Norton 1992).
171 Such differences in terms of propagule dispersal between the infralittoral fringe and
172 the subtidal zone have recently been evidenced by comparing genetic connectivity of
173 *L. digitata* and *L. hyperborea* populations (Robuchon *et al.* 2014). Therefore,
174 variation in community composition should be observed at a finer spatial scale in
175 infralittoral fringe communities compared to subtidal ones.

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

181 **Materials and methods**

182 *Study area and data sources*

183 To determine the drivers of seaweeds' community structure across spatial scales, we
184 compiled data on floristic composition and environmental variables across 19 sites
185 distributed in four sectors of Brittany (France, Fig. 2). These sectors were chosen
186 because they display distinct features which characterised the environmental
187 heterogeneity of the Brittany coastline: St Malo Bay shows a more irregular
188 topography and is characterised by the presence of cyclonic and anticyclonic gyres
189 that increase the water mass residence times and may affect propagule dispersal
190 (Salomon & Breton 1993), water bodies of Southern Brittany are stratified (Le Fèvre
191 1987) and between these two regions, Iroise Sea and Morlaix Bay form a cold and
192 resilient water pocket (Gallon *et al.* 2014). Floristic composition was assessed during
193 a survey of seaweed diversity conducted in winter 2011 by scuba-diving and
194 targeting the flora living beneath the canopy of *Laminaria digitata* and *L. hyperborea*,
195 which differ by their distributions along the tidal zone: *L. digitata* occupies the
196 infralittoral fringe, between + 1 and – 1 m depth whereas *L. hyperborea* occupies the
197 infralittoral zone between –1 and – 30 m (reviewed by Robuchon *et al.* 2014). This
198 difference in vertical distribution implies that *L. digitata* populations and associated
199 understory communities are sometimes emerged (83 hours over the year 2011 based
200 on the SHOM data - <http://www.shom.fr/> - for the city of Roscoff, in Morlaix Bay)
201 whereas *L. hyperborea* populations and associated understory communities are
202 always underwater. At each site, six quadrats of 0.10 m² were randomly placed
203 among the kelps holdfasts at a few meters of distance (three among *L. digitata* and
204 three among *L. hyperborea*) and sampled for all macroscopic specimens of
205 seaweeds (except crustose seaweeds) present in these quadrats. Then, specimens

206 were sorted by morphotype and identified using the floristic keys and field guides
207 available for the region (Dixon & Irvine 1977; Irvine 1983; Fletcher 1987; Burrows
208 1991; Maggs & Hommersand 1993; Irvine, Chamberlain & Maggs 1994; Brodie &
209 Irvine 2003; Cabioc'h *et al.* 2006). The number of individuals per morphotype within
210 each quadrat was counted, allowing generating one quadrat-by-species and one site-
211 by-species abundance matrices.

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

217 *Hierarchical analyses of diversity indices*

218 Species richness (SR) and Shannon diversity index based on $\log_e(H')$ (Shannon
219 1948) were calculated for the infralittoral fringe communities and the subtidal
220 communities at three spatial scales: sector (4 levels), site (19 levels) and quadrat (57
221 levels). Variability in SR and H' was examined at the different spatial scales with
222 nested analysis of variance (ANOVA) conducted with the R package BiodiversityR
223 (Kindt & Coe 2005). The design was fully hierarchical; sectors were fixed while
224 nested factors were treated as random. As neither SR nor H' fit the assumptions of
225 normality and homogeneity of variance, a dissimilarity matrix based on Bray-Curtis
226 coefficients (Bray & Curtis 1957) derived from untransformed SR and H' (using a
227 dummy variable equal to 1) was generated for the analyses, which used 999
228 permutations.

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

236 *Multivariate spatial analyses*

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

245 We carried out this approach independently for infralittoral fringe communities
246 and for subtidal communities. To that purpose, we considered two initial site-by-
247 species abundance matrices, one for infralittoral fringe communities and one for
248 subtidal communities as well as the two corresponding site-by-environment matrices
249 containing explanatory environmental variables (i.e. the environmental matrices). The
250 environmental matrices were generated by testing correlations among all variables
251 listed in Table 1 and removing variables driving absolute values of pair-wise
252 correlations superior to 0.75 using the R package *caret* (Kuhn & Contributions from

253 Jed Wing 2015). The community matrices were transformed using the Hellinger
254 transformation to put emphasis on abundant species as recommended by Rao
255 (1995). Then, we performed a principal component analysis (PCA) to identify the
256 main patterns in community data.

257 Redundancy analysis (RDA) was conducted to reveal the main structures in
258 community data explained by environmental variables (i.e. analysis of the two fitted
259 matrices) using a forward selection procedure to retain informative environmental
260 variables only, whereas partial residual analysis (PRA) was performed to identify the
261 structures in community data not explained by environmental variables (i.e. analysis
262 of the two residual matrices). To generate the spatial explanatory variables, we
263 conducted a classical distance-based MEMs approach (formally called Principal
264 Coordinates of Neighbour Matrices) following guidelines in Borcard, Gillet and
265 Legendre (2011): i) we computed a matrix of geographic distances among sites using
266 the shortest path by the sea, ii) we truncated the matrix using a distance threshold
267 equal to the maximum distance between two consecutive sites across the coastline,
268 iii) we performed a principal coordinates analysis (PCoA) on the truncated distance
269 matrix and iv) we retained 18 eigenvectors that model spatial correlation as spatial
270 explanatory variables. Scalograms were computed for the community, the fitted and
271 the residual matrices by projecting the sites scores on the first two axes of the
272 different analyses (PCA, RDA, and PRA, respectively) onto the spatial basis formed
273 by the 18 MEMs, therefore representing a partitioning of the respective variances
274 across multiple spatial scales ranked from the broadest to the finest. They are
275 represented in a smoothed version (as in Munoz 2009) with six spatial components
276 formed by groups of three successive MEMs, which is a way to avoid undesired
277 sampling artefacts at fine scales (aliasing effects, Platt & Denman 1975). The

278 individual R^2 values that form the scalograms and correspond to the amount of
279 variation explained by a given scale are expected to be uniformly distributed in the
280 absence of spatial structure (Ollier, Coueron & Chessel 2006). To uncover significant
281 spatial structure, we therefore tested if the maximum observed R^2 was significantly
282 larger than values obtained in the absence of spatial structure using a permutation
283 procedure with 999 repetitions.

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

286 **Results**

287 In total, 5292 specimens corresponding to 69 species were identified from the 57
288 quadrat samples of the infralittoral fringe communities and 5179 specimens
289 corresponding to 68 species were identified from the 57 quadrat samples of the
290 subtidal communities. For both infralittoral fringe and subtidal communities, red
291 seaweeds constituted the most abundant and the most diverse seaweed lineage
292 (respectively 94% and 92% of total abundance/ 78% and 76% of total species
293 richness), followed by brown seaweeds (respectively 3.9% and 7.2% of total
294 abundance/ 14% and 18% of total species richness) and green seaweeds
295 (respectively 0.2% and 0.1% of total abundance/ 5.8% and 4.4% of total species
296 richness).

297 At the scale of sector and for both infralittoral fringe and subtidal communities,
298 species richness (SR) was minimum in St Malo Bay and maximum in Iroise Sea
299 (equally maximum in Morlaix Bay for infralittoral fringe communities, Fig. 3a).
300 Shannon diversity (H') was also minimum in St Malo Bay for both infralittoral fringe
301 and subtidal communities; however, it reached its maximum in Southern Brittany for
302 infralittoral fringe communities and in Morlaix Bay for subtidal communities (Fig. 3b).
303 At the scale of site and for both communities, SR encountered its minimum in site 4
304 (a site in St Malo Bay) and its maximum in site 19 (a site in Southern Brittany), and
305 could be markedly variable among sites within the same sector as reported in Morlaix
306 Bay and Iroise Sea (Fig. 3c). Finally, H' was minimum in sites of St Malo Bay and
307 very variable both among sites and between kelp communities (Fig. 3d). For both
308 infralittoral fringe and subtidal communities, nested ANOVA indicated that both SR
309 and H' were considerably and significantly variable at all spatial scales (Table 2). In
310 all cases, the examination of variance components suggested that the relative

311 importance of fine scale variability (i.e. site and residuals) outweighed that of broad-
312 scale variability (i.e. sector), although the relative importance of broad-scale
313 variability was higher for SR than for H'.

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

320 Regarding the computation of the environmental matrices, 10 out of 32
321 environmental variables were retained for the infralittoral fringe as well as for the
322 subtidal zone of which 8 are common to the two matrices (Table 1). After a forward
323 selection procedure to retain environmental variables which best explained the
324 variations of the community matrices, 4 out of the 10 previously retained
325 environmental variables were selected for explaining the infralittoral fringe community
326 matrix (i.e. bathymetry, maximum monthly sea surface temperature, maximum
327 monthly wave energy flux and mean annual sea water velocity) and 4 out of the 8
328 previously retained environmental variables were selected for explaining the subtidal
329 community matrix (i.e. density of *L. hyperborea*, distance to shore, bathymetric slope,
330 annual range in sea surface temperature).

331 The environmental variables explained a significant proportion of the variation
332 of both the infralittoral fringe community matrix ($R^2 = 0.457$, $P = 0.001$) and the
333 subtidal community matrix ($R^2 = 0.461$, $P = 0.001$). The fitted matrix of the infralittoral
334 fringe exhibited two prominent axes representing a total of 83.9 % of the total

335 variance, correlating mainly with maximum monthly sea surface temperature ($r = -$
336 0.79 for the first axis and -0.58 on the second axis) and bathymetry ($r = -0.29$ for the
337 first axis and -0.52 on the second axis). Representing a total of 78.0% of the total
338 variance, the first two axes of the subtidal fitted matrix correlated mainly with density
339 of *Laminaria hyperborea* ($r = -0.60$ for the first axis and -0.78 on the second axis) and
340 annual range in sea surface temperature ($r = -0.83$ for the first axis and 0.29 on the
341 second axis).

342 Figures 4 to 6 show ordination of sites and the associated scalograms of the
343 main ordination axes for the community matrices (Fig. 4), the fitted matrices (Fig. 5)
344 and the residual matrices (Fig. 6). The scalograms for the first two axes exhibited
345 distinct shapes for the infralittoral fringe community matrix and the subtidal
346 community matrix, with variance accumulation in both broad - (axes 1 and 2) and
347 fine-scale (axis 1 only) components for the infralittoral fringe community matrix (Fig.
348 4a) and accumulation in broad-scale components only for the subtidal community
349 matrix (Fig. 4b). Indeed, the first axis of the infralittoral fringe community matrix
350 exhibited a fine-scale non-random spatial pattern ($R^2_{\text{Max}} = 0.53$, $P = 0.008$) and an
351 important but nonsignificant broad-scale component ($R^2_{\text{Max}} = 0.38$, $P = 0.073$) while
352 its second axis showed a broad-scale non-random spatial pattern ($R^2_{\text{Max}} = 0.47$, $P =$
353 0.007). In contrast, the main axis of the subtidal community matrix exhibited
354 significantly skewed distributions towards the broad-scale components solely (axis 1:
355 $R^2_{\text{Max}} = 0.79$, $P = 0.001$; axis 2: $R^2_{\text{Max}} = 0.44$, $P = 0.023$). These results regarding
356 community matrices signify that community variability is important at both broad and
357 fine scales for infralittoral fringe communities and at broad-scale only for subtidal
358 communities.

359 Regarding the fitted matrices (Fig. 5), scalograms of the first two axes
360 displayed a broad-scale non-random spatial pattern for both the subtidal fitted matrix
361 (axis 1: $R^2_{\text{Max}} = 0.47$, $P = 0.011$; axis 2: $R^2_{\text{Max}} = 0.68$, $P = 0.004$) and the infralittoral
362 fringe fitted matrix (axis 1: $R^2_{\text{Max}} = 0.76$, $P = 0.001$; axis 2: $R^2_{\text{Max}} = 0.37$, $P = 0.048$). In
363 addition, the first axis of the infralittoral fringe fitted matrix showed a fine-scale non-
364 random spatial pattern ($R^2_{\text{Max}} = 0.47$, $P = 0.013$) while the second axis of the subtidal
365 fitted matrix exhibited an important but nonsignificant medium-scale component
366 ($R^2_{\text{Max}} = 0.32$, $P = 0.109$). These results regarding fitted matrices are similar to those
367 observed for the community matrices and indicate that environmental variables well
368 explain community variability at broad spatial scales for both infralittoral fringe and
369 subtidal communities, and, additionally, at fine scale for infralittoral fringe
370 communities.

371 Finally, the scalograms for the first two axes of the residual matrices exhibited
372 distinct patterns for the infralittoral fringe fitted matrix (Fig. 6a), showing variation
373 accumulated mainly and significantly in broad-scale components (axis 1: $R^2_{\text{Max}} =$
374 0.37 , $P = 0.046$; axis 2: $R^2_{\text{Max}} = 0.52$, $P = 0.005$), and the subtidal fitted matrix (Fig.
375 6b), displaying variation accumulated in medium-scale components (and only
376 significantly for axis 1: $R^2_{\text{Max}} = 0.41$, $P = 0.043$). Regarding infralittoral fringe
377 communities, this indicates that a significant broad-scale spatial pattern remained in
378 the data after the effects attributable to the measured environmental variables
379 (mainly a combination of maximum temperature and bathymetry) were partialled out.
380 Regarding subtidal communities, this reveals that a significant medium-scale spatial
381 pattern remained in the data after the broad-scale effects related to the measured
382 environmental variables (mainly temperature range and kelp density) were removed.

383 **Discussion**

384 In marine ecology, the variation of community patterns along the vertical gradient of
385 tidal heights is a longstanding issue (Raffaelli & Hawkins 1996) while its examination
386 along a gradient of multiple spatial scales is more recent and still scarce in major
387 coastal ecosystems such as kelp forests (but see Smale, Kendrick & Wernberg
388 2011). In this study of kelp-dominated seaweed communities, we sought to
389 understand how the relative roles of stochastic (i.e. ecological drift and limited
390 dispersal) and deterministic (i.e. environmental filtering and biotic interactions)
391 processes in structuring communities vary both along the vertical gradient of tidal
392 heights and across multiple spatial scales. Specifically, we highlight the crucial role of
393 deterministic processes in shaping these communities, we identify environmental
394 correlates of community composition and we show that the scale of variation in
395 community composition differs across tidal heights.

396 *Relative importance of deterministic processes in structuring communities*

397 Our results show that variability in α and β species diversity differed from
398 expectations under a null model at all spatial scales for infralittoral fringe
399 communities, indicating that they are largely shaped by deterministic processes at all
400 scales from the finest (the quadrats, separated by a few meters) to the broadest (the
401 sectors, separated by more than 60 km). The same pattern was observed for subtidal
402 communities, except for the variability in β species richness which did not differ from
403 null expectations at the intermediate scale of sites (separated by more than 300 m),
404 suggesting that variability in species richness between sites can be explained by the
405 action of stochastic processes only. Therefore, the relative importance of
406 deterministic processes in structuring communities appears to be slightly greater in

407 infralittoral fringe communities than in subtidal ones. Such differences might be
408 related to the fact that infralittoral fringe communities inhabit a more disturbed
409 environment than subtidal communities: the prevalence of deterministic processes in
410 disturbed environments has been advocated to explain variation in community
411 patterns along a gradient of disturbance in a variety of other organisms (i.e. small
412 freshwater ponds: Chase, 2007 and plants: Myers & Harms, 2011). Nevertheless, it
413 does not imply that deterministic processes do not structure subtidal communities. In
414 particular, α diversity was lower than expected for the three spatial scales and the
415 two diversity metrics examined. These results suggest that distribution of kelp
416 understory seaweeds is far from random and may be the result of species-specific
417 factors such as biogeographic history and dispersal ability as well as deterministic
418 processes of environmental filtering and/or biotic interactions.

419 *Environmental correlates of community composition*

420 The relative importance of abiotic over biotic variables in driving community
421 composition established from the list of variables retained in our analysis was slightly
422 greater in infralittoral fringe communities compared to subtidal ones: four abiotic
423 variables correlated with composition of infralittoral fringe communities whereas a
424 combination of one biotic and three abiotic variables correlated with composition of
425 subtidal communities. Community composition was correlated with variables related
426 to sea surface temperature for both infralittoral fringe and subtidal communities. This
427 finding is consistent with previous studies on kelp forests showing that distribution of
428 understory red seaweeds was mainly driven by annual amplitude in sea surface
429 temperature (Gallon *et al.* 2014) and that large scale community variation was related
430 to the differences in species temperature affinities (Smale, Kendrick & Wernberg
431 2011; Derrien-Courtel, Le Gal & Grall 2013). In agreement with recent reports

432 documenting the sensitivity of kelp species (e.g. Pehlke & Bartsch 2008; Oppliger *et*
433 *al.* 2014) and associated communities (e.g. Gallon *et al.* 2014; Wernberg *et al.* 2016)
434 to rising temperatures, our study therefore suggests that kelp forests would be largely
435 affected by climate change.

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

444 Moreover, some variables were correlates of composition for infralittoral fringe
445 communities but not for subtidal ones, and *vice versa*. As such, current and wave
446 energy explained variation in composition for infralittoral fringe communities but not
447 for subtidal ones, a finding which is logical since infralittoral fringe communities are
448 located closer to the sea surface and are therefore more prone to be affected by the
449 action of currents and waves than subtidal communities. A strong hydrodynamism
450 can affect kelp-dominated communities either directly through dislodgement of
451 individual kelps (Wernberg *et al.* 2008) or indirectly by modulating herbivores'
452 abundances (Vanderklift *et al.* 2009). Furthermore, kelp density explained variation
453 in composition for subtidal communities but not for infralittoral fringe communities.
454 This outcome might reflect an interaction between *L. hyperborea* canopy and its
455 understory community. Such canopy-understory interaction can be either competitive
456 or facilitative. Specifically, canopy formers may competitively exclude understory

457 species by shading their environment and scouring recruits or juveniles or facilitate
458 the recruitment and existence of other species by mitigating physical stress such as
459 hydrodynamic forces (e.g. Kain 1979; Wernberg, Kendrick & Toohy 2005; Bennett &
460 Wernberg 2014). As we recorded lower species diversity in sites characterised by a
461 high kelp density, the canopy-understory interactions we detected in subtidal
462 communities are likely dominated by competition.

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

471 *Multi-scale variation in community composition*

472 We found that variation in community composition was concentrated at both fine and
473 broad spatial scales in infralittoral fringe communities, and only at broad spatial
474 scales in subtidal ones. Expected lower dispersal distances in infralittoral fringe than
475 in subtidal communities may contribute to this difference, promoting finer scale
476 variation in community composition in the infralittoral fringe. In accordance to this
477 hypothesis, some studies have shown that genetic connectivity among populations
478 decreased with tidal height for different organisms of rocky shores (e.g. Engel,
479 Destombe & Valero 2004; Kelly & Palumbi 2010; Valero *et al.* 2011), including the
480 two kelps *L. digitata* and *L. hyperborea* (Robuchon *et al.* 2014). Alternatively, our

481 results also indicate that environmental variables were good correlates of community
482 composition at fine scale for infralittoral fringe communities. Thus, fine-scale
483 variability in the composition of infralittoral fringe communities may also be the result
484 of environmental filters acting at a fine scale.

485 *Study limitations and future directions*

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

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

520 **Author's Contributions**

521 MR, MV and LL conceived the ideas and designed methodology; MR and LL
522 collected the data; MR analysed the data; ET critically interpreted the first results and
523 contributed to reorient the analyses; MR led the writing of the manuscript. All authors
524 contributed critically to the drafts and gave final approval for publication.

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537 **Data accessibility**

538 Data deposited in the Dryad repository: doi:10.5061/dryad.3s96n

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

Name (abbreviation)	Description (units)	Type (resolution)	Source
Density of <i>Laminaria digitata</i> (Ld.density) ‡	Density of <i>L. digitata</i> individuals (semi-quantitative measure ranging from 1 (low density) to 4 (high density))	<i>In-situ</i> measure	This study
Density of <i>Laminaria hyperborea</i> (Lh.density) ¶	Density of <i>L. hyperborea</i> individuals (semi-quantitative measure ranging from 1 (low density) to 4 (high density))	<i>In-situ</i> measure	This study
Bathymetry (bathy)	Depth of the seafloor (meters)	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 (kilometres)	Derived from remotely sensed shoreline (30 arc-second)	MARSPEC*
Bathymetric slope (slope) ‡ ¶¶	Slope of the seafloor (degrees)	Derived from remotely sensed bathymetry (30 arc-second)	MARSPEC*
Concavity	Slope of the bathymetric slope	Derived from remotely sensed	MARSPEC*

(conrav)	(degrees)	bathymetry	
		(30 arc-second)	
Mean annual SSS (sss.mean)	Mean sea surface salinity averaged over the period 1955-2006 (psu)	Derived from <i>in-situ</i> 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 <i>in-situ</i> measures (30 arc-second)	MARSPEC*
Maximum monthly SSS (sss.max)	Salinity of the saltiest month averaged over the period 1955-2006 (psu)	Derived from <i>in-situ</i> 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 <i>in-situ</i> measures (30 arc-second)	MARSPEC*
Annual variance in SSS (sss.var)	Annual variance in sea surface salinity averaged over the period 1955-2006	Derived from <i>in-situ</i> measures (30 arc-second)	MARSPEC*

	(psu)		
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-calmer 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

Number of CGE extreme measures within the 3 months preceding the floristic survey (cge.next.3months)	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-caldest 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	Derived from model outputs in HOMERE database †	This study

	(m. s ⁻¹)	(value from the nearest node)	
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.3months)	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

746 **Table 2.** Results of nested ANOVA for factor “site” nested in factor “sector” based on
 747 Bray-Curtis dissimilarity coefficients derived from untransformed species richness
 748 (SR) and Shannon diversity (H') using a dummy variable equal to 1; all tests used
 749 999 permutations

	Df	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

750 Df = degrees of freedom, SS = sum of squares, F = F-ratio, P = p-value estimating
 751 the significance of F-ratios; Var.comp = estimated relative contribution to total
 752 variance

753

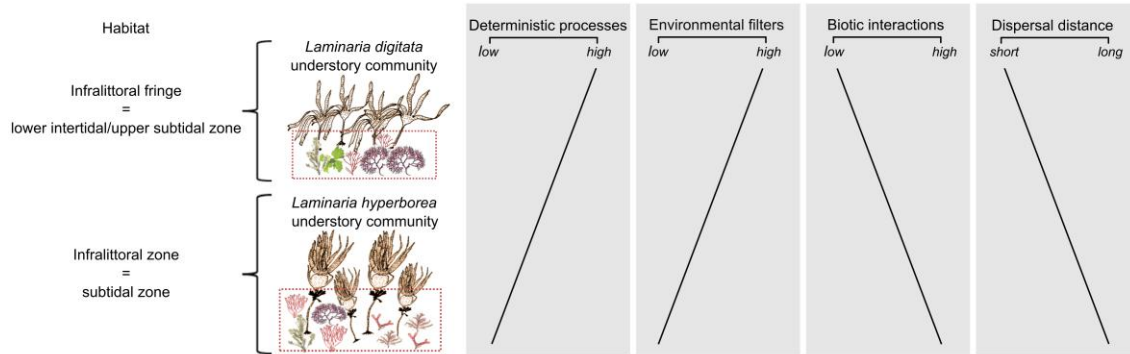
754 **Table 3.** Results of additive diversity partitioning from untransformed species
755 richness (SR) and Shannon diversity (H') comparing simulated statistics under a null-
756 model to observed statistics of α and β diversity at three levels of sampling hierarchy
757 ("quadrat", "site" and "sector") as well as γ diversity of the entire dataset; all tests
758 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

759 SES = standardised effect sizes of the observed statistic quantifying the size of the
760 difference between expected and observed values, P = p-value of the statistic based
761 on simulations

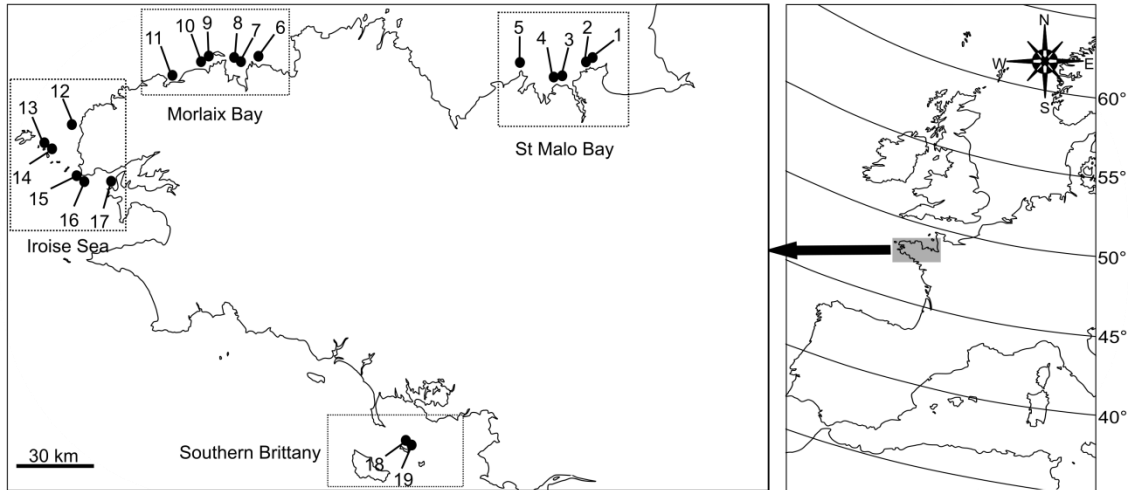
762 **Figures**



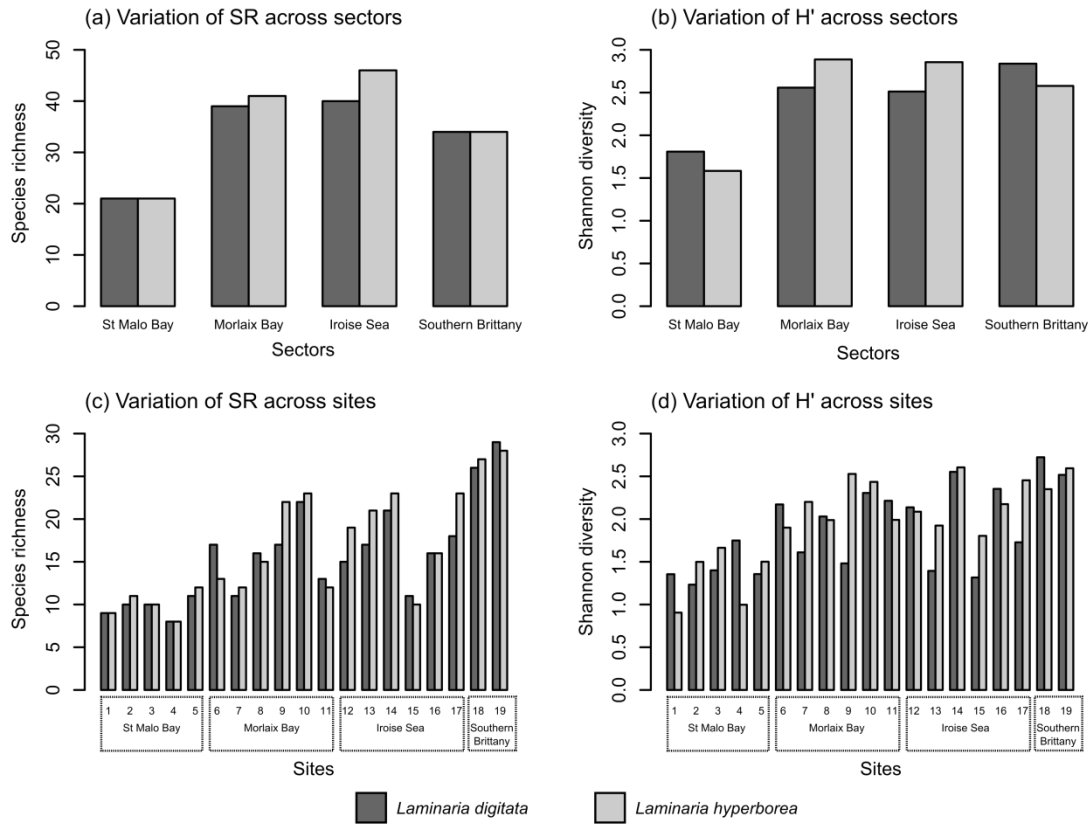
763

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

767

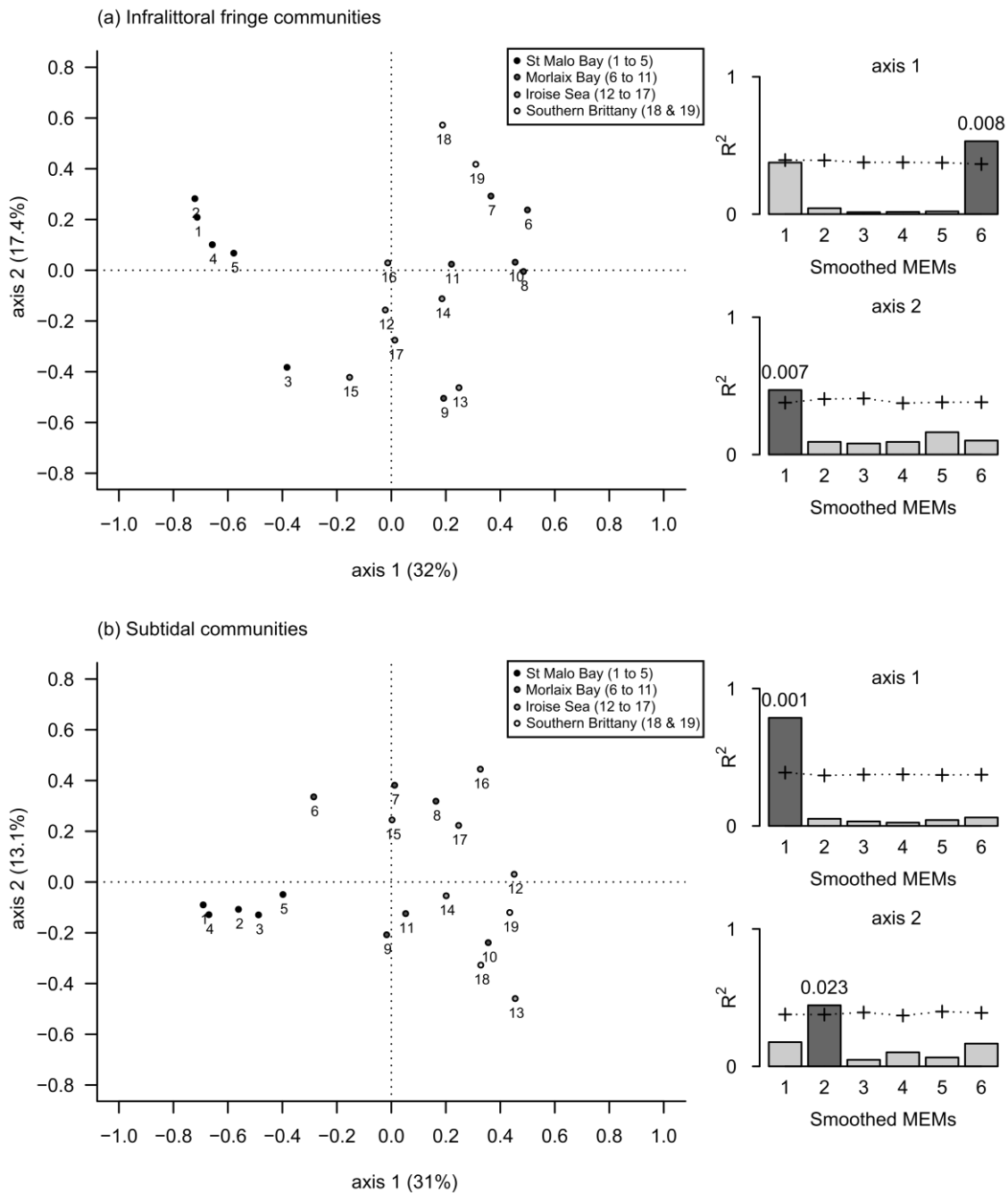


768 **Fig. 2.** Map showing the 19 sampling sites distributed in the four sectors along the
769 Brittany coastline, France. Sites are: Guimereux (1), La Bigne (2), Nerput (3), Le
770 Moulin (4), Les Amas du Cap (5), Primel (6), Duons Est (7), Duons Ouest (8), Santec
771 2 (9), Santec 1 (10), Les Amiettes (11), Les Linious (12), Men Vriant (13), Klosenn
772 Malaga (14), Les Rospects (15), St Mathieu (16), Pointe du Grand Gouin (17), Houat
773 2 (18) and Houat 1 (19). For site coordinates, see Appendix S1.



774

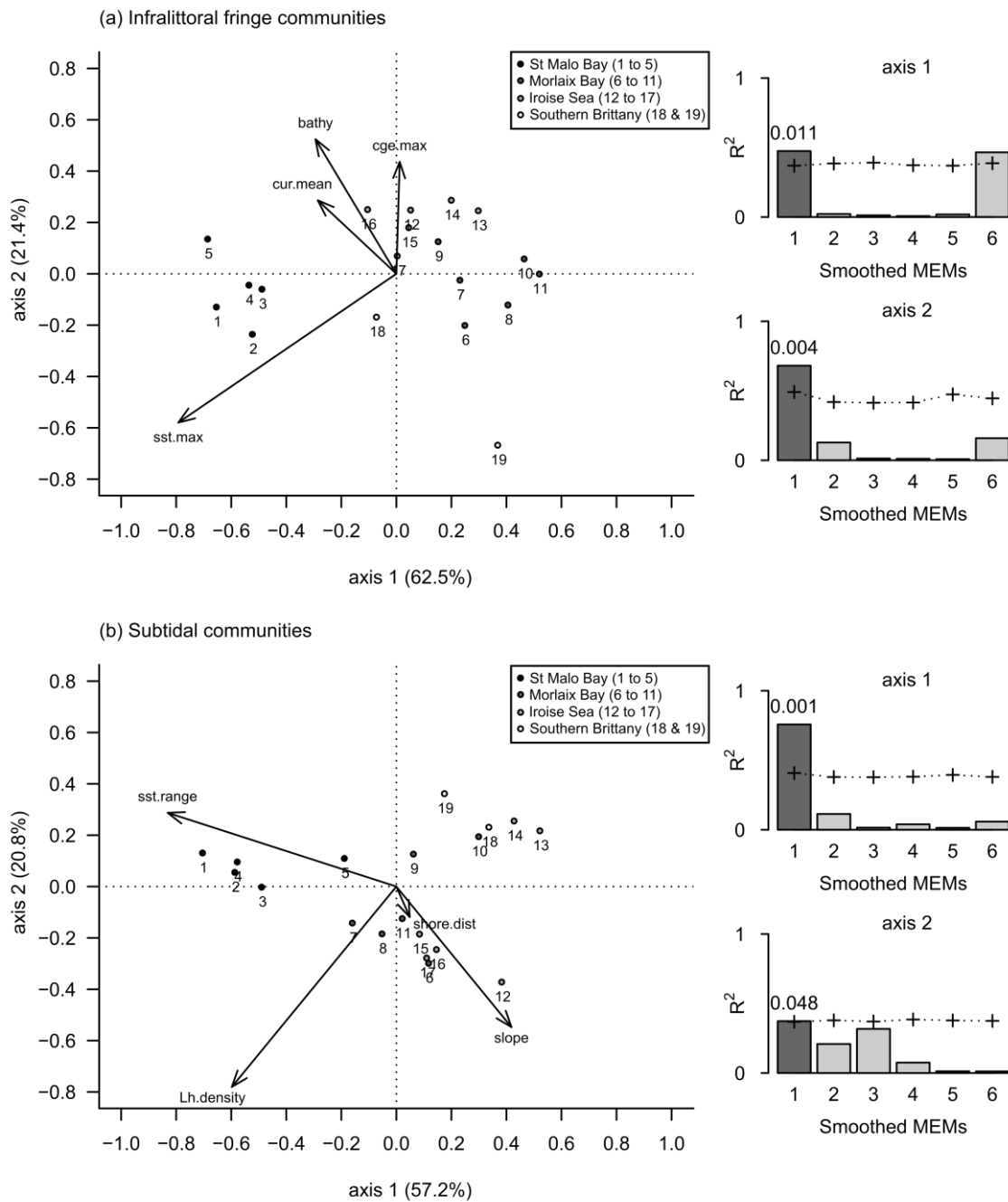
775 **Fig. 3.** Comparison of species diversity estimates between infralittoral fringe
 776 communities and subtidal communities across space. (a) Species richness (SR) by
 777 sector, (b) Shannon diversity (H') by sector, (c) SR by site and (d) H' by site. For site
 778 names, see Fig. 2.



779

780 **Fig. 4.** Plots of site scores on the first two axes of the principal components analyses
 781 of site-by-species abundance matrices (a) for infralittoral fringe communities and (b)
 782 for subtidal communities. For each score, a smoothed scalogram (the 18 Moran's
 783 eigenvector maps [MEMs] are assembled in 6 groups) indicates the portion of
 784 variance (R^2) explained by each spatial scale ranked from the broadest to the finest.
 785 For each scalogram, the scale corresponding to the highest R^2 (in dark gray) is

786 tested using 999 permutations of the observed values (P values are given). The 95%
787 confidence limit is also represented by the line of plus signs.

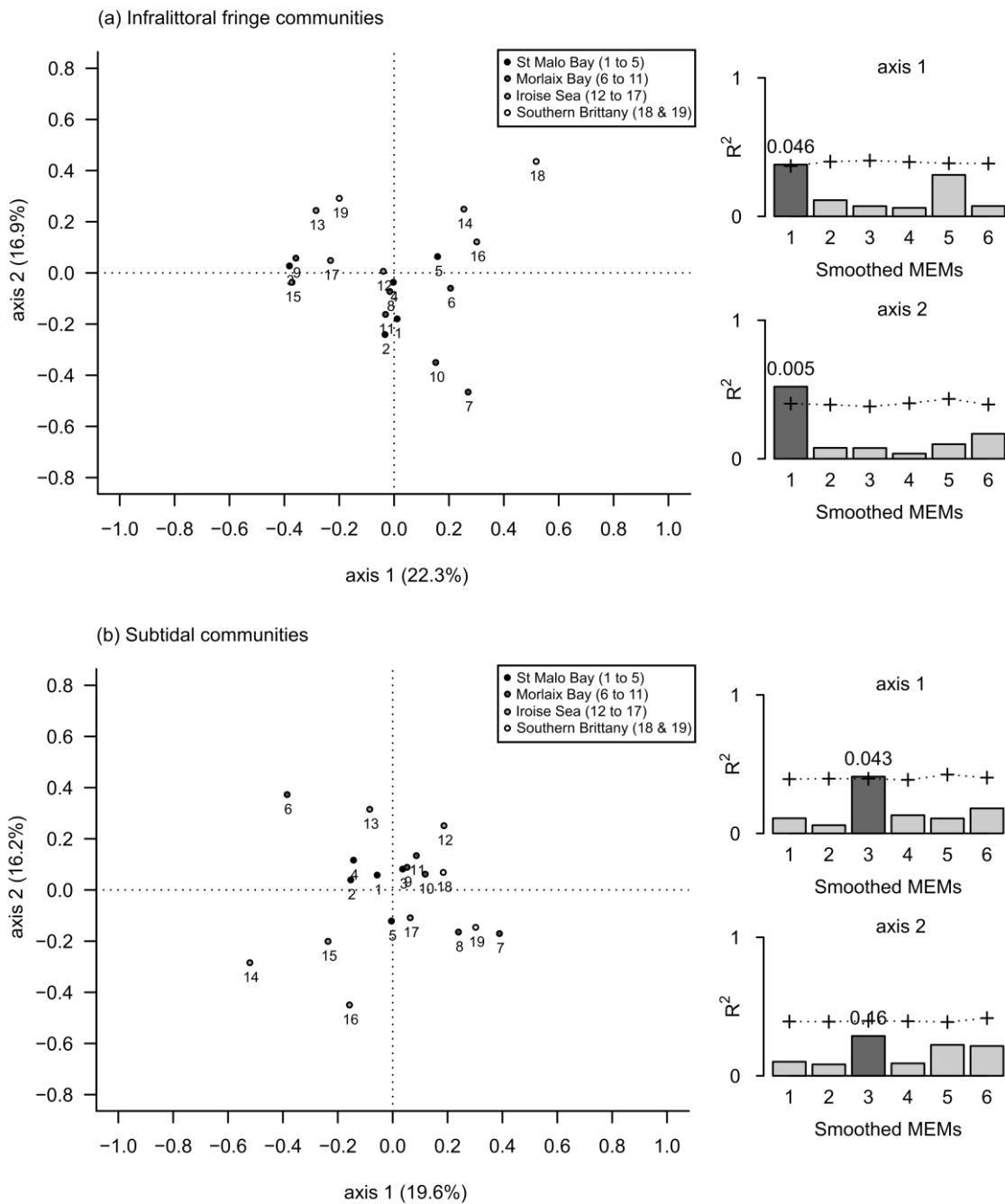


788

789 **Fig. 5.** Plots of site scores on the first two axes of the redundancy analyses using the
 790 site-by-environment matrices as predictors (a) for infralittoral fringe communities and
 791 (b) for subtidal communities. For each score, a smoothed scalogram (the 18 Moran's
 792 eigenvector maps [MEMs] are assembled in 6 groups) indicates the portion of
 793 variance (R^2) explained by each spatial scale ranked from the broadest to the finest.
 794 For each scalogram, the scale corresponding to the highest R^2 (in dark gray) is

795 tested using 999 permutations of the observed values (P values are given). The 95%
796 confidence limit is also represented by the line of plus signs.

797



798

799 **Fig. 6.** Plots of site scores on the first two axes of the partial principal component
 800 analysis using the site-by-environment matrices as co-variables (a) for infralittoral
 801 fringe communities and (b) for subtidal communities. For each score, a smoothed
 802 scalogram (the 18 Moran's eigenvector maps [MEMs] are assembled in 6 groups)
 803 indicates the portion of variance (R^2) explained by each spatial scale ranked from the
 804 broadest to the finest. For each scalogram, the scale corresponding to the highest R^2

805 (in dark gray) is tested using 999 permutations of the observed values (P values are
806 given). The 95% confidence limit is also represented by the line of plus signs.

807 **Supporting information**

808 Additional Supporting Information may be found in the online version of this article:

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

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

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

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

816 **Appendix S5.** R script to reproduce the analyses using data of Appendices S1 to S4