

1 **Matrix composition and patch edges influence plant-**
2 **herbivore interactions in marine landscapes**

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18

19 **Abstract**

20 1. The functioning of ecosystems can be strongly driven by landscape attributes.
21 Despite its importance, however, our understanding of how landscape influences
22 ecosystem function derives mostly from species richness and abundance patterns, with
23 few studies assessing how these relate to actual functional rates.

24 2. We examined the influence of landscape attributes on the rates of herbivory in
25 seagrass meadows, where herbivory has been identified as a key process structuring
26 these relatively simple systems. The study was conducted in three representative
27 *Posidonia oceanica* meadows. The principal herbivores in these meadows are the fish
28 *Sarpa salpa* and the sea urchin *Paracentrotus lividus*, and we hypothesised that
29 differences in their interaction with landscape attributes would significantly influence
30 herbivory rates.

31 3. We measured herbivore abundance, herbivory rates, primary production and plant
32 quality (C:N) in seagrass patches embedded either in rock or in sand (matrix attribute),
33 in patches either near or far from a rocky reef (distance attribute) and at the edges and
34 interior of meadows.

35 4. Our results show that matrix and meadow edges significantly affected the actual
36 levels of herbivory. Herbivory rates were higher in seagrass patches embedded in a
37 rocky matrix compared to those on sand, and herbivory at the centre of seagrass
38 meadows was higher than at the edges. In contrast, patch distance to rocky reefs did not
39 affect herbivory. Neither herbivore abundance nor food quality explained the patterns
40 across different landscape attributes. This suggests that variation in herbivory across the
41 landscape may be related much more to behavioural differences between species in their
42 evaluation of risk, movement, and food preference in relation to the landscape structure.

43 5. Our results indicate that richness and abundance patterns may mask critical
44 interactions between landscape attributes and species responses, which result in
45 considerable heterogeneity in the way key functional processes like herbivory are
46 distributed across the ecosystem mosaic.

47

48 **Key-words:** behaviour; ecosystem function; Mediterranean; movement;
49 *Paracentrotus lividus*; *Posidonia oceanica*; *Sarpa salpa*; seagrass; seascape.

50

51 **Introduction**

52 Landscape often exerts a strong influence on the functioning of systems, and can
53 mediate population structure, community composition and a range of ecosystem
54 processes (Pickett & Cadenasso 1995). Traditionally, most landscape studies have
55 focused on assessing the influence of landscape attributes on species distribution,
56 abundance or richness (Diekötter *et al.* 2007). In contrast, far fewer studies have
57 focused on the effects of these attributes on ecosystem processes, functions or indirect
58 interactions (but see Andren & Angelstam 1988; Cronin 2003; Diekötter *et al.* 2007;
59 Macreadie, Geraldi & Peterson 2012) with most studies assuming that species richness
60 and abundance patterns are a reasonable proxy for functional processes (Valladares,
61 Salvo & Cagnolo 2006). It is unclear if this critical assumption is always valid
62 particularly when species with very different behaviours and life histories together
63 contribute to a single ecosystem function.

64

65 Few processes are as ubiquitous and central to ecosystem functioning as herbivory
66 (Burkepile 2013), regulating rates of primary production and nutrient cycling (Abbas *et*
67 *al.* 2012; Gera *et al.* 2013), influencing species interactions (Pringle *et al.* 2007; Pagès

68 *et al.* 2012) and being a strong determinant of community composition, diversity and
69 biomass (Knapp *et al.* 1999) among others. As a process, herbivory is known to be
70 highly affected by the landscape mosaic (e.g. Diekötter *et al.* 2007; Haynes & Crist
71 2009), but our understanding of the influence of landscape attributes on herbivores'
72 activity has been drawn mostly from indirect evidence such as herbivore abundance or
73 distribution (e.g. Diekötter *et al.* 2007) or visual assessments of damaged tissues (e.g.
74 Thies, Steffan-Dewenter & Tschardtke 2003). There is compelling evidence that
75 herbivores do not distribute randomly across the habitat mosaic, and often concentrate
76 or disperse in space as a function of the landscape configuration, potentially generating
77 spatial heterogeneity in herbivory function (Pickett & Cadenasso 1995; Vergés *et al.*
78 2011). This is due, in part, to species-specific perception abilities (Thies *et al.* 2003). In
79 addition, different herbivores may interact with landscapes at very different scales
80 (Dunning, Danielson & Pulliam 1992), according to their degree of mobility (Ricketts
81 2001).

82

83 Mobile generalist herbivores may make foraging choices based on their social
84 behaviour (e.g. McNaughton 1984; Black *et al.* 1992) or based on specific patch
85 properties: choosing foraging locations as a function of patch resource availability (i.e.
86 patch size, MacArthur & Pianka 1966), food quality (i.e. high-quality, less-defended
87 patches are expected to be preferred; Haynes & Cronin 2004), predation risk (the so-
88 called landscape of fear; e.g. Brown & Kotler 2004). In addition, the matrix within
89 which the patch is embedded (i.e. the landscape) may also influence foraging decisions.
90 Generalist mobile herbivores have been shown to choose landscapes where their focal
91 habitat is embedded in a matrix with other complementary or supplementary diet

92 elements (i.e. complementation or supplementation hypotheses, Dunning *et al.* 1992;
93 Haynes, Diekötter & Crist 2007).

94

95 In contrast, low-mobility herbivores likely respond to landscape features very
96 differently. They are much more prone to be affected by the presence of edges, which
97 may be a barrier for their movement (Ricketts 2001). In these cases, patch-specific
98 patterns may dominate, and recruitment-mortality processes within the patch may
99 become the main driver of herbivore abundance and eventually of herbivory pressure.

100 Indeed, herbivores may either aggregate in areas close to habitat edges (e.g. Haynes &
101 Cronin 2003) or avoid them, as predation is known to be more intense at the edges of
102 habitats than in the centre (e.g. Andren & Angelstam 1988), both mechanisms
103 generating potential edge-related heterogeneities. However, if edges are more
104 permeable (i.e. soft edges, e.g. between two types of vegetated areas) low-mobility
105 herbivores may be able to move between areas, and their choices and foraging
106 behaviour may be influenced by similar factors as mobile herbivores (see previous
107 paragraph). Again, the composition of the matrix has been shown to be crucial in
108 determining how edges will be perceived (Cronin 2003; Haynes & Cronin 2003). If the
109 matrix habitat contrasts strongly with the patch habitat, edges may be perceived as hard,
110 thus inhibiting migration; conversely, less contrasting matrix types, with similar
111 structure to patch habitat, may favour softer patch edges (i.e. low contrast), with higher
112 permeability (Stamps, Buechner & Krishnan 1987). These factors will influence the
113 movement and abundance-distribution patterns of low mobility herbivores thus
114 affecting the processes they contribute to within focal habitat patches (Haynes & Cronin
115 2003; Haynes & Cronin 2006).

116

117 Underwater landscapes in the coastal zone (seascapes), like many other linear habitats
118 (riverine ecosystems, mountain ridges, among others), are characterised by being
119 relatively small patches of habitat isolated from each other by matrices of a different
120 nature and with a tendency of being miniaturized (Goodsell, Chapman & Underwood
121 2007). This makes them ideal candidates to study ecosystem processes at a scale that is
122 relevant for the landscape. However, seascapes have specific features that make them
123 unique. They are generally more connected than terrestrial systems, and potentially less
124 affected by barriers, particularly during larval and dispersal phases (Tanner 2006).
125 However, many shallow-water systems have significant hard edges which become
126 particularly important for adult life stages of animals with restricted movement (e.g.
127 echinoderms, Hereu 2005).

128

129 Seagrass meadows are a common nearshore vegetated ecosystem, frequently
130 interspersed with rock or sandy habitats and with a propensity to form differently sized
131 patches, specially in shallow coastal waters (i.e. 0-10 m). They create a seascape mosaic
132 that raises critical questions of how ecological functions are distributed across the
133 habitat. It is known that seagrass patch size influences within-patch species richness and
134 abundance (e.g. MacReadie *et al.* 2009), that patches embedded in different matrices
135 display contrasting species abundances (e.g. Tanner 2006), that edges can modify
136 within-patch species abundance and distribution (Smith *et al.* 2010), and that seagrass
137 patches display shorter canopies near coral reefs than away from them (Valentine *et al.*
138 2007). More recently, ecosystem processes, such as primary production and nutrient
139 cycling have also been observed to change as a result of seagrass patch size (Gera *et al.*
140 2013), and specifically, herbivory increases with the reduction of the meadow size
141 (Prado *et al.* 2008). However, studies dealing with the effects of landscape attributes on

142 seagrass ecosystem processes are scarce, and those assessing the effects of landscape
143 attributes other than patch size, on seagrass functioning are, to our knowledge, very
144 limited.

145

146 We take advantage of a relatively simple plant-herbivore system with one primary
147 producer (the Mediterranean endemic seagrass *Posidonia oceanica*) and its two
148 dominant consumers, a fish and an echinoderm. Both are generalists and interact
149 strongly between them (Pagès *et al.* 2012). They also show very different adult
150 mobility patterns, which we expect to be highly influenced by landscape configuration,
151 with consequences for how their rates of herbivory are distributed across the mosaic. In
152 this study we examined if landscape configuration could drive patterns of herbivory by
153 these two herbivores across the meadow. Specifically, we assessed actual levels of
154 herbivory of each herbivore in (i) seagrass patches embedded either in rock or in sand
155 matrices (hereafter matrix attribute), (ii) seagrass patches embedded in a sand matrix,
156 either near or far from rocky reefs (hereafter distance attribute) and (iii) at the centre
157 and edges of seagrass meadows bordered on one side with rock (rock edge) and on the
158 other with sand (sand edge; hereafter edge attribute) (Fig. 1). Additionally, we evaluated
159 plant production and nutrients in each of these patches to test if forage quality
160 differences could help explain observed patterns of herbivory across the seagrass
161 mosaic.

162

163 **Materials and Methods**

164 *Study system*

165 *Posidonia oceanica* (L.) Delile is a habitat-forming seagrass whose meadows,
166 considered among the most productive communities in the Mediterranean (Cebrian et al

167 1996), provide shelter, food or substrate to a large diversity of species (Francour 1997).
168 This seagrass typically grows as patchy meadows, specially in shallow areas, and can be
169 found growing either between rocky substrates (i.e. embedded within a rock matrix) or
170 in sandy areas (i.e. embedded within a sand matrix). The macroherbivore guild is
171 limited in this system, with just two key species responsible for the bulk of the
172 herbivory: the sparid fish *Sarpa salpa* (L.) and the sea urchin *Paracentrotus lividus*
173 (Lam.) (Tomas, Turon & Romero 2005). Both are generalist herbivores and can have
174 significant impacts on macrophyte communities, consuming on average more than 40%
175 of seagrass leaf production (Prado *et al.* 2007). The activity of both species peaks
176 during summer months and is concentrated in the upper infralittoral zone (Prado *et al.*
177 2007).

178

179 The sparid *S. salpa* is a roving herbivore with home ranges that often span several
180 hectares (Jadot *et al.* 2006; Pagès *et al.* in press). It is a generalist capable of connecting
181 distant habitats (several kilometres apart, Pagès *et al.* in press). Adults tend to prefer
182 seagrass leaves (but they also feed frequently on macroalgae) while juveniles typically
183 consume macroalgae (Verlaque 1990). It travels in large shoals of hundreds of
184 individuals, and has few (if any) extant predators. In contrast, the sea urchin *P. lividus*
185 displays a considerably restricted movement pattern (average distance from initial
186 position after 3 months = 1.5 m, Hereu 2005), and generally do not cross sandy areas
187 (Dance 1987). The *P. lividus* diet is also varied, and includes different species of
188 macroalgae, as well as seagrass leaves. In addition, both adults and the juveniles of this
189 species are highly preyed by a wide variety of fishes (Sala 1997). Given that *S. salpa*
190 and *P. lividus* are the only important herbivores in Western Mediterranean seagrass
191 meadows, these differences in movement, behaviour and predation risk may determine

192 their ability to forage in different landscape configurations and may influence their
193 overall impacts on the ecosystem.

194

195 *Field design*

196 To assess the importance of different seascape attributes (matrix, distance to
197 neighbouring habitats and matrix dependent edge effects) in determining herbivory rates
198 we selected three shallow *P. oceanica* seagrass meadows (5-8 m depth) with similar
199 seascape configurations. The sites, separated by few kilometres, are situated along the
200 northern Catalan coast (NW Mediterranean). At each site, we tested the influence of
201 seascape attributes on actual herbivory rates. For the matrix attribute we selected eight
202 seagrass patches of similar sizes (mean size = $5.1 \pm 0.9 \text{ m}^2$) embedded in two different
203 matrices: 4 patches in 'rock' and 4 patches in 'sand' (Fig. 1a). For the distance attribute,
204 we selected another set of eight seagrass patches of similar sizes (mean size = 4.1 ± 0.5
205 m^2) all embedded in a sand matrix, either 'near' (4 patches, mean distance from a rocky
206 reef = $5.6 \pm 0.7 \text{ m}$) or 'far' from a rocky reef (4 patches, mean distance from a rocky
207 reef = $23.1 \pm 2 \text{ m}$) (Fig. 1b). For the edge attribute, we selected 15 zones (approx. 5 m^2)
208 within a continuous meadow at 3 locations: 5 at the centre of the meadow, 5 at edges
209 bordered with rock ('rock edge') and 5 at edges bordered with sand ('sand edge') (Fig.
210 1c). At each of the selected patches (or zones) we measured total herbivory rates and
211 herbivore-specific herbivory rates (fish or sea urchin). To compare impacts of herbivory
212 between patches we measured primary production at every patch. In addition, we
213 measured herbivore abundance to test if rates of herbivory were related to site-specific
214 or attribute-specific herbivore numbers. Additionally, to test if plant quality was
215 responsible for any of the observed patterns we analysed plant tissues nutrient content
216 (carbon:nitrogen ratio) from every patch.

217

218 *Response variable assessments*

219 We measured direct herbivory rates and leaf growth (as a surrogate of primary
220 production) in July 2011, when herbivory is at its seasonal maximum (Prado et al. 2007),
221 on the same *P. oceanica* shoots. Primary production was estimated using a modified
222 Zieman's method (Zieman 1974; Pérez & Romero 1994) and herbivory was assessed
223 with a tethering technique similar to the one used in Prado *et al.* (2007). SCUBA divers
224 marked 5 shoots per patch for matrix and distance experiments (5 shoots per patch, 4
225 patches, 2 conditions, 3 sites, resulting in a total of 120 marked shoots for each
226 experiment [matrix and distance]) and 3 shoots per zone for the edge experiment (3
227 shoots per zone, 5 zones, 3 positions, 3 sites, resulting in a total of 135 marked shoots).
228 In each shoot we marked the base of the leaves (piercing the leaf with a needle) to
229 measure leaf elongation. We also counted the initial number of leaves, measured the
230 initial leaf length and recorded the state of the apical part of each leaf (broken, eaten by
231 fish, eaten by sea urchin or intact). 15 days later all marked shoots were collected and
232 transported to the lab for sorting. For each shoot, we counted the number of leaves, and,
233 for each leaf, we measured its length and examined the state of its apex. For each leaf,
234 the new leaf tissue produced (between the pierced mark and the ligula) was also
235 measured (i.e. leaf elongation). Primary production ($\text{cm shoot}^{-1} \text{ day}^{-1}$) of pierced shoots
236 was determined by dividing the cm of new tissue produced by the number of days
237 elapsed since marking. Shoot herbivory rates ($\text{cm shoot}^{-1} \text{ day}^{-1}$) were estimated for each
238 of the collected shoots by adding leaf elongation (cm of new tissues produced) to the
239 initial length and subtracting this total from the final leaf length, finally divided by the
240 number of days elapsed since marking (Prado *et al.* 2007). Only leaves that had clear
241 herbivore bite marks were assigned to herbivory and the rest were discarded to avoid

242 herbivory overestimates. Both herbivores leave bite marks of distinctly identifiable
243 shapes (e.g. Tomas *et al.* 2005), and we were able to separately estimate seagrass
244 removal rates for sea urchins and for fish (herbivore-specific herbivory rates). In
245 statistical analyses, the mean of these 3-5 marked shoots was taken as the primary
246 production and herbivory rate of each experimental unit (i.e. patch [matrix, distance
247 experiments] or zone of the meadow [edges experiments]). Production-herbivory
248 balances were obtained by subtracting herbivory ($\text{cm shoot}^{-1} \text{ day}^{-1}$) from production (as
249 leaf elongation, $\text{cm shoot}^{-1} \text{ day}^{-1}$) to assess if shoot length (and, consequently, canopy
250 height) was overall increasing (if production outpaced herbivory) or decreasing (if
251 herbivory was greater than production) for the period considered (July, i.e. early
252 summer).

253

254 We estimated sea urchin density at each experimental location by counting adult sea
255 urchin abundance (test size ≥ 3 cm) in quadrats randomly placed in each patch for matrix
256 and distance experiments (3 quadrats per patch, 4 patches, 2 conditions, 3 sites,
257 resulting in a total of 72 quadrats for each experiment) or zone for the edge experiment
258 (2 quadrats per zone, 5 zones, 3 positions, 3 sites, resulting in a total of 90 quadrats). In
259 statistical analyses, the mean of these 2-3 quadrats was taken as the sea urchin density
260 of each experimental unit (i.e. patch [matrix, distance experiments] or zone of the
261 meadow [edge experiments]). We did not assess fish herbivore abundance in each
262 condition since *S. salpa* are very mobile and display a home range greater than our
263 experimental scale (i.e. on the order of hectares; Jadot *et al.* 2006; Pagès *et al.* in press).
264 We therefore assume that within each site, every patch or zone is equally likely of being
265 visited by *S. salpa* fishes with no physical barriers restricting their movements. As a

266 result, potential differences in fish herbivory between matrices, distances to the rocky
267 reef or zones will be the result of behavioural choices made by these fishes.

268

269 To assess food (plant) quality, we measured leaf nitrogen (% N) and carbon (% C) to
270 obtain C:N ratios from leaves at each site (see for e.g. Haynes & Cronin 2004). To
271 obtain adequate leaf biomass for these analyses we pooled 3-5 shoots together resulting
272 in one sample per experimental unit (i.e. per patch [matrix and distance experiments, 4
273 patches, 2 conditions, 3 sites, 24 samples in total] or per zone [edge experiment, 5 zones
274 per position, 3 positions, 3 sites, 45 samples in total]). Leaf nitrogen and carbon
275 concentration were measured using an elemental analyser EA1108 (Carlo Erba
276 Instruments) at Unidade de Técnicas Instrumentais de Análise (Universidade de
277 Coruña).

278

279 *Statistical analyses*

280 We used linear mixed effects models to determine how seagrass response variables (i.e.
281 total herbivory rates, herbivore-specific herbivory rates, sea urchin density, primary
282 production, production-herbivory balance and plant quality [C:N ratio]) varied across
283 the different landscape attributes studied (i.e. matrix composition, distance to the
284 nearest rocky reef, edge effects). For the matrix attribute, ‘matrix’ was considered a
285 fixed factor with 2 levels (rock and sand); for the distance attribute, ‘distance’ was
286 considered a fixed factor with 2 levels (near and far); and for the edge attribute,
287 ‘position’ was the fixed factor with 3 levels (rock edge, centre, sand edge). In addition,
288 ‘site’ was included as a random factor to account for the variance shared between those
289 measurements taken from the same site (3 levels, the 3 sites [except for the variables
290 related to herbivory in the edge experiment, which only had 2 suitable sites, since the

291 third showed virtually no herbivory, possibly due to a problem with the shoot marking
292 technique]). In those attributes that involved patches (matrix and distance attributes)
293 patch size (m²) was also included in the models as a covariate to control for this
294 possible source of variation. Finally, to assess the response variable herbivore-specific
295 herbivory rate, ‘animal’ was also included into the model as a fixed factor with 2 levels
296 (fish and sea urchin).

297

298 We conducted multiple comparisons using Tukey’s HSD on those dependent variables
299 that showed a significant effect in our linear mixed effects analyses. This enabled us to
300 test pairwise differences between variables. Normality and homogeneity of variances
301 were checked graphically by inspecting residuals and fitted values. Whenever a variable
302 was clearly heteroscedastic its variance structure was included as weights within the
303 linear mixed effects model and the best weighted model was selected using Akaike’s
304 Information Criterion (AIC) (Zuur *et al.* 2009). All data were analysed with the
305 packages nlme and lme4 in the statistical software R (Bates, Maechler & Bolker 2011;
306 Pinheiro *et al.* 2011; RDevelopmentCoreTeam 2012).

307

308 **Results**

309 Matrix composition had a significant effect on total herbivory rates (Table 1). Meadows
310 embedded in a rock matrix sustained herbivory rates three-times higher than those
311 surrounded by sandy habitats (Fig. 2a), independent of the site (Table 1). There were no
312 significant differences between herbivore-specific rates in any of the matrix types,
313 although fish herbivory (57 ± 15 %) appeared to be marginally higher than sea urchin
314 herbivory in both matrices (Fig. 2b). We did not find any shift in the proportion of
315 herbivory caused by each herbivore species according to matrix composition (matrix ×

316 animal effect not significant, Fig. 2b, Table 1). Sea urchin density was not significantly
317 different across matrices, despite slightly higher sea urchin densities in patches
318 embedded in the rock matrix compared to sandy matrices (Fig. 2c, Table 1). Seagrass
319 primary production was not affected by the intervening matrix composition either
320 (Table 1) and was very similar between patches embedded in both matrix types (mean =
321 1.7 ± 0.3 cm shoot⁻¹ day⁻¹, Fig. 2d). As a result, the production-herbivory balance in
322 shoots from patches within the rock matrix was negative, with a daily mean of leaf
323 length loss of 0.82 ± 0.3 cm; in contrast, shoots in sand patches showed a neutral
324 balance between herbivory and production (Fig. 2e, Table 1). There were no differences
325 in plant quality between seagrass patches on sand or rock matrices (Fig. 2f).

326

327 Patch distance from rocky reefs did not influence total herbivory rates, with very similar
328 values between patches near and far from rocky reefs (Fig. 3a, Table 2). However, fish
329 herbivory was significantly higher than urchin herbivory (Table 2) only in patches
330 further away from rocky reefs according to pairwise comparisons (i.e. differences
331 between grazers not significant in 'near' patches). Specifically, while each herbivore
332 accounted for half of the total herbivory rates in 'near' patches, in 'far' patches fish
333 herbivores made up three-quarters of the total herbivory (Fig. 3b). Distance to rocky
334 reefs did not have an effect on sea urchin densities, despite a tendency of lower
335 densities in distant patches compared to patches closer to rocky reefs (Fig. 3c, Table 2).
336 Similarly, we found no effects of distance on primary production, production-herbivory
337 balances or plant quality (Fig. 3d,e,f, Table 2). The random factor 'site' did not show
338 significant effects on any of the response variables studied (Table 2).

339

340 Position within the meadow had a clear influence on herbivory (Fig. 4a, Table 3). Both
341 edges showed lower levels of herbivory compared to the centre of the meadow, but
342 differences were only significant between the rock edge and the centre of the meadow
343 according to Tukey's HSD pairwise comparison. Specifically, herbivory rates were 3.6
344 times higher at the centre of the meadow compared to the rock edge (Fig. 4a). These
345 differences were due to increased herbivory pressure exerted by fish grazers at the
346 centre of the meadow (as shown by the significant grazer effect; Fig. 4b, Table 3),
347 which accounted for the 80% of total herbivory at this zone. Sea urchin density was not
348 significantly different between positions in the meadow, despite a non-significant trend
349 of lower sea urchin density from the rock towards the sand edge (Fig. 4c, Table 3).
350 Primary production and plant quality did not differ with meadow position (Fig. 4d,f,
351 Table 3). As a result, significant differences in production-herbivory balances were
352 evident (Table 3), with a highly negative balance at the centre of the meadow (shoots
353 shortening) compared to the edges, particularly rocky edges, whose shoots showed a
354 slightly positive balance (Fig. 4e). The random factor 'site' did not show significant
355 effects on any of the response variables studied (Table 3).

356

357 For the experiments that involved the use of discrete patches as experimental units, the
358 covariate patch size presented significant relationships with primary production (Tables
359 1 and 2) and plant quality (Table 2), as has been previously found in studies with the
360 same seagrass species (Gera *et al.* 2013).

361

362 **Discussion**

363 Landscape appears to play a critical role in mediating the way ecological functions are
364 distributed in the seagrass ecosystems we studied. Both the landscape matrix

365 composition and edges influenced overall rates of herbivory within the meadow, while
366 distance did not appear to affect herbivore consumption rates. Herbivory rates were
367 higher in seagrass patches embedded in a rocky matrix compared to sandy matrices; and
368 herbivory was higher at the centre of seagrass meadows compared to its edges.
369 Moreover, edge effects appeared to be matrix dependent. In contrast, patch distance to
370 rocky reefs did not play any role at determining plant-herbivore interactions or
371 ecological processes in *P. oceanica* seagrass meadows, at least at the scale tested.
372 Previous studies on terrestrial systems found that matrix composition affected herbivore
373 abundances (Haynes *et al.* 2007; Haynes & Crist 2009; Öckinger *et al.* 2012), pollinator
374 visitation (Diekötter *et al.* 2007), herbivore movements (Ricketts 2001; Haynes &
375 Cronin 2003), and plant damage (Thies *et al.* 2003). Here we show that matrix and
376 patch edges significantly affected the actual levels of herbivory, driven largely by
377 differences in the foraging behaviour of the two key herbivores of the system, and not
378 by differences in food quality across the landscape as has been widely reported (Haynes
379 & Cronin 2004).

380

381 Herbivory was highest at the centre of seagrass patches while edges were less grazed
382 (rocky edges in particular). This grazing peak at the centre of meadows was likely
383 related to fish herbivore behaviour, since fish herbivory was particularly high in
384 meadow interiors, accounting for 80 % of the total herbivory rates measured at the
385 meadow centre (Fig. 4b). Other studies in marine systems have proposed that similar
386 heterogeneity in the distribution of herbivory could be driven by a greater risk of
387 predation at habitat edges, which causes herbivores to be less abundant and reduce their
388 feeding behaviour at these edge habitats (Macreadie *et al.* 2012). This mechanism is
389 highly unlikely in Mediterranean waters, given the rarity of extant predators of *S. salpa*.

390 Perhaps more likely, the grazing peak at the centre of meadows is driven by the shoal
391 feeding behaviour this species. It may be an optimal strategy for schooling fish to start
392 foraging from the centre of meadows, as has been observed for goose flocks (Black *et al.*
393 1992): because flocks land in the middle of fields and forage outwards, the centre of
394 fields are exploited more heavily than the edges (Krebs & Davies 1993). Sea urchin
395 herbivory, in contrast, appeared to play a minor role in explaining the observed
396 herbivory patterns. Sea urchin abundance at the rock-seagrass edge was slightly
397 (although non-significantly) higher than at the centre and at the seagrass-sand edge,
398 possibly due to a migration of recruits from the rocky matrix (Prado *et al.* 2012). These
399 differences in abundance were not reflected in total herbivory rates.

400

401 Matrix composition played a major role in influencing herbivory rates of both generalist
402 herbivores of the system, with herbivory rates in seagrass patches embedded in rocks
403 three times higher than patches embedded in sand. This is consistent with several
404 studies that have observed that generalist species are more likely to be affected by the
405 intervening matrix than specialists (Brotons, Mönkkönen & Martin 2003; Steffan-
406 Dewenter 2003; Diekötter *et al.* 2007). Eventually, the feeding specialization of the
407 principal herbivores of the system will determine the manner and strength with which
408 landscape attributes affect levels of herbivory (Haynes & Crist 2009), since generalists
409 may feed both on the focal habitat (in this case the seagrass) and in the intervening
410 matrix (in this case, the sand or rocky matrix). Since unlike the sandy matrix, rocky
411 areas also sustain macroalgae that herbivores may complement or supplement their diet
412 with (see Dunning *et al.* 1992), it is perhaps unsurprising that these matrices are
413 favoured. Complementation or supplementation hypotheses propose that many mobile
414 species may have a diversity of nutritional requirements that may change as they grow

415 and which may require them to utilise multiple ecosystems, effectively linking these
416 habitats together (Dunning *et al.* 1992; Haynes *et al.* 2007).

417

418 Another factor that could potentially influence habitat use across the matrix is plant
419 quality, which is often itself strongly influenced by landscape configuration (see Haynes
420 & Cronin 2004 for a review). Nutrient availability, water movement, light availability
421 and plant competitive interactions could all be heavily modified by the matrix and
422 determine animal foraging choices (Haynes & Cronin 2004). However, plant quality
423 did not covary with the matrix in the present study, and seagrass leaves had similar
424 carbon and nitrogen contents in both matrices, indicating that forage quality was not a
425 factor influencing foraging differences. Another potential reason for clearly higher
426 herbivory rates in rocky matrix is that these may be preferred areas for sea urchins. Sea
427 urchins recruit preferentially in rocky habitats (Prado *et al.* 2012), which provide ample
428 shelter for the species from which they have been observed to migrate to seagrass
429 patches (Ceccherelli *et al.* 2009). In contrast, sea urchins cannot recruit, forage or
430 shelter in sandy areas, and they generally do not cross seagrass-sand edges (Dance
431 1987). Indeed, matrix type has been shown to affect edge-mediated behaviour and
432 emigration rates of various species (Ricketts 2001; Haynes & Cronin 2003; Haynes &
433 Cronin 2006). This has been attributed to differential predation risk according to the
434 matrix they are in. Thus, although we did not find significant differences in sea urchin
435 abundance between patches embedded in rock or in sand, sea urchins sheltering or
436 foraging within the rock matrix (ignored in our abundance estimates) may cross the
437 rock-seagrass edge and feed on seagrass, further increasing herbivory in these patches.
438 Conversely, no sea urchin immigration occurs in patches surrounded by sand, since it
439 involves crossing a hard edge (sand-seagrass), and moving across a risky matrix (Farina

440 et al. unpublished manuscript). These factors could further explain the differences in
441 herbivory rates we recorded between in seagrass patches embedded in rocky matrices
442 and those embedded in sand.

443

444 The distance of patches from rocky reefs did not play a role in determining herbivory
445 rates despite several studies on coral reefs that have found that herbivory is usually
446 higher close to reefs, decreasing with distance (Valentine *et al.* 2007; Vergés *et al.*
447 2011). However, in this case, the distance between rocky reefs and the farthest patches
448 was clearly insufficient to determine any pattern given the known mobility of *S. salpa*,
449 which can connect habitats several kilometres apart (Pagès *et al.* in press). It is
450 interesting to note, however, that fish contributed more to total herbivory at these more
451 distant patches compared to the patches near the rocky reef. This was possibly linked to
452 a slightly higher (though non-significant) abundance of sea urchin in patches closer to
453 the rocks.

454

455 This study shows that matrix and edges landscape attributes are capable of introducing
456 considerable spatial heterogeneity in herbivory rates, a key ecological process in
457 seagrass meadows. The high herbivory rates found in patches embedded in rock
458 compared to sand, and at the interior of meadows compared to the edges may have
459 important consequences for other ecological processes, particularly when these rates
460 exceed leaf growth. This negative balance does not necessary imply a meadow decline,
461 since it only occurs in early summer, when herbivory is at its maximum and leaf growth
462 at sub-maximum, and is largely compensated for across the annual cycle (Prado *et al.*
463 2007). However the daily reduction in canopy height (at a rate of ca. 1 cm per shoot per
464 day) can expose other seagrass-dwelling species (including sea urchins) to increased

465 predation risk (Pagès *et al.* 2012). Moreover, seagrass shoots subject to these
466 imbalances between production and herbivory have been observed to decrease shoot
467 nutrient stocks (Vergés *et al.* 2008), likely limiting their long-term primary production
468 and even decreasing reproduction (Planes *et al.* 2011). In spite of the high levels of
469 herbivory that some seagrass areas receive, we should bear in mind that herbivory in the
470 Mediterranean is highly seasonal, with high rates during summer and low rates in winter
471 (Prado *et al.* 2007). This seasonality may be critical for the survival of *P. oceanica*
472 meadows in areas of the landscape where herbivory is most intense.

473

474 Our results reinforce the view that a more nuanced understanding of landscape
475 processes will require us to go beyond describing species abundance and distribution
476 patterns across mosaics. While these may serve to provide a rough idea of how
477 landscape configuration influences ecosystem processes, they often mask much more
478 complex interactions. Our results show that the abundance of herbivores at a patch did
479 not completely correspond to their functional impact: areas with very similar
480 abundances of herbivores had very different levels herbivory. This mismatch was driven
481 by differences in life history, movement and predation risk between the two dominant
482 herbivores that resulted in very different patterns of foraging in relation to landscape
483 attributes. These behavioural and movement patterns of the key species of the system
484 may be fundamental to predict the spatial heterogeneity of ecological processes, which
485 may have important consequences for plant production, nutrient cycling, plant
486 reproductive success and the trophic pathways of the system.

487

488

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651

652 **Table 1.** Model results for the matrix experiment. The significance of random factors
 653 was assessed comparing the mixed effects with the linear model using the Akaike's
 654 Information Criterion (AIC); thus, we cannot display the F-values of these tests. d.f.
 655 degrees of freedom. Significance codes: P -value < 0.001 ***, < 0.01 ** , ≤ 0.05 *

656	Response variable	Effects	d.f.	F	P-value
657	Herbivory	Site (random)	2	-	0.812
658		Matrix	1	23.2	0.000 ***
659		Size	1	595.7	0.000 ***
660		Matrix × size	1	15.1	0.001 **
661		Residual	18		
662	Herbivore-specific herbivory	Site (random)	2	-	0.648
663		Matrix	1	4.1	0.050 *
664		Animal	1	0.4	0.520
665		Size	1	1.6	0.214
666		Matrix × animal	1	0.4	0.516
667		Matrix × size	1	0.9	0.342
668		Animal × size	1	0.8	0.379
669		Matrix × animal × size	1	0.6	0.441
670		Residual	36		
671	Sea urchin density	Site (random)	2	-	0.999
672		Matrix	1	1.8	0.195
673		Size	1	0.9	0.352
674		Matrix × size	1	0.0	0.996
675		Residual	18		

676

677	Primary production	Site (random)	2	-	0.01 **
678		Matrix	1	0.6	0.466
679		Size	1	1.8	0.194 ***
680		Matrix × size	1	1.1	0.314
681		Residual	18		
682	Production-	Site (random)	2	-	1
683	herbivory balance	Matrix	1	13.2	0.002 **
684		Size	1	443.4	0.000 ***
685		Matrix × size	1	5.5	0.030 *
686		Residual	18		
687	Plant quality (C:N)	Site (random)	2	-	0.028 *
688		Matrix	1	0.0	0.920
689		Size	1	0.5	0.487
690		Matrix × size	1	6.0	0.026 *
691		Residual	16		
692					
693					

694 **Table 2.** Model results for the distance experiment. The significance of random factors
 695 was assessed comparing mixed effects with linear models using the Akaike's
 696 Information Criterion (AIC); thus, we cannot display the F-values of these tests. d.f.
 697 Degrees of freedom. Significance codes: P -value < 0.001 ***, < 0.01 ** , ≤ 0.05 *

698	Response variable	Effects	d.f.	F	<i>P</i>-value
699	Herbivory	Site (random)	2	-	0.532
700		Distance	1	0.0	0.947
701		Size	1	0.1	0.708
702		Distance × size	1	0.3	0.562
703		Residual	19		
704	Herbivore-specific herbivory	Site (random)	2	-	0.222
705		Distance	1	0.0	0.933
706		Animal	1	5.5	0.025 *
707		Size	1	0.1	0.757
708		Distance × animal	1	1.0	0.321
709		Distance × size	1	0.5	0.474
710		Animal × size	1	0.0	0.894
711		Distance × animal × size	1	0.0	0.968
712	Residual	40			
713	Sea urchin density	Site (random)	2	-	0.173
714		Distance	1	0.0	0.905
715		Size	1	6.9	0.017 *
716		Distance × size	1	4.7	0.047 *
717		Residual	18		
718					

719	Primary production	Site (random)	2	-	1
720		Distance	1	0.0	0.845
721		Size	1	5.7	0.027 *
722		Distance × size	1	0.0	0.948
723		Residual	18		
724	Production-	Site (random)	2	-	0.113
725	herbivory balance	Distance	1	0.0	0.900
726		Size	1	0.0	0.860
727		Distance × size	1	0.4	0.549
728		Residual	18		
729	Plant quality (C:N)	Site (random)	2	-	0.992
730		Distance	1	0.1	0.762
731		Size	1	10.5	0.004 **
732		Distance × size	1	0.2	0.672
733		Residual	19		
734					
735					
736					

737 **Table 3.** Model results for the edges experiment. The significance of random factors
 738 was assessed comparing the mixed effects with the linear model using the Akaike's
 739 Information Criterion (AIC); thus, we cannot display the F-values of these tests. d.f.
 740 degrees of freedom. Significance codes: P -value $< 0.001^{***}$, $< 0.01^{**}$, $\leq 0.05^*$

741	Response variable	Effects	d.f.	F	<i>P</i>-value
742	Herbivory	Site (random)	1	-	1
743		Position	2	6.8	0.004 **
744		Residual	25		
745	Herbivore-specific herbivory	Site (random)	1	-	1
746		Position	2	3.6	0.036 *
747		Animal	1	5.3	0.026 *
748		Position × animal	1	1.8	0.183
749		Residual	50		
750	Sea urchin density	Site (random)	2	-	1
751		Position	2	0.8	0.467
752		Residual	24		
753	Primary production	Site (random)	2	-	1
754		Position	2	2.7	0.08
755		Residual	40		
756	Plant quality (C:N)	Site (random)	2	-	1
757		Position	2	1	0.3802
758		Residual	40		
759	Production- herbivory balance	Site (random)	2	-	0.107
760		Position	2	4.9	0.012 *
761		Residual	40		

762 **Figure legends**

763

764 **Fig. 1.** Experimental design. (a) Matrix experiment consisted of measuring ecological
765 features from seagrass patches embedded in a rock matrix ($n = 4$) and patches in a sand
766 matrix ($n = 4$), in 3 sites. (b) Distance experiment involved measuring ecological
767 parameters from seagrass patches embedded in a sand matrix and either near (ca. 5 m, n
768 = 4) or far (ca. 20 m, $n = 4$) from a rocky reef, in 3 sites. (c) In the edges experiment we
769 measured ecological features in 5 zones at the centre of a meadow (ca. 200 m²) and 5
770 zones at the rock and sand edges, also in 3 sites.

771

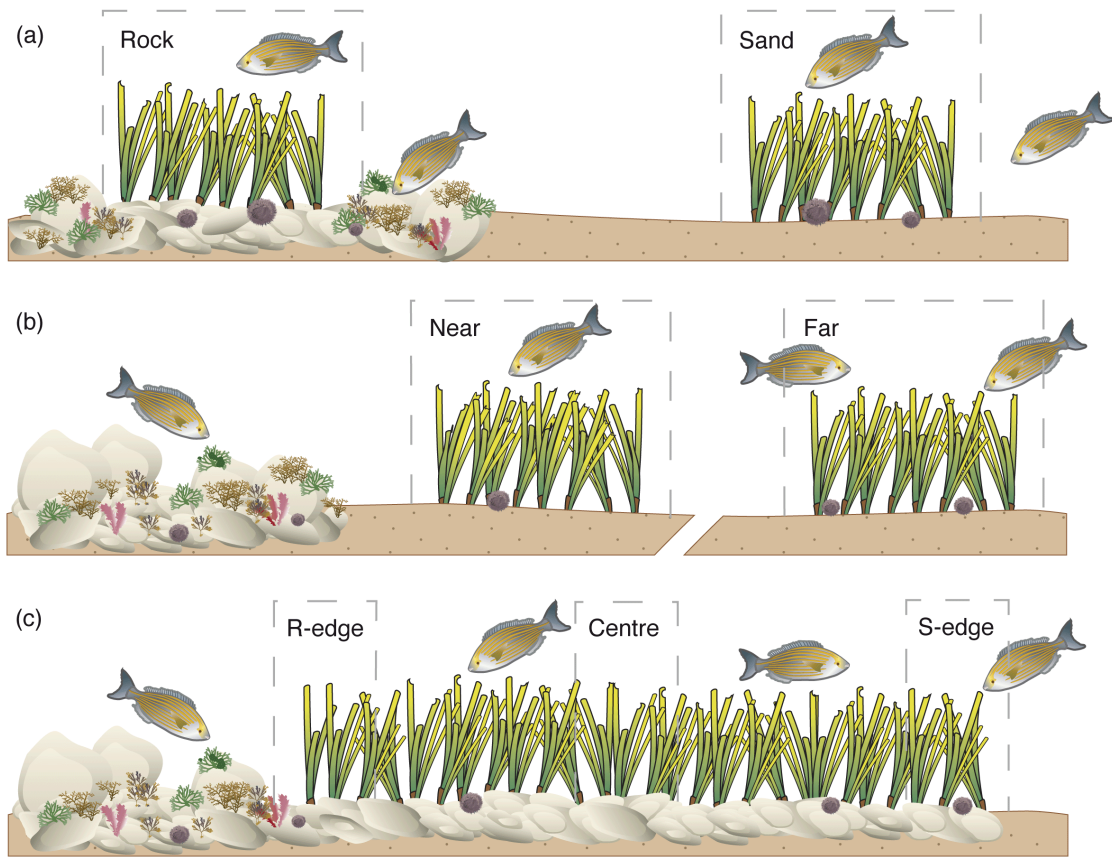
772 **Fig. 2.** Matrix experiment. (a) Total herbivory rates, (b) percentage of herbivory rate
773 accounted by each herbivore (dark grey bars correspond to fish herbivory [*S. salpa*] and
774 light grey ones to urchin herbivory [*P. lividus*]), (c) sea urchin density, (d) seagrass
775 primary production, (e) balance between production and herbivory (cm shoot⁻¹ day⁻¹)
776 and (f) plant quality (leaves' C:N ratio) in *P. oceanica* patches embedded in a rock or in
777 a sand matrix. Bars labelled with the same letter do not differ significantly according to
778 a Tukey HSD post hoc test.

779

780 **Fig. 3.** Distance experiment. (a) Total herbivory rates, (b) percentage of herbivory rate
781 accounted by each herbivore (dark grey bars correspond to fish herbivory [*S. salpa*] and
782 light grey ones to urchin herbivory [*P. lividus*]), (c) sea urchin density, (d) seagrass
783 primary production, (e) balance between production and herbivory (cm shoot⁻¹ day⁻¹)
784 and (f) plant quality (leaves' C:N ratio) in *P. oceanica* patches placed either near or far
785 from a rocky reef. Bars labelled with the same letter do not differ significantly
786 according to a Tukey HSD post hoc test.

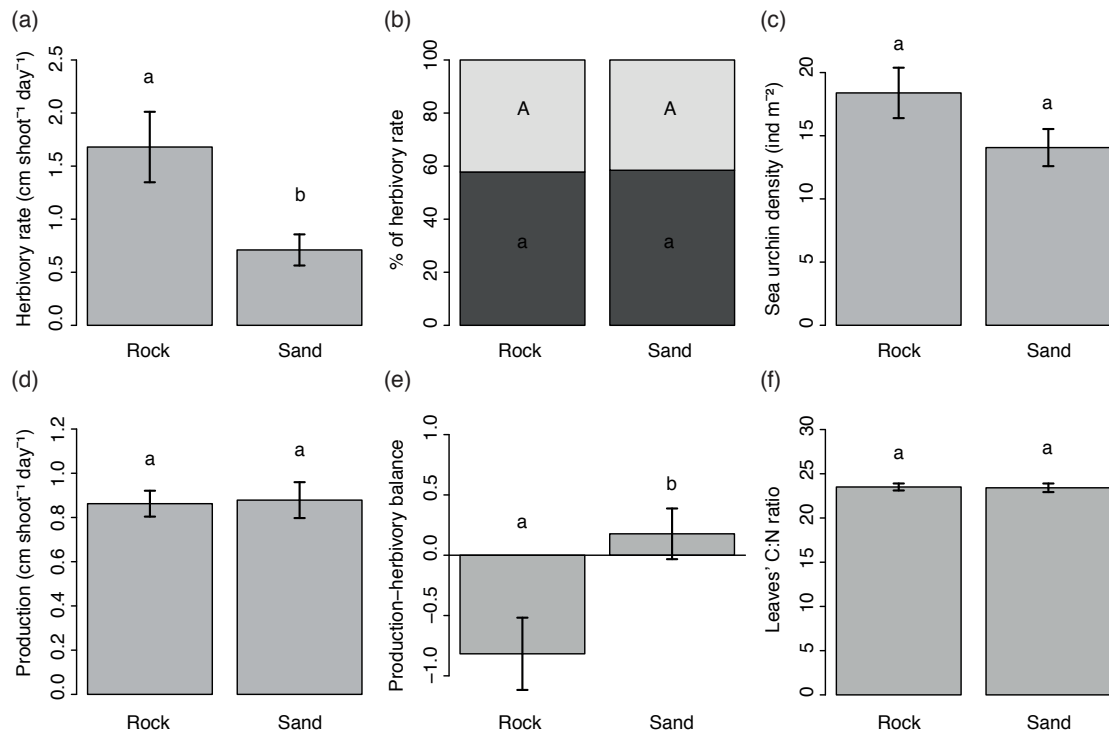
787 **Fig. 4.** Edges experiment. (a) Total herbivory rates, (b) percentage of herbivory rate
788 accounted by each herbivore (dark grey bars correspond to fish herbivory [*S. salpa*] and
789 light grey ones to urchin herbivory [*P. lividus*]), (c) sea urchin density, (d) seagrass
790 primary production, (e) balance between production and herbivory (cm shoot⁻¹ day⁻¹)
791 and (f) plant quality (leaves' C:N ratio) in areas placed at the rock edge, at the centre or
792 at the sand edge of *P. oceanica* meadows. Bars labelled with the same letter do not
793 differ significantly according to a Tukey HSD post hoc test.
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795

796 **Fig. 1.**



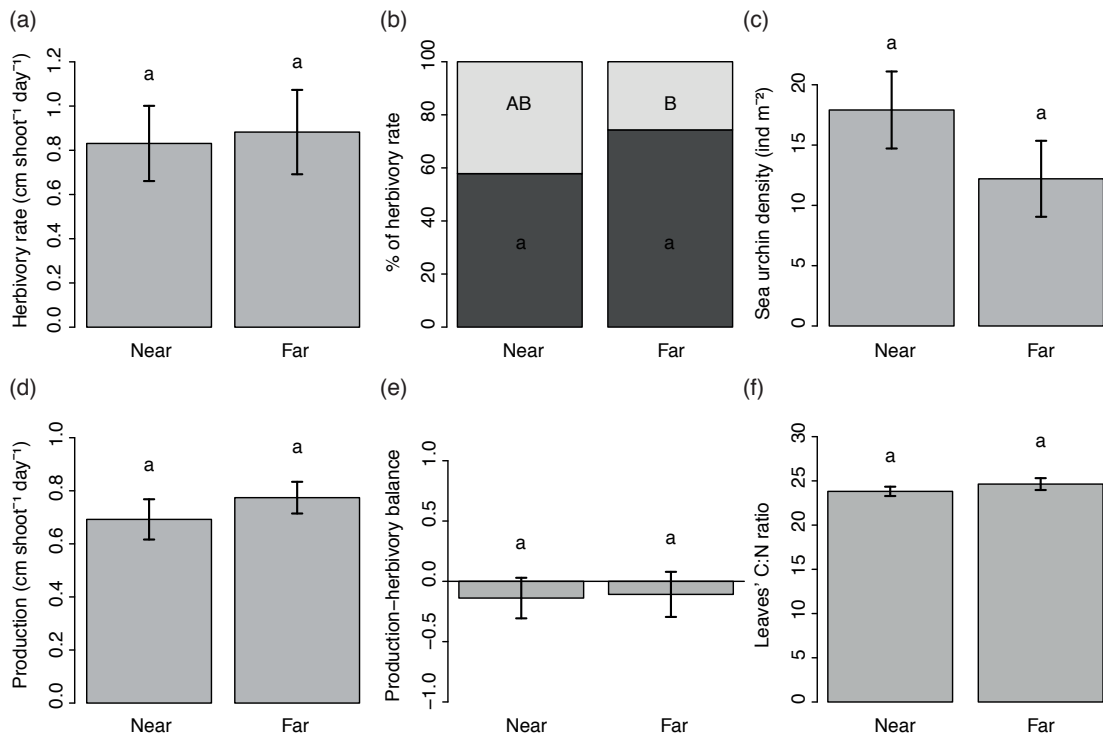
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802 **Fig. 3.**

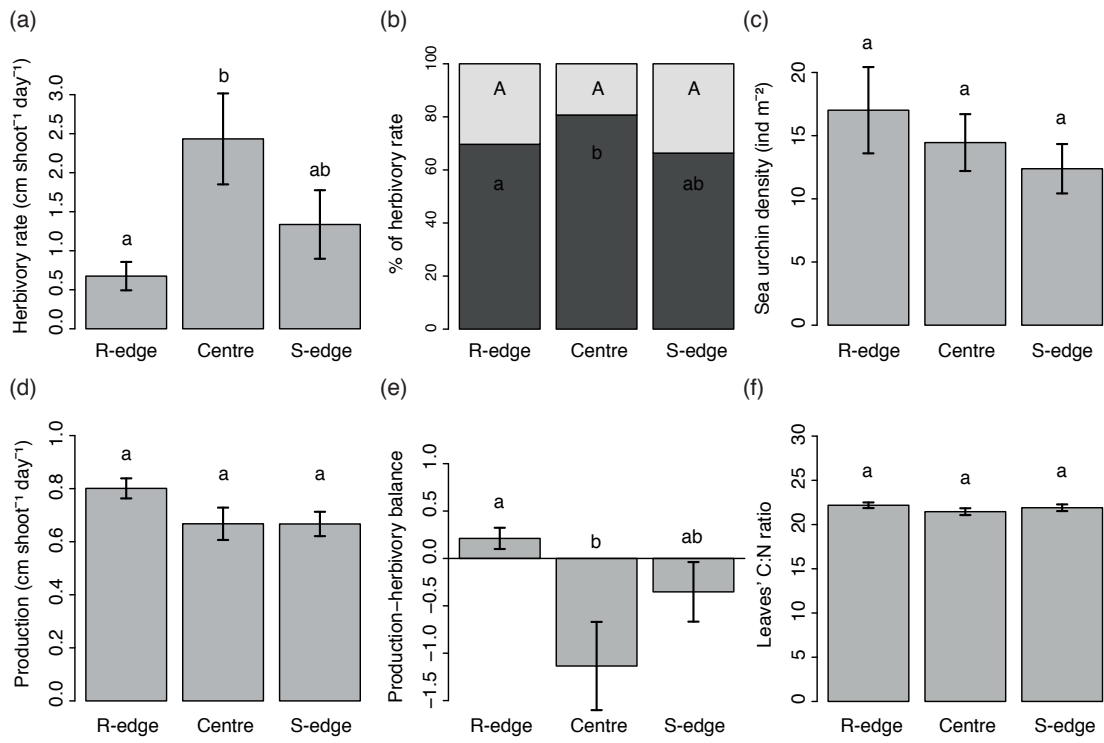
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805 **Fig. 4.**

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