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1 **Interannual fluctuations in rainfall shift the functional structure of Mediterranean**
2 **grasslands across gradients of productivity and disturbance**

3

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13 **ABSTRACT**

14 **Questions:** How do interannual fluctuations in water availability affect the functional trait
15 patterns along spatial gradients of resource availability and disturbance?

16 **Location:** Mediterranean grasslands in central Spain, near Madrid

17 **Methods:** We surveyed plant communities from 66 sites under different grazing regimes (from
18 heavy grazing to grazing abandonment) in productive and unproductive habitats (corresponding
19 to upper and lower topographic zones) in two years with contrasting rainfall conditions.

20 Community weighted mean (CWM) and Rao quadratic entropy for three key plant ecology
21 strategy traits (specific leaf area, height and seed mass) were calculated for each community. We
22 used null models to estimate functional richness (FR) and functional divergence (FD), the two
23 components of functional diversity with the highest power to detect changes in community
24 assembly processes across environmental gradients.

25 **Results:** The patterns of CWM remained rather constant across years, with the only exception
26 being seed mass, which experienced considerable temporal changes that suggested that heavy-
27 seeded species are favored under stressful conditions. Marked and unchanging differences in FR
28 between the two habitats revealed the existence of trait convergence -observed for vegetative
29 traits in unproductive habitats and seed mass in productive ones- and divergence -seed mass in
30 unproductive habitats and vegetative traits in productive ones- for different niche axes. In
31 contrast, the patterns of FD of the vegetative traits changed considerably between years.

32 **Conclusions:** Increased water availability during the wet year had a greater impact on the
33 functional structure of unproductive habitats. The appearance of taller species in unproductive
34 habitats during the wet year suggested a relaxation of the abiotic filters. In addition, differences
35 in the direction of the interannual changes of FD indicated that increased competition for light

36 can lead to increased niche partitioning in unproductive habitats, but also to the exclusion of
37 weak competitors in undisturbed productive sites. Our results show that the temporal changes in
38 the abundance of the species of Mediterranean grasslands largely depend on the species' traits,
39 leading to great interannual changes in its functional structure, and that the patterns of trait
40 convergence/divergence are, not only trait-dependent, but also depend on the complex
41 interaction between productivity and disturbance.

42 **Keywords:** Annual plants; community assembly; dehesa; functional divergence; functional
43 richness; grazing; productivity; species pool.

44 **Nomenclature:** Flora Europea (Tutin et al. 1964-1980)

45 **Running head:** Functional structure in Mediterranean grasslands

46 **INTRODUCTION**

47 Functional trait diversity is emerging as a powerful indicator of community assembly
48 processes in plant communities (Mason *et al.* 2005, 2012a; Vileger *et al.* 2008; de Bello *et al.*
49 2010). Recent work has used functional diversity indices to reveal changes in assembly processes
50 along spatial gradients of resource availability and disturbance (e.g. Cornwell & Ackerly 2009;
51 Pakeman *et al.* 2011; Mason *et al.* 2011, 2012). However, it remains unclear how temporal
52 variation in resource availability interacts with spatial gradients of stress and disturbance to
53 influence assembly processes in plant communities. This study uses functional diversity for plant
54 traits to explore how temporal and spatial variations in resource availability interact with grazing
55 disturbance to influence assembly processes in Mediterranean grassland communities.

56 Limitations in resource availability reduce the range of vegetative trait values that are viable
57 within a given site, favouring species adapted to the local conditions (Grime 2006). This may
58 increase the likelihood of co-existence between species with trait values similar to the local

59 optimum (Mouillot et al. 2007; Mason et al. 2012; Spasojevic & Suding 2012), leading to
60 reduced functional diversity (convergence; Grime 2006). On the other hand, the principle of
61 limiting similarity (MacArthur & Levins 1967) predicts that competition will impose a limit to
62 how similar coexisting species can be. According to this principle, the traits of coexisting species
63 should be more different than expected at random (divergence; Mason et al. 2012; Spasojevic &
64 Suding 2012). However, competition can also increase similarity among coexisting species by
65 excluding species bearing traits associated with low competitive ability (Chesson 2000, Grime
66 2006, Mayfield and Levine 2010). Local increases in productivity produce a shift in the limiting
67 factors for plant growth from soil resources to light, thus increasing the intensity of above-
68 ground competition (Tilman 1988). For instance, low productivity selects for species with
69 resource-retaining strategies (Cornwell & Ackerly 2009). Conversely, increased productivity,
70 and hence increased competition for light, should enhance the abundance of fast-growing
71 species, and lead to higher functional diversity for vegetative traits (Mason et al. 2011;
72 Spasojevic & Suding 2012; Gross et al. 2013), although the latter may not be true when
73 competition for light is very intense (e.g. Bernard-Verdier et al. 2012).

74 Grazing also plays an important role as a determinant of the functional structure of plant
75 communities (Carmona et al. 2012). Plants deal with grazing adopting two main strategies:
76 avoidance and tolerance (Anderson & Briske 2005; Cingolani et al. 2005). The avoidance
77 strategy involves vegetative traits that allow plants to reduce its accessibility and palatability
78 (such as short statures, small leaves or rosette growth forms). In contrast, grazing-tolerant plants,
79 which have the capacity to regrow quickly after defoliation, have traits associated with high rates
80 of resource capture relative to their size, such as a high specific leaf area or high concentrations
81 of Nitrogen in the leaves. As a result, tolerant plants are highly palatable and selected by

82 herbivores, often leading to a positive feedback between grazing and plant quality (Cingolani et
83 al. 2005). Nevertheless, traits associated to grazing tolerance also entail a less efficient
84 conservation of resources, and therefore grazing tolerant responses are only expected to increase
85 with grazing when there is a sufficient availability of resources (Cingolani et al. 2005). With
86 respect to the distribution of trait values, disturbance has been considered as the most important
87 source of trait divergence, because biomass removal should prevent the exclusion of weak
88 competitors (Grime 2006; de Bello et al. 2013). However, recent studies have shown that
89 disturbance can also result in trait convergence (Mason et al. 2011; Pakeman et al. 2011;
90 Carmona et al. 2012; Laliberté et al. 2013), especially under harsh environmental conditions
91 (Carmona et al. 2012).

92 Indeed, the predominant assembly processes can differ between niche axes; Grime (2006)
93 suggested that, while divergence is common for reproductive traits, patterns of convergence
94 predominate for vegetative traits. Traits related with the regeneration stage of plants, such as
95 seed mass, play a crucial role in Mediterranean grasslands, where annual species are very
96 abundant, accentuating the influence of the germination and establishment stages on the species
97 composition of these systems (Espigares & Peco 1995). Seedlings coming from larger seeds are
98 known to have higher survival rates (Metz et al. 2010), especially under stressful conditions,
99 such as low availability of light and water (Moles & Westoby 2004). Therefore, high levels of
100 productivity, associated with low light availability, should enhance the abundance of species
101 with large seeds. On the other hand, small-seeded species produce greater numbers of seeds,
102 which in turn result in a better capacity to colonise the gaps produced by livestock and leads to
103 the increased abundance of such species under grazing conditions (Kohler et al. 2006; Peco et al.
104 2012; Dobarro et al. 2013).

105 In this context, temporal increases in water availability are very likely to alter the functional
106 structure of annual plant communities, by selecting for species with higher growth rates over
107 species that can tolerate low resource levels (Angert et al. 2009). Moreover, given that the effect
108 of grazing is strongly mediated by resource availability (Díaz et al. 2007a; Carmona et al. 2012,
109 2013), increased water availability is also likely to affect the patterns of functional structure
110 across grazing gradients, by enhancing the abundance of grazing-tolerant species along grazing
111 gradients. In addition, temporal increases in water availability, and hence enhanced seedling
112 survivorship, should result in increases in the abundance of small seeded species, especially
113 considering that small seeds persist in the seed banks for longer periods (Thompson et al. 1993).

114 Mediterranean grasslands are an excellent system for testing whether or not spatial patterns
115 in functional community structure are stable in the face of temporal fluctuation in resource
116 availability. One of the main features of Mediterranean climate is the high level of interannual
117 variability in rainfall, which generates a great variability in the productivity of Mediterranean
118 grasslands. This translates into significant interannual differences in the productivity, species
119 composition and diversity of these systems (Peco 1989; St. Clair et al. 2009; Fernández-Going et
120 al. 2012; Pérez-Camacho et al. 2012; Carmona et al. 2012). In this paper, we examine the
121 functional structure for three key plant traits (specific leaf area, height and seed mass; Westoby
122 1998) between two habitats differing in resource availability situated along a grazing intensity
123 gradient, in a wet and a dry year. We test whether patterns in functional community structure
124 across spatial gradients of resource availability and grazing vary between years of differing
125 rainfall. We expect that interannual changes in rainfall will change the most successful functional
126 strategies, resulting in changes in the functional structure patterns. Specifically, we hypothesize
127 that: (1) increased water availability during the wet year should favour traits associated with

128 resource-acquiring strategies, such as high SLA or height; (2) these changes should be
129 particularly evident in unproductive environments, because of the relaxation of the strong abiotic
130 filters that impose a great constraint to trait values during the dry year; (3) because productivity
131 modulates the effect of disturbance, interannual differences in water availability should alter the
132 plant strategies selected by grazing, from grazing-avoidance strategies (characterised by low
133 SLA values) in the dry year to grazing-tolerance strategies (characterised by high SLA values) in
134 the wet year; (4) higher levels of water availability during the wet year should intensify
135 competition for light leading to increased divergence in traits related with light use and
136 acquisition; however, in productive habitats with little or no grazing, very intense competition
137 for light may result in convergence by the exclusion of traits that confer weak competitive
138 ability; (5) given that large-seeded species are more likely to overcome stressful germination and
139 establishment conditions, enhanced conditions for small-seeded species during the wet year
140 should be reflected in a reduction in average seed mass accompanied by an increase in the range
141 of values of this trait (Table 1).

142 **MATERIAL AND METHODS**

143 **Study area**

144 The study area (5 × 4 km) is situated 35 km north of Madrid, in central Spain (40°38' N;
145 3°70' W; mean elevation 860 m). Climate is Mediterranean, with annual rainfall (average ca. 540
146 mm, with high interannual variability) concentrated mainly in spring and autumn, with very dry
147 summers. Mean annual temperature is *c.* 13°C. The landscape is characterised by moderate
148 slopes, shallow acidic soils over a gneiss substratum and many rocky outcrops. Clearing of the
149 original forest, where *Quercus ilex* subsp. *ballota* L. and *Juniperus oxycedrus* L. were the

150 dominant tree species, resulted in a typical “dehesa” landscape with *c.* 40 trees/ha over a
151 grassland understorey with a high proportion (ca. 70%) of annual species.

152 Extensive grazing has been the dominant use in the region for centuries, but currently there
153 is great spatial variability in grazing intensity, with intensification in some areas and
154 abandonment in others (Peco et al. 2006). In order to cover a wide range of situations, we
155 selected sites with four different levels of grazing intensity: (1) areas in which grazing has been
156 abandoned; (2) areas grazed only occasionally; (3) areas where livestock is permanently present,
157 but in which grazing pressure is moderate because they are distant from points of livestock
158 concentration such as water and feeding points; (4) areas under permanent high levels of grazing
159 because they are close to points of livestock concentration. We made sure that the grazing status
160 of all the selected areas has remained unchanged for at least 30 years. Two different habitat types
161 can be distinguished within each of the grazing intensity levels: (1) productive habitats, located
162 at the bottom of slopes, characterised by their deep soils, and that receive water and nutrient
163 inflows; (2) unproductive habitats, on the upper slopes with shallower soils, and nutrient and
164 water outflows. In each of these eight ‘habitat × grazing’ levels we selected eight or nine
165 independent sites, always situated in areas with slopes under 5% (total of 66 sites). In order to
166 guarantee the independency of our sampling units, we made sure that all sites were sufficiently
167 separated, with a minimum distance between adjacent sites of 45 m, and an average of 106 m.

168 The differing topographic positions of the two types of habitats have led to differences in
169 their levels of soil water availability, clay percentage, total nitrogen and soil organic matter (Peco
170 et al. 2006), which result in a much lower plant productivity of upper-slope habitats (Casado et
171 al. 1985). For instance, soil analyses in the same 66 sites have revealed that the two habitats
172 differ in Total N ($0.39 \text{ g}/100 \text{ g} \pm 0.03$ in productive vs. $0.18 \text{ g}/100 \text{ g} \pm 0.01$ in unproductive

173 habitats) and organic matter contents ($7.02 \text{ g}/100 \text{ g} \pm 0.77$ in productive vs. $2.68 \text{ g}/100 \text{ g} \pm 0.16$
174 in unproductive habitats), but not in P content ($7.78 \text{ ppm} \pm 1.50 \text{ ppm}$ in productive vs. 8.34 ppm
175 $\pm 1.73 \text{ ppm}$ in unproductive habitats; Navarro 2013). In order to corroborate the differences in
176 soil water content between habitats, we collected and oven-dried a soil sample (5-cm cylinder of
177 98.17 cm^3) from each site in April 2012. We defined the water content of these soil samples as
178 the ratio of the mass of water to the dry weight of the sample. As expected, we found significant
179 differences between the mean soil water contents of productive ($33.04\% \pm 1.39\% \text{ SE}$) and
180 unproductive habitats ($14.60\% \pm 1.09\%$). Accordingly, total plant cover in lower-slope habitats
181 is substantially higher than in upper-slope ones (ca. 82% vs 62%; Carmona et al. 2013).

182 **Vegetation and functional traits sampling**

183 At each site we set up three sampling quadrats ($20 \times 20 \text{ cm}$), always in the same relative
184 positions (1 m N, E and W from the site centre). We surveyed these quadrats twice, in the spring
185 of 2009 (dry year, with 315 mm of precipitation between October and June, which is ca. 65% of
186 the long term average during that period) and 2010 (wet year, with 575 mm of precipitation, ca.
187 119% of the average precipitation between October and June). Interannual differences in
188 precipitation have an important effect on the productivity of grasslands, especially of those
189 situated in dry environments such as the studied ones (Yang et al. 2008; St. Clair et al. 2009). We
190 estimated the abundance of each species in each quadrat, using six cover classes: (0) absent; (1)
191 cover $< 1\%$; (2) $1\% < \text{cover} \leq 12\%$; (3) $12\% < \text{cover} \leq 25\%$; (4) $25\% < \text{cover} \leq 50\%$; and (5)
192 cover $> 50\%$. Subsequently, we assigned to each species the median value of its cover class, and
193 transformed these covers, by ensuring that the sum of all the covers of the species at each quadrat
194 was always 1.

195 We found a total of 177 species in the surveys (Appendix S1). For each species we collected
196 data on three functional traits –height, specific leaf area (SLA) and seed mass – related to
197 species’ strategies in response to disturbance and productivity. Data on SLA and height were
198 taken from Peco et al. (2005) or measured in the cases in which such information was not
199 available. Plant height (distance between the plant base and the highest photosynthetic leaf) was
200 measured on 10 non-grazed mature individuals of each species, at least 25 m from each other, in
201 the areas where the species was more abundant. Height regulates plant responses to resource
202 availability and disturbance and can be interpreted as an indicator of successional status and
203 response to grazing (Westoby et al. 2002; Díaz et al. 2007a). Specific leaf area (SLA; mm²/mg)
204 was measured on the same individuals, dividing the leaf area by its oven-dried mass. SLA is an
205 indicator of resource-use strategies, with low SLA values being associated with long-lived
206 leaves, low relative growth rates and long residence times of nutrients (Westoby et al. 2002).
207 Seed mass was obtained in most cases from Azcárate et al. (2002), and new measurements were
208 taken for the species not included in that paper, following the same protocol (30 dry seeds per
209 species). Seed mass influences seedling survival -large-seeded species produce large seedlings
210 that survive better under difficult conditions such as shade, drought or defoliation- as well as the
211 colonisation capacity of species -species with large seed produce smaller numbers of seeds per
212 unit of mass (Westoby 1998; Moles & Westoby 2004). The three traits were independent, as
213 revealed by Mantel tests (9,999 permutations) performed between the respective matrices of trait
214 distances between species (SLA-Height: $r = -0.006$, $p = 0.495$; SLA-Seed mass: $r = -0.007$,
215 $p=0.423$; Height-Seed mass: $r = 0.02$, $p=0.249$)

216 **Functional structure calculation**

217 The study of the variation in community functional structure along ecological gradients
218 requires the combined use of indicators of shifts in the functional composition and in the patterns
219 of trait convergence and divergence (Spasojevic & Suding 2012; Bernard-Verdier et al. 2012).
220 Changes in the functional composition of communities can be detected by analysing the patterns
221 of community average trait values (Pakeman et al. 2011; Mason et al. 2012). On the other hand,
222 functional diversity reveals the changes in the patterns of trait convergence/divergence
223 associated to changes in community assembly. Among the different components of functional
224 diversity, we analysed functional richness and functional divergence. Functional richness, an
225 indicator of the amount of niche space occupied by the species in a community (Mason et al.
226 2005), reveals the influence of trait-based assembly processes on species' occurrence.
227 Additionally, functional divergence, an indicator of the degree of trait divergence between the
228 most abundant species, can reveal effects of trait-based assembly processes on species' relative
229 abundances (Mason et al. 2012, 2013). While limiting similarity is associated with high
230 functional richness and divergence, abiotic filters reduce the values of these indicators (Mouchet
231 et al. 2010; Mason et al 2012).

232 To calculate these indices, we first log-transformed and standardised the SLA, height, and
233 seed mass values to a 0–1 scale. For each quadrat j we calculated the community weighted mean
234 (Díaz et al. 2007b) of each trait (CWM_{SLA} , CWM_{Height} and CWM_{Seed}). Additionally, we
235 calculated, for each trait, a matrix of Euclidean distances between all possible species-pairs. In
236 order to have an indication of functional richness and functional divergence, we calculated the
237 Rao quadratic entropy (henceforth “Rao”; Rao 1982; de Bello et al. 2010) for each trait in each
238 quadrat and year. The Rao Index can be expressed as:

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$$Rao = \sum_{i=1}^S \sum_{j=1}^S d_{ij} p_i p_j,$$

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where d_{ij} expresses the dissimilarity between each pair of coexisting species i and j and varies from 0 (two species with exactly the same trait values) and 1 (two species with completely different traits). p_i and p_j indicate the relative abundances (in this case relative cover) of species i and j . Rao is a combination of both functional richness and functional divergence (Mouchet et al. 2010). We chose Rao because it has been found to be a reliable index when analysing changes in assembly processes across gradients of stress (Mason et al. 2012, 2013) and can take species' relative abundances into account (de Bello et al. 2010). For each quadrat and year we calculated two Rao values. The first one was calculated taking into account species' covers ("Rao_{ab}"). For the second Rao value we took into account only species' presences (i.e. assigning the same abundance value to all the species in a quadrat; "Rao_{pr}").

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Both raw Rao values may be influenced by species richness (i.e. may be correlated with species richness even in randomly generated data), especially when using presence/absence data (Pavoine et al. 2013). Consequently, relationships between Rao and environmental gradients can arise simply due to variation in species richness. To remove spurious effects of species richness on Rao values, we compared observed Rao values with two different null models. First, we compared the observed Rao_{pr} of each quadrat with null values generated using a matrix-swap null model (using 2000 initial swaps and 2000 swaps between calculation of each null value) based on the species presence-absence matrix (177 species x 198 quadrats; Manly 1995). Given the reduced geographical extension of our study area, we considered a common species pool for all quadrats. Comparisons of observed Rao_{pr} values with null values obtained following this procedure are a powerful method to detect the effects of ecological processes on species'

261 occurrences, and are good estimators of functional richness (Mason et al. 2013). Second, we
262 compared observed Rao_{ab} with null values generated by randomising abundances across species
263 but within quadrats (Hardy 2008; Mason et al. 2012). This procedure preserves all the processes
264 that led to the observed composition, except those determining the abundances of species (Mason
265 et al. 2012). Comparing the observed Rao_{ab} values with the Rao_{ab} obtained in this second type of
266 randomisation provides a pure estimation of functional divergence. Simulation studies indicate
267 that these indices collectively provide a high level of power to detect changes in assembly
268 processes along environmental gradients (Mason et al. 2013). This method has been used before
269 in field-based studies (Mason et al 2011, 2012), showing its reliability to detect changes along
270 gradients.

271 We performed 10,000 randomisations of each null-model in order to calculate the
272 standardised effect size ($SESRao = [\text{observed Rao} - \text{mean of simulated Rao}] / \text{standard deviation}$
273 of simulated Rao; Gotelli &McCabe 2002). Subsequently, we averaged the values of the three
274 quadrats of each site, thus obtaining two $SESRao$ values per site: $SESRao_{pr}$ (observed Rao_{pr}
275 compared with the matrix-swap null model) and $SESRao_{ab}$, (observed Rao_{ab} compared with the
276 null model randomising abundances across species but within 20 cm x 20 cm sampling
277 quadrats). For convenience, we refer to them respectively as FR and FD henceforth.

278 **Statistical analyses**

279 We examined the influence of grazing intensity, habitat type and year on the CWM, FR and
280 FD of the three studied traits by means of mixed effects models, with site as a random factor
281 (Table 1). Given that in many occasions the variability between the groups was not uniform, we
282 fitted 7 different models for each response variable: one model with no different spread per
283 stratum and 6 models in which we allowed the variance to vary within groups. Such groups were

284 defined as the levels of each of the studied factors (grazing intensity, habitat type and year), as
285 well as their pairwise combinations. Subsequently, for each response variable, we selected the
286 model with the lowest AIC value (Zuur et al. 2009). We checked for spatial autocorrelation in
287 the residuals of the models using Mantel tests. Because our models included two observations of
288 each site (two different years), we performed two Mantel test for each model, with the matrix of
289 distances of the residuals of the dry and of the wet year, respectively, and the matrix of spatial
290 distances. Finally, for each model, we performed Bonferroni-corrected pairwise comparisons to
291 detect differences between grazing intensities within habitat types and year as well as interannual
292 changes within sites (differences between years within habitat types and grazing intensities). All
293 analyses were performed using R (R Development Core Team 2013).

294 **RESULTS**

295 For CWM and FD, AIC values indicated that the models that considered different variances
296 within groups were generally more parsimonious than those that assumed equal variance across
297 strata. In contrast, the models with the lowest AIC scores for FR were those that did not
298 considered differences in variance among groups (Appendix S2). In addition, the Mantel tests
299 performed for each year and model revealed that there was not spatial autocorrelation in the
300 residuals of the models (Appendix S3).

301 **Patterns in the functional structure of vegetative traits**

302 Species with high SLA and low stature were more abundant under higher grazing intensities,
303 regardless of the year or habitat type (Table 2a; Fig. 1; Appendix S4). The communities of
304 productive habitats were composed of taller plants with lower SLA values than those of
305 unproductive habitats (Table 2a; Fig. 1). Although the patterns of average values of the studied
306 traits across grazing intensities and habitat types were consistent across years, the CWM_{SLA} of

307 the communities sited in unproductive habitats experienced significant interannual variations
308 (Table 2; Appendix S4). Importantly, the direction of this change was modulated by grazing
309 intensity, resulting in increased SLA values during the wet year in the most intensively grazed
310 areas and the opposite pattern in the less intensively grazed areas (Fig. 1a). In contrast,
311 CWM_{Height} was rather constant across years in both habitat types across the whole grazing
312 gradient (Fig. 1b; Appendix S4).

313 High grazing pressures reduced the range of height values in unproductive habitats in both
314 years, but did not have any effect on productive habitats (Table 2b; Fig. 2b). In contrast, FR_{SLA}
315 was not affected by grazing in any of the studied scenarios (habitats and years). Again, habitat
316 type played a very important role (Table 2b), with higher FR values in productive than in
317 unproductive habitats, for both SLA and height, during both years (Fig. 2b; Appendix S4). With
318 the exception of FR_{Height} in unproductive habitats, which generally increased during the wet year,
319 the temporal variability in FR within habitats and grazing intensities was minor compared to the
320 differences between habitats (Fig. 2b).

321 On the contrary, the values of FD for vegetative traits experienced a much higher degree of
322 interannual variability. For instance, the effect of grazing on FD_{SLA} contrasted markedly between
323 years, regardless of habitat type, with grazing having a significant and generally negative effect
324 on FD_{SLA} during the dry year, and no effect during the wet year (Fig. 3). Interestingly, the
325 interannual variability in FD_{SLA} within sites was contingent on habitat type: during the wet year
326 FD_{SLA} increased in unproductive habitats throughout the grazing gradient, whereas it underwent
327 an important decrease in the communities of the productive habitats where grazing had been
328 abandoned (Fig. 3a). The high within-site temporal variability of FD_{SLA} contrasted with the
329 temporal constancy observed in FD_{Height} (Fig. 3a; Appendix S4).

330 **Patterns in the functional structure of seed mass**

331 The average values of seed mass displayed a very complex response to grazing and
332 productivity. During the dry year, CWM_{Seed} was higher in unproductive than in productive
333 habitats, but that relationship reversed during the wet year, especially in the most intensively
334 grazed sites, that experienced great interannual increases (in productive habitats) or reductions
335 (in unproductive habitats) in seed mass (Fig. 1c; Appendix S4). Seed mass decreased with
336 grazing, but only during the dry year in productive habitats and during the wet year in
337 unproductive ones (Fig. 1c).

338 The lack of any effect of grazing on the functional richness of seed mass contrasted with the
339 remarkable differences between habitats in this parameter. FR_{Seed} was much higher in
340 unproductive than in productive habitats, a tendency that became even more evident during the
341 wet year (Fig. 2c; Appendix S4). Finally, none of the studied factors affected FD_{Seed} or its
342 temporal variability (Table 2b and Fig. 3c).

343 **DISCUSSION**

344 Temporal and spatial variations in resource availability interact with disturbance in complex
345 ways, altering the functional structure of plant communities. Our results show that temporal
346 fluctuations can drive considerable variation in the functional trait patterns across gradients. As
347 we expected, the functional structure of unproductive habitats experienced greater interannual
348 variations than that of productive habitats (Hypothesis 2). Interannual changes in unproductive
349 habitats indicated a relaxation of the strength of abiotic filters during the wet year. The habitat-
350 dependent direction of the interannual changes in functional divergence patterns suggested that
351 the outcome of competition for light depend on its intensity (Hypothesis 4). Grazing selected for
352 tolerance strategies more strongly during the wet year in unproductive environments, confirming

353 the role of productivity as a modulator of the effects of grazing on plant communities
354 (Hypothesis 3). Below, we discuss our main results in more detail, focussing successively on the
355 different traits considered.

356 **Patterns in vegetative traits**

357 Average SLA increased with grazing in all but the less productive scenario -unproductive
358 environments, dry year-, showing that grazing selects for tolerance strategies when there is
359 sufficient resource availability (Eskelinen et al. 2012). In addition, higher mean SLA values
360 during the wet year in the most intensively grazed sites of unproductive habitats was consistent
361 with the expected shift towards grazing-tolerance strategies when water availability increased
362 (Hypothesis 3). This shift can be mediated by a few abundant species; for instance, the
363 abundance of *Poa bulbosa*, a species with fast growth rates and a relatively high SLA value,
364 increased remarkably during the wet year (Appendix S5; Fig. A1). This increase is probably
365 related to the high sensitivity of *P. bulbosa* to water deficits (Mamolos et al. 2001) and with its
366 increased tolerance to grazing under high-resource-availability conditions (Staalduinen et al.
367 2010). Simultaneously, the abundances of species with rosette form and intermediate SLA
368 values, such as *Leontodon taraxacoides* or *Hypochaeris glabra*, decreased in unproductive
369 habitats during the wet year, suggesting that dry conditions favour grazing-avoidance strategies,
370 whereas more humid conditions favour grazing-tolerance strategies (Díaz et al. 2007a). On the
371 contrary, mean SLA decreased in the non-grazed sites during the wet year (Fig. 1a), suggesting
372 that within-site interannual changes in the most successful resource-use strategies are mediated
373 by the disturbance regime.

374 There were important differences between habitats in the patterns of functional richness for
375 SLA, which were much higher in productive than in unproductive habitats. In contrast, habitat

376 type did not stand out as the main determinant of the patterns of functional divergence of SLA
377 (Table 2c). According to Hypothesis 4, we expected to observe trait convergence among the
378 most abundant species under low water availability and increased divergence under higher water
379 availability. The generalised increase in the divergence of SLA in unproductive habitats during
380 the wet year partially confirmed these predictions. The enhanced abundance of *Vulpia myuros*, a
381 graminoid with a much lower SLA value than the dominant *P. bulbosa*, contributed decisively to
382 this increase (Fig. 3a and Appendix S5; Fig. A2). In contrast, we also observed a great decrease
383 in the functional divergence of SLA during the wet year in the grazing-abandoned productive
384 habitats' communities (Fig. 3a and Appendix S5; Fig. A3). Apparently, under conditions that
385 favor strong competition for light (i.e. wet year, productive habitats and no grazing disturbance),
386 large differences in competitive abilities led to the preeminence of equalizing fitness mechanisms
387 and, as a consequence, to trait convergence (Chesson 2000; Grime 2006; Mayfield & Levine
388 2010). Our results suggest that functional divergence for SLA peaks at intermediate productivity
389 levels, a pattern similar to that reported by Bernard-Verdier et al. (2012) in Mediterranean
390 rangelands.

391 Unproductive habitats had, on average, shorter species than productive ones, which suggests
392 that the importance of competition for light increased with higher resource availability (Bernard-
393 Verdier et al. 2012; Spasojevic & Suding 2012). In addition, grazing decreased average height, in
394 agreement with the results of previous studies (Peco et al. 2005; de Bello et al. 2005; Díaz et al.
395 2007a). Again, habitat type was the main driver of FR_{Height} , with higher functional richness in
396 productive than in unproductive environments. This result, along with the above-mentioned for
397 FR_{SLA} , corroborates that environmental filters impose significant restrictions to the range of
398 vegetative trait values present at a given site (Hypothesis 2; Grime 2006). This was further

399 confirmed by the increase in FR_{Height} in unproductive habitats during the wet year (Fig. 2b),
400 where reduced water stress increased the occurrences of tall species. However, the enhanced
401 presence of these species was not accompanied by great increases in their abundances, as
402 suggested by the temporal consistency of mean height. Additionally, high grazing intensities
403 reinforced the effects of aridity, further reducing the small FR_{Height} values in unproductive
404 habitats (Cingolani et al. 2005; Carmona et al. 2012). These results provide support for the
405 notion of disturbance as a force that leads to convergence in trait patterns (Mason et al. 2011;
406 Pakeman et al. 2011; Laliberté et al. 2013).

407 In general, the patterns of vegetative traits across the grazing gradient depended strongly on
408 rainfall conditions. Functional divergence decreased with grazing during the dry year, with the
409 only exception of height in productive habitats. However, the non-significant effect of grazing on
410 functional divergence observed during the wet year (Fig. 3) confirms that the effects of grazing
411 are highly influenced by the productivity level (Milchunas et al. 1988, de Bello et al. 2006;
412 Carmona et al. 2012). Future studies including a wider range of productivity conditions would
413 help to discern the conditions in which disturbance acts as a driver of trait divergence (Grime
414 2006) or convergence.

415 **Seed mass**

416 As expected, grazing reduced mean seed size (Peco et al; 2005; Kohler et al. 2006; Dobarro
417 et al. 2013), but these reductions were highly context-dependent. Interannual differences in mean
418 seed size increased with grazing intensity, but the direction of this change depended on habitat
419 type. As a result, average seed size was higher in unproductive habitats during the dry year,
420 whereas it maximized in productive habitats during the wet year (Fig. 1c). These results, which
421 are in agreement with Hypothesis 5, suggest that increased stress levels, manifested as increased

422 shading in productive habitats during the wet year, and as severe constraints on water availability
423 in unproductive habitats during the dry year, select for large-seeded species with higher
424 survivorship rates in stressed conditions (Moles & Westoby 2004). In addition, the increase in
425 average seed mass experienced by the most intensively grazed productive sites during the wet
426 year is consistent with a reduction in the availability of regeneration gaps -of which small seeded
427 species take advantage (Kohler et al. 2006)- caused by livestock trampling and defoliation.

428 Between-habitat differences in productivity played a major role determining the functional
429 richness of seed mass, which was greater in unproductive than in productive habitats. These
430 differences further increased during the wet year (Table 2b), associated with the aforementioned
431 reduction in average seed mass in unproductive habitats and the increase in productive habitats.
432 For instance, in unproductive habitats, we observed increased presence and abundance of small-
433 seeded species (e.g. *Tuberaria guttata*, *Spergula arvensis* or *Vulpia myuros*) during the wet year,
434 combined with a decline of species with heavy seeds (e.g. *Biserrula pelecinus*, *Brassica*
435 *barrelieri* or *Erodium cicutarium*). The functional richness of seed size displayed the opposite
436 pattern in productive habitats (Appendix S5; Fig. A4). The interannual changes observed for
437 FR_{Seed} can be caused by the capacity of small seeds to persist in the seed bank for longer times
438 than large seeds (Thompson et al. 1993). Thus, small-seeded species present in the seed bank
439 probably experienced buffered population growth (Chesson 2000), i.e. enhanced germination and
440 seedling survivorship under less stressful environmental conditions (higher water availability in
441 unproductive habitats during the wet year and higher light availability in productive habitats
442 during the dry year, respectively). The appearance of small-seeded species along with the
443 presence of large-seeded ones in the communities regardless of water availability would
444 therefore explain the increase in FR_{Seed} values under favourable conditions.

445 Finally, the lack of effect of any of the studied factors on the functional divergence of seed
446 mass is in line with previous results (Viard-Crétat et al. 2011). In this sense, it is important to
447 note that patterns of divergence or convergence in seed size would indicate a great importance of
448 seedling-seedling interactions, which rarely occur in natural or experimental conditions (Peco &
449 Espigares 1994; Moles & Westoby 2004; Ben-Hur et al. 2012).

450 **Concluding remarks**

451 Our results suggest that wet years foster trait diversity in unproductive habitats, while dry
452 years allow resource-retaining species, which are poor competitors for light, to remain in the
453 communities. Therefore, resource fluctuations seem to promote the diversity of trait values,
454 playing an important role in the maintenance of diversity (Chesson et al. 2004). The present
455 study provides support for the consideration of disturbance as a driver of functional convergence
456 (e.g. Pakeman et al. 2011), rather than a source of trait divergence (Grime 2006).

457 The application of an approach similar to the one presented here can help to reduce the
458 number and importance of possible confounding factors, opening a new and promising venue for
459 the study of changes in patterns of trait convergence/divergence associated to shifts in resource
460 availability or disturbance. However, we are aware of the potential confounding effects of factors
461 other than the total amount of rainfall, which are likely to have changed between years. For
462 example, small-seeded species are favored in years with early autumn rains, whereas large-
463 seeded species are more abundant after dry autumns (Peco et al. 2009). Another possible caveat
464 of our study is the lack of consideration of dispersal limitation, which might reduce the
465 functional pool available at each site (Myers & Harms 2009), and have a confounding effect on
466 our FR analyses. Finally, we want to stress that we only considered a single average trait value
467 per species regardless of the year. Therefore, our study only considers differences in functional

468 structure caused by changes in species composition, but not those due to within-species
469 variability (Lepš et al. 2011). Among the studied traits, height is the most likely to experience
470 within-species variation associated to environmental changes (Garnier et al. 2007), a feature that
471 can be behind the lack of interannual changes in mean height values. Studies using a similar
472 research framework, but including a higher number of years, as well as considering the possible
473 effects of dispersal limitation and within-species variability in trait values, are needed in order to
474 adequately describe the role of temporal variation in resource availability.

475 The temporal consistency and the importance of the differences in average trait values and
476 functional richness between habitats indicate that long-term and sustained differences, such as
477 the ones produced by the different topographical positions between unproductive and productive
478 habitats, have a great influence on these values through trait-mediated changes in the species
479 pool. This contrasted with the great interannual changes observed for the functional divergence
480 of the vegetative traits, particularly for SLA. Interannual changes in functional divergence show
481 that the temporal fluctuations in the abundance of the species of Mediterranean grasslands
482 largely depend on the species' traits. Our results illustrate that the patterns of trait
483 convergence/divergence are, not only trait-dependent, but also depend on the complex
484 interaction between productivity and disturbance. Most importantly, we provide evidence
485 showing that the conclusions drawn from studies analysing the trait patterns across ecological
486 gradients can be substantially modified by temporal fluctuations in resource availability. Our
487 findings indicate that the results derived from a single year should be considered with caution.
488 Consequently, we recommend that future studies analysing these patterns should take into
489 account the temporal fluctuations in resource availability, especially in plant communities
490 dominated by annual species.

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673

674 **Supporting Information**

675 **Appendix S1.** Species recorded in the study.

676 **Appendix S2.** AIC values of the different linear mixed effects models.

677 **Appendix S3.** Results of the Mantel tests performed to check for spatial autocorrelation in the
678 residuals of the models

679 **Appendix S4.** Mean values of the different indicators of functional structure for each functional
680 trait and combination of grazing, habitat productivity and year.

681 **Appendix S5.** Additional figures.

682

683 **Table 1** Main hypotheses tested, reasoning for each and expected results.

Hypothesis	Reasoning	Expected results
1. Higher SLA or Height during the wet year.	Increased water availability favours resource-acquiring strategies.	Significant <i>Year</i> effect.
2. Greater increases in SLA or Height in unproductive habitats.	The constraint to trait values imposed during dry years is greater in unproductive habitats.	Significant <i>Year x Habitat</i> interaction.
3. Plant strategies selected by grazing differ among years.	Productivity modulates the effect of grazing.	Significant <i>Year x Grazing</i> interaction.
4. Higher FD for traits related with light acquisition during the wet year; especially in unproductive habitats or ungrazed and productive sites.	Intensified competition for light during the wet year may leave to greater trait divergence, but can also increase dominance in undisturbed productive environments.	Significant <i>Year x Grazing x Habitat</i> interaction.
5. Smaller seeds, and greater FRSeed during the wet year.	Enhanced conditions for small-seeded species during the wet year, but no reason for heavy seeds to disappear.	Significant <i>Year</i> effect.

685 **Table 2** Results of the linear mixed models analysing the values of the community weighted
686 mean (CWM), functional richness (FR) and functional divergence (FD) for each
687 functional trait. Grazing intensity, habitat type and year as well as their interactions were
688 used as fixed-effects explanatory variables. Site was used as a random factor. *P*-values
689 are shown in brackets. Significant results ($P < 0.05$) are in bold.

	df	SLA	Height	Seed mass
		<i>F</i>	<i>F</i>	<i>F</i>
a) CWM				
Grazing intensity	3	19.88 (<0.001)	65.02 (<0.001)	4.99 (0.004)
Habitat	1	109.64 (<0.001)	208.73 (<0.001)	1.47 (0.230)
Year	1	<0.001 (0.989)	0.02 (0.877)	5.46 (0.022)
Grazing × Habitat	3	3.39 (0.012)	3.21 (0.029)	1.19 (0.321)
Grazing × Year	3	9.93 (<0.001)	1.31 (0.279)	0.03 (0.993)
Habitat × Year	1	10.96 (0.002)	1.31 (0.257)	57.75 (<0.001)
Grazing × Habitat × Year	3	0.39 (0.764)	1.39 (0.253)	4.20 (0.009)
b) FR				
Grazing intensity	3	0.57 (0.639)	7.28 (<0.001)	1.02 (0.393)
Habitat	1	122.75 (<0.001)	128.78 (<0.001)	99.11 (<0.001)
Year	1	0.93 (0.338)	3.36 (0.072)	0.04 (0.834)
Grazing × Habitat	3	0.23 (0.873)	14.94 (<0.001)	1.59 (0.201)
Grazing × Year	3	0.72 (0.546)	1.82 (0.154)	0.270 (0.847)
Habitat × Year	1	0.20 (0.660)	14.46 (<0.001)	16.16 (<0.001)
Grazing × Habitat × Year	3	2.28 (0.089)	0.485 (0.694)	0.01 (0.999)
c) FD				
Grazing intensity	3	5.21 (0.003)	3.93 (0.013)	0.21 (0.890)
Habitat	1	5.28 (0.025)	26.21 (<0.001)	2.21 (0.143)
Year	1	17.32 (<0.001)	6.60 (0.013)	<0.001 (0.987)
Grazing × Habitat	3	1.64 (0.191)	2.25 (0.093)	0.56 (0.643)
Grazing × Year	3	3.24 (0.028)	0.97 (0.414)	0.43 (0.735)
Habitat × Year	1	49.70 (<0.001)	0.219 (0.641)	0.11 (0.739)
Grazing × Habitat × Year	3	5.21 (0.003)	5.36 (0.003)	0.23 (0.874)

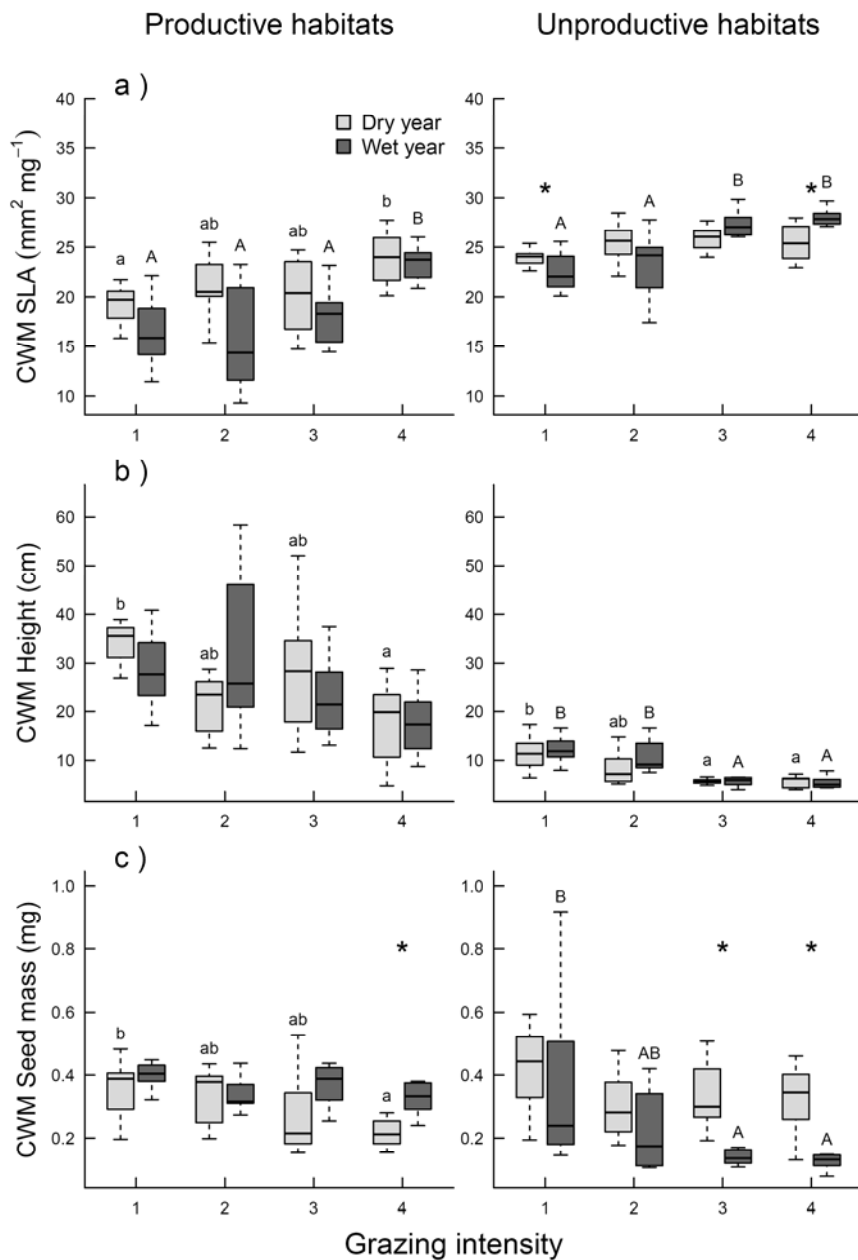
691 **FIGURE LEGENDS**

692 **Figure 1.** Boxplots showing the effect of grazing intensity (1: abandoned; 2: grazed
693 occasionally; 3: grazed moderately; 4: overgrazed) and year (dry and wet) on the community
694 weighted mean values of the different functional traits for each grazing intensity level and year,
695 in productive (left) and unproductive (right) habitats. When the effect of grazing is significant,
696 different letters for each year (lower case for the dry year and upper case for the wet year)
697 indicate significant differences between grazing intensity levels. Similarly, asterisks show
698 significant differences between years for a given habitat type and grazing intensity level. Outliers
699 are not shown to improve the clarity of the figures.

700 **Figure 2.** Boxplots showing the effect of grazing intensity (1: abandoned; 2: grazed
701 occasionally; 3: grazed moderately; 4: overgrazed) and year (dry and wet) on functional richness
702 (FR; $SESR_{ao_{pr}}$) values of the different functional traits for each grazing intensity level and year,
703 in productive (left) and unproductive (right) habitats. Interpretation of the statistical results is as
704 in Fig. 1. Outliers are not shown to improve the clarity of the figures.

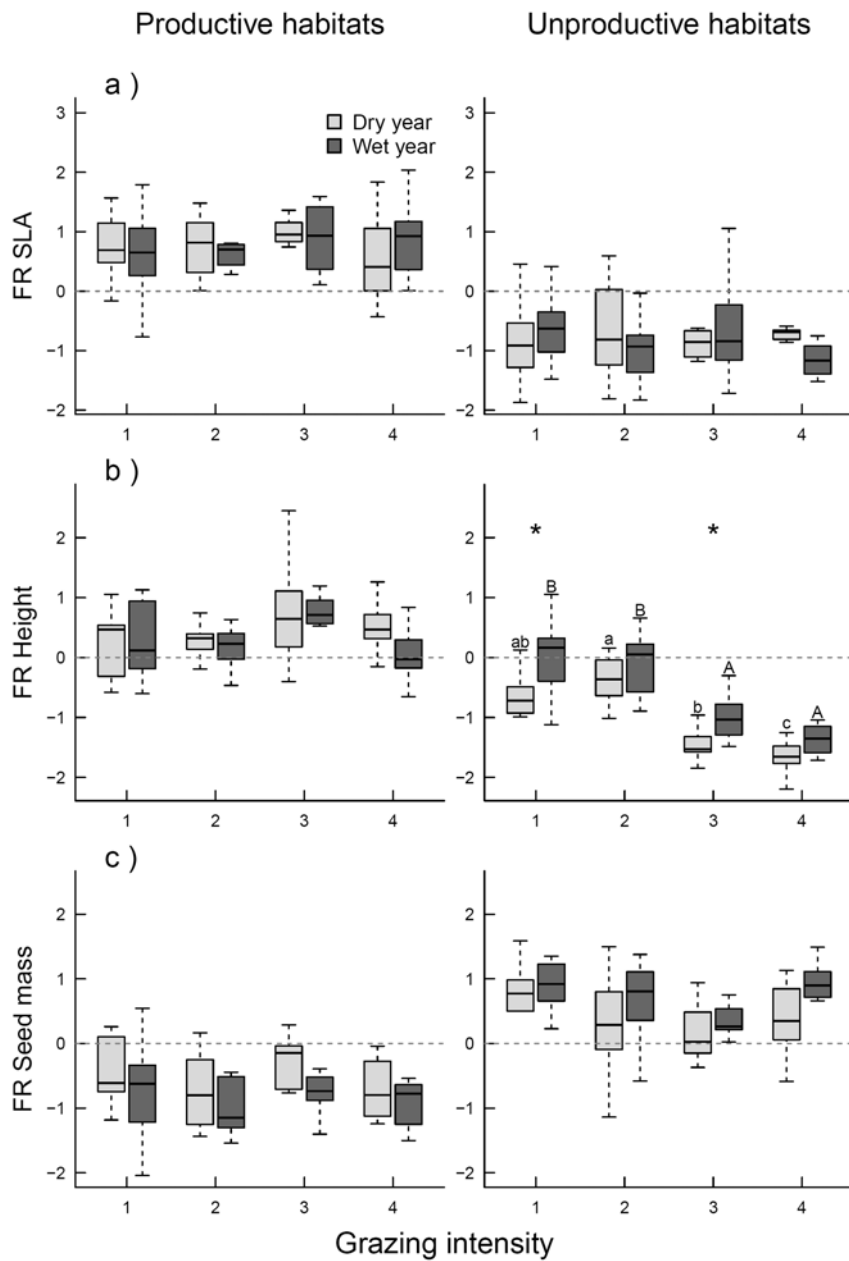
705 **Figure 3.** Boxplots showing the effect of grazing intensity (1: abandoned; 2: grazed
706 occasionally; 3: grazed moderately; 4: overgrazed) and year (dry and wet) on functional
707 divergence (FD; $SESR_{ao_{ab}}$) values of the different functional traits for each grazing intensity
708 level and year, in productive (left) and unproductive (right) habitats. Interpretation of the
709 statistical results is as in Fig. 1. Outliers are not shown to improve the clarity of the figures.

710



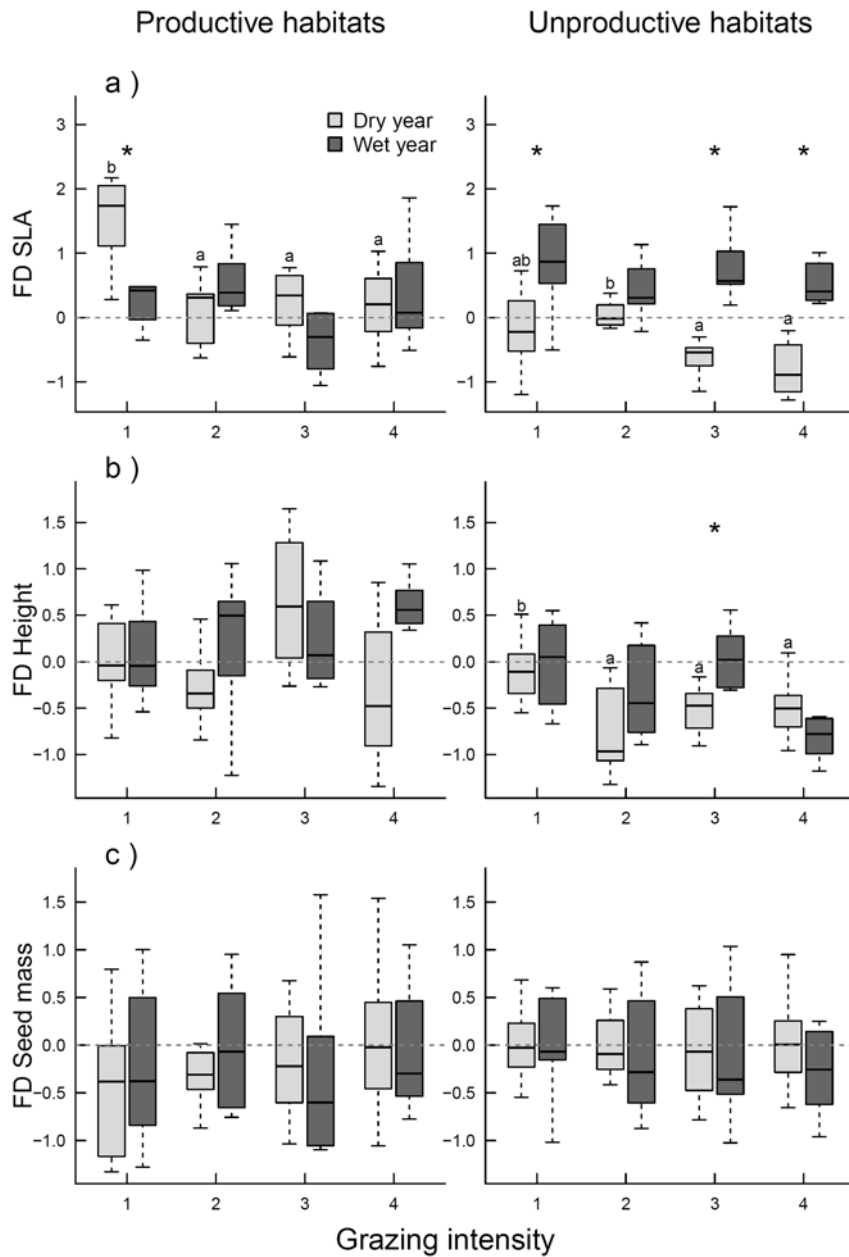
712

713 **Figure 1.** Boxplots showing the effect of grazing intensity and year on the community weighted
 714 mean values of the different functional traits for each grazing intensity level and year, in
 715 productive (left) and unproductive (right) habitats. When the effect of grazing is significant,
 716 different letters for each year (lower case for the dry year and upper case for the wet year)
 717 indicate significant differences between grazing intensity levels. Similarly, asterisks show
 718 significant differences between years for a given habitat type and grazing intensity level. Outliers
 719 are not shown to improve the clarity of the figures.
 720



722

723 **Figure 2.** Boxplots showing the effect of grazing intensity and year on functional richness (FR;
 724 SESRao_{pr}) values of the different functional traits for each grazing intensity level and year, in
 725 productive (left) and unproductive (right) habitats. Interpretation of the statistical results is as in
 726 Fig. 1. Outliers are not shown to improve the clarity of the figures.
 727



730 **Figure 3.** Boxplots showing the effect of grazing intensity and year on functional divergence
 731 (FD; SESRao_{ab}) values of the different functional traits for each grazing intensity level and year,
 732 in productive (left) and unproductive (right) habitats. Interpretation of the statistical results is as
 733 in Fig. 1. Outliers are not shown to improve the clarity of the figures.