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1 RESEARCH ARTICLE

2 **Species dominance rather than complementarity drives community digestibility and litter**
3 **decomposition in species-rich Mediterranean rangelands**

4
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18
19 **Running head:** Digestibility and decomposability linkages

20 **ABSTRACT**

21 **Questions:** Management practices in permanent grasslands affect plant communities structure and
22 thus resources for both the herbivore and the decomposer subsystems. While their effects on
23 digestibility or litter decomposition had been studied separately, few, if any, studies have tested
24 their responses simultaneously and the underlying relationships with communities functional
25 structure. We tested whether the mass ratio hypothesis or the niche complementarity hypothesis
26 held in the scaling-up from species to community level.

27 **Location:** Dry calcareous rangelands of southern France on a limestone plateau

28 **Methods:** We measured digestibility and litter decomposability of 24 communities in three
29 management regimes representing an intensification gradient corresponding to a combination of
30 increased fertility and grazing. Key structural leaf traits (e.g. Leaf Dry Matter Content, LDMC) and
31 chemical traits (e.g. Leaf Nitrogen content, LNC and Leaf Neutral Detergent Fibre, LNDF) were
32 measured as well as communities mean (i.e. Community Weighted Means, CWM) and variance (i.e.
33 Community Weighted Variances, CWV).

34 **Results:** Digestibility and litter decomposability were higher in intensively grazed and fertilized
35 than in lightly grazed and abandoned communities. Increased nutrient availability combined with
36 more intense grazing induced an increase in CWM LNC and a decrease in CWM LDMC and CWM
37 LNDF. Communities in these regimes were less functionally diversified, with lower CWV LDMC and
38 lower CWV LNDF.

39 **Conclusions:** The close relationship between digestibility and decomposability was maintained at
40 the community level. Relationships between CWM, community digestibility and decomposability
41 were more consistent across the management regimes than relationships with CWV, supporting the
42 dominance rather than the complementarity hypothesis.

43
44 **KEYWORDS:** Community weighted mean (CWM); community weighted variance (CWV);
45 decomposability; dry matter digestibility; functional trait; management regime; rangeland

47 **Introduction**

48 Permanent grasslands are of great importance for food production, nature conservation and other
49 ecosystem services due to their high biodiversity (Habel et al., 2013; Bullock et al.; Lemaire et al.,
50 2011). In these systems, in addition to the pedoclimatic conditions, management practices such as
51 grazing, mowing and mineral or organic fertilization, affect plant communities structure and
52 composition by filtering species according to their responses on these practices (Garnier et al.,
53 2016). Understanding the effects of management practices on the functional composition of plant
54 communities is essential, as this composition affect carbon and nutrient cycling by providing
55 resources for both herbivores and the decomposer subsystem (Hobbie, 1992; Berendse, 1994; Aerts
56 & Chapin, 1980). More precisely, plant communities control two major ecosystem properties in
57 permanent grasslands, namely green dry mass digestibility, a critical component of herbage
58 nutritive value, and litter decomposition. Dry mass digestibility and litter decomposition can be
59 considered as two degradation processes, the first one occurring in the digestive tracts of herbivores
60 and the second one mediated by soil macrofauna and microbial activity. On the one hand, dry
61 matter digestibility is a critical component of herbage nutritive value and provides a synthetic
62 measure of the amount of energy available for herbivores in plant constituents (Bruinenberg et al.,
63 2002). On the other hand, decomposition of dead plant material is a key component of nutrient and
64 carbon fluxes in most terrestrial ecosystems (Chapin et al., 2002), since it determines the rate at
65 which carbon and nutrients are mineralized from plant litter. It is thus essential to understand how
66 changes in grassland management modify community functional composition and consequently
67 stocks and fluxes of carbon and nitrogen in ecosystems *via* these key processes.

68 The “afterlife effect” hypothesis (Grime et al., 1996) postulates that variations in functional
69 traits of green plants leading to high palatability or digestibility, such as high nitrogen and low
70 structural carbohydrate contents, affect the rate at which senescent leaves decompose (Grime et al.,
71 1996; Cornelissen et al. 1999; 2004; 2004; Pérez-Harguindeguy et al., 2000; Wardle et al. 2002). At
72 the species level, structural traits such as leaf dry matter content (the ratio of leaf dry mass to water

73 saturated fresh mass; LDMC), which relates to fiber content, was found to be negatively related to
74 both digestibility (Al Haj Khaled et al., 2006; Pontes et al., 2007; Bumb et al., 2018) and litter
75 decomposition (Kazakou et al., 2006, 2009; Bumb et al., 2018), while chemical traits, such as leaf
76 nitrogen content *per* unit mass (LNC) were found to be positively linked to digestibility (Al Haj
77 Khaled et al., 2006; Pontes et al., 2007) and litter decomposition (Cornwell et al., 2008). Carbon-
78 rich structural compounds, particularly lignin, strengthen leaves significantly and influence leaf
79 digestibility and litter decomposition (Schadler et al.2003). Whether this holds at the community
80 level in species-rich grasslands, where plants grow and decompose in mixtures remains to be tested.
81 This will allow us to predict the consequences of management practices on plant species
82 diversification and ecosystem processes in permanent grasslands.

83 The effects of management practices in permanent grasslands on digestibility and litter
84 decomposition have been studied separately for each process (e.g. Gardarin et al., 2014 for
85 digestibility and Fortunel et al., 2009 for litter decomposition), but few, if any, studies have tested
86 the responses of these two processes simultaneously and how they relate to the functional structure
87 of communities. More specifically, the identification of the respective roles of the distinct
88 components of this structure, namely the *mean value* and the *variability* of the traits of individuals
89 affecting digestibility and decomposition remains an open question (see Garnier et al., 2016 for a
90 review on these effects on a range of ecosystem properties). The dominance hypothesis, based on
91 the idea that dominant species have a major impact on ecosystem processes comparatively to other
92 species, appears to apply in explaining the digestibility of the biomass and decomposability of
93 species-rich communities. Studies conducted at the community level on either properties showed
94 that leaf dry matter content (LDMC), a trait affecting the trade-off between fast-growth vs. physical
95 or chemical protection of herbaceous species, had consistent effects on both digestibility (Duru et
96 al., 2008; Ansquer et al., 2008; Andueza et al., 2010; Gardarin et al., 2014) and litter mass loss via
97 decomposition (Garnier et al., 2004; Quested et al., 2007; Cortez et al., 2007; Quétier et al., 2007;
98 Fortunel et al., 2009). High grazing and fertilization can induce a modification in species

99 composition over time (Chollet et al., 2014), favorizing species with acquisition strategies with high
100 nitrogen concentration and low fiber content and low dry matter content likely to allow
101 compensatory growth after grazing (Herms and Mattson, 1992) resulting in higher digestibility and
102 decomposability. By contrast communities experiencing lower disturbance intensity or longer time
103 since last disturbance, will be dominated by conservative species with high LDMC (Pontes et al.,
104 2007), tannin concentration and fiber content, protecting plants from herbivory *via* efficient defence
105 mechanisms (Herms and Mattson, 1992) and thus lower digestibility and decomposability.

106 However, in most studies, mixed litters (*i.e.* composed of several species) decompose more
107 rapidly than the expected average value of decomposition from single-species litter experiments and
108 this synergistic effect of litter mixing can be explained by higher trait dissimilarities (Porre *et al.*
109 2020). However, the effects of functional divergence postulated by the niche complementarity
110 hypothesis, on biomass digestibility and litter decomposition, have been harder to demonstrate as
111 studies suggested either positive, either negative, or non-existent effects among species with
112 different trait values (Diaz et al., 2007; Mokany et al., 2008; Laughlin et al., 2011; but see
113 Schumacher & Roscher, 2009). To explain non-additive mass loss, the nutrient transfer hypothesis
114 is most frequently mentioned. This hypothesis states that decomposers preferentially feed on high
115 nitrogen litters. Subsequently nitrogen is released and could then be transferred to the low nitrogen
116 litter and thus facilitate the decomposition of the more recalcitrant litter, resulting in non-additive
117 mass loss in mixtures by accelerating the decomposition rate of the more recalcitrant litter
118 (Hättenschwiler et al., 2005). Other potential mechanisms of leaf litter diversity effects on
119 decomposition include also transfer of deterrent compounds by leaching decomposers'
120 complementary use of resources (Hättenschwiler et al., 2005) and changes in stimulation and
121 suppression of decomposers' activity (Gessner et al. 2010).

122 In the present study we propose to test whether the relationships between dry matter
123 digestibility and decomposition in Mediterranean rangelands, subject to management regimes
124 differing in intensity of grazing and fertilization, found at the species level (Bumb et al., 2018) were

125 maintained at the community level. More precisely, we expect that higher levels of disturbance, as
126 intense grazing and fertilization, would allow only acquisitive species to thrive, thus increasing the
127 communities digestibility and decomposition. This species selection would also decrease
128 communities' functional divergence leading to synergistic effects on digestibility and
129 decomposability. More precisely, we hypothesized that leaf and litter of higher qualities could share
130 nutrients with lower quality leaves and litters to promote digestibility and decomposability, while
131 lower quality leaves and litters might transmit specific secondary compounds (tannins or phenolics).
132 In long-abandoned grasslands, where more conservative species whose leaves have a high LDMC
133 and low nitrogen contents become dominant (Peco et al., 2012; Kahmen & Poschlod, 2004), we
134 hypothesize that trait functional convergence can lead to a decrease of the two processes, as
135 recalcitrant compounds that leach from low-quality leaf and litter could decrease digestibility and
136 retard the decomposition of high-quality litter in mixtures. To summarize, we asked the four
137 following questions: (1) how do communities digestibility and litter decomposition differ among
138 management regimes? (2) how do these management regimes affect the community weighted mean
139 (CWM hereafter) and the community weighted variance (CWV hereafter) different leaf traits? (3)
140 are differences in digestibility and litter mass loss best explained by dominance or complementarity
141 effects? (4) which trait best relates to the two processes?

142

143 **Material and methods**

144 *Study site, experimental design and plant species*

145 The study was conducted in dry calcareous rangelands of southern France located on a limestone
146 plateau (Larzac Causse) at the INRA "La Fage" experimental station (French National Institute for
147 Agricultural Research) (43°56'N, 3°06'E, 765-830 m above sea level) (Molenat et al., 2005). The
148 climate of the plateau is sub-humid with a Mediterranean influence, with cool wet winters and
149 warm dry summers. Annual mean precipitation of 1070 mm occurs mainly during spring and
150 autumn, and mean monthly temperatures vary from 1°C in January to 19°C in August (data from

151 1973-2006). Vegetation is dominated by perennial herbaceous species (*Bromopsis erecta*), along
152 with loosely scattered shrubs and trees (*Buxus sempervirens* and *Juniperus oxycedrus*) (Bernard,
153 1996). Since 1972, the station's 280 ha of rangelands have been grazed by a sheep flock (Romane
154 breed) raised outdoors year-round for meat production.

155 The experimental station is divided into paddocks that vary from 4.7 to 24.5 ha which are
156 subjected to three different management regimes representing an intensification gradient
157 corresponding to an a combination of increased fertility and grazing (for a detailed description see
158 Garnier et al., 2018). We selected seven of these paddocks which were close to one another and
159 comparable in terms of soil composition and topography. The first most intense regime consisted of
160 fertilization and grazing ("G+F" regime hereafter) and corresponds to three paddocks, which were
161 fertilized with nitrogen (60 kg/ha each year, half of them in spring and the other half in autumn) and
162 phosphorus (40 kg/ha during spring every 3 years) over the 1978–2005 period. In these G+F
163 paddocks, increased fertilization was accompanied by an increase in the intensity of disturbance: the
164 proportion of biomass removed annually by grazing relative to the total biomass produced increased
165 from 0.20 kg kg⁻¹ (which corresponds to a stocking rate of c. 1 sheep/ha) to 0.61 kg kg⁻¹, with the
166 establishment of intense grazing in spring during the peak of biomass production. The second
167 management regime, applied since 1972, consisted of moderate grazing starting in early May of
168 0.20 kg kg⁻¹, without fertilization ("GU" regime hereafter) and corresponds to three unfertilized
169 paddocks, maintained under traditional management practices. Finally, a third management regime
170 consisting in suppression of grazing without fertilization was applied since 1987 ("UU" hereafter),
171 corresponds only to one paddocks as this regime is not a main practice of the experimental station.

172 *Species abundance and sampling of green and standing litter biomass*

173 Plant material was collected in several plots which covered 200-500 m² in each of the different
174 paddocks (9 plots of the G+F and GU regimes and 6 plots of the UU regime). In total we considered
175 24 plots. Biomass sampling was conducted during two periods: at the peak of biomass production
176

177 for the green material used for measuring dry mass digestibility and during plant senescence at the
178 end of the summer for estimating litter decomposability. More precisely, during spring 2014,
179 species abundance in each plot was estimated using the point quadrat method at the peak of
180 biomass, which differed according to management regime (end of May for the G+F regime, early
181 June for the GU and mid-June for the UU regime, in order to have species at same phenological
182 stage for all the management regime). We used one 0.75 m² quadrat per plot, i.e. 24 quadrats in
183 total. Then, the green plant material present in each quadrat was sampled and all dead plant parts
184 were removed from the sample. The 24 samples were dried in the oven during 72h at 60°C. In
185 August 2014, at the season of maximum standing litter mass, vegetation present in 0.75 m² quadrats
186 located close to those used for botanical relevés, was collected. Vegetation was then sorted in order
187 to keep only the litter of the community present at that time (mixing litter of leaves, stems and
188 reproductive parts of the different species present) and dried in an oven during 72h at 60°C.

189

190 *Measurements of dry matter digestibility*

191 Dry matter digestibility was determined at the community level from the green vegetation sampled
192 in each quadrat. Dried and ground samples of plant communities were analysed using near-infrared
193 reflectance spectroscopy in ring cells equipped with quartz glass. Reflectance spectra were collected
194 from duplicate samples using a FOSS Nirsystem 6500 spectrometer (FOSS Nirsystems, Silver
195 Spring, MD, USA) operating at 400-2500 nm. Calibrations previously available were updated and
196 adapted to our samples with reference analyses of 24 samples representative of our dataset.
197 Calibration was performed using modified partial least square regression using the WINISI software
198 (Infrasoft International, Port Matilda, PA, USA) (for more details see Bumb et al., 2016). In order to
199 perform new calibrations dry matter digestibility (g kg⁻¹) was estimated *via* measurements of in
200 vitro Dry matter digestibility by the pepsin-cellulase method of Aufrère et al. (2007).

201

202 *Litter mass loss measurements*

203 The litter collected in each quadrat was divided into four sub-samples (*i.e.* four litterbags per plot)
204 treated as replicates. During autumn 2014, the litter of each community was incubated in
205 microcosms in the laboratory, under controlled temperature and humidity conditions. The four
206 subsamples of each litter community (between 0.40 and 2.10 g \pm 0.01 g) per management regime
207 were sealed in a nylon litter bag of 1 mm mesh (Northern Mesh, Oldham, UK). Each litter sample
208 (96 samples in total) was weighed in order to have the exact initial mass (*Litter mass_{initial}*).
209 Microcosms, as simplified analogues of natural ecosystems, allow the study of litter decomposition
210 by controlling temperature and humidity, with similar soil conditions and decomposer populations,
211 while maintaining a sufficiently natural situation so that results of laboratory tests may be
212 extrapolated to the field situation with confidence (Taylor & Parkinson, 1988). This method allows
213 to test only the effect of litter quality on litter mass loss (hereafter “decomposability”) by limiting
214 the effect of pedoclimatic conditions and soil organisms. The microcosm type used for this
215 experiment was described by Taylor and Parkinson (1988). Each microcosm chamber, 15 cm high,
216 was made of a 15 cm diameter polyvinylchloride pipe, fitted with a lid and a sealed bottom. The lid
217 could be opened to allow gas exchange and the plug at the bottom could be removed to drain excess
218 water. A grid, 2 cm above the bottom, divided the chamber into two unequal parts: a usable space of
219 1.5 L capacity and a drainage compartment of 300 mL. One kilogram of soil, of known water-
220 holding capacity, was placed on the grid. The soil was a standardized humus substrat composed by
221 a 3:1 mixture of mineral soil and surface organic horizon taken from the experimental garden of
222 CEFE in Montpellier (43°38’N, 3°52’E). The soil was subsequently moistened up to 80% of field
223 capacity. The microcosms were kept in the dark at 24°C in mean throughout the experiment and
224 watered once a week to maintain constant soil moisture during the eight weeks of incubation. After
225 eight weeks, the litter bags were taken out of the microcosms. Soil particles were carefully removed
226 from the litter bags and the litter samples were weighed after drying for 48 h at 60 °C to determine
227 the percentage of litter mass loss. Litter mass loss was calculated as:

228
$$\text{Litter mass loss (\%)} = \left(\frac{\text{Litter mass}_{\text{initial}} - \text{Litter mass}_{\text{after incubation}}}{\text{Litter mass}_{\text{initial}}} \right) \times 100\%$$

229 where *Litter mass_{initial}* (g) is initial litter mass before incubation and *Litter mass_{after incubation}* (g) is the
230 remaining mass after 8 weeks of incubation in microcosms.

231

232 *Traits of green and litter organs: sampling and measurements*

233 Based on botanical surveys of the plots, we selected 26 species among the most abundant ones
234 (Appendix 1), representing a large range of botanical families, growth forms and trait values. More
235 precisely, plant species were classified into three form categories: “tussocks” (mostly Poaceae
236 species), “rosettes” and “extensive and stemmed herbs” (Appendix 1). Among these species, 16
237 were collected and measured at the peak of biomass (end of May for G+F and mid-June for GU and
238 UU) in 2013 (data published in Bumb et al., 2018) and 10 additional species in 2014. In total we
239 considered 35 plant populations (i.e. species present in a treatment regime, Appendix 1).

240 Measurements on green leaves were conducted on at least 12 individuals per species in each plot
241 during spring 2013 or 2014, according to species considered, on the youngest fully expanded, well-
242 lit leaves at their peak period of growth (we measured 35 populations x 12 repetitions= 420 leaves
243 collected outside the quadrats as a whole). After harvesting, leaves were immediately placed in a
244 test tube filled with water and placed in a cool box. The tubes were then stored at 4°C for at least 6
245 h to insure full rehydration of the samples (cf. Garnier et al., 2001). Each sample was gently blotted
246 dry before weighing to obtain its water-saturated fresh mass. It was then dried for 72 h at 60°C and
247 weighed to measure dry mass. Leaf dry matter content (LDMC) was calculated as the ratio between
248 the dry mass of leaves and their water-saturated fresh mass. Leaf Nitrogen content *per* mass (LNC)
249 and Leaf fibre content *per* mass (Leaf Neutral Detergent Fibre, LNDF %) for each species were
250 measured using NIRS method. Calibrations were based on the Kjeldhal analysis for NC and Van
251 Soest sequential detergent method with an amyolytic and protease pre-treatment (Van Soest et al.,
252 1991) for NDF.

253

254 *Trait distributions in communities*

255 To characterize the functional structure of communities, we calculated the mean and the variance of
256 trait values, weighted by species abundances. The community-weighted mean (CWM) for each trait
257 t was calculated as the sum for the S species in each plot, of the mean trait value of species i in a
258 given treatment (species population per management regime), t_i , weighted by its relative abundance,
259 p_i (Garnier et al., 2004):

$$260 \quad CWM_{trait_i} = \sum_{i=1}^s p_i \times t_i$$

261 Community-weighted trait variances (CWV) were computed for each trait in each plot as follows
262 (Sonnier et al., 2010):

$$263 \quad CWV_{trait_i} = \sum_{i=1}^s p_i \times (t_i - CWM)^2$$

264 *Data analysis*

265 Statistical analyses were performed with R software (R Development Core Team 2010). ANOVA
266 was used to test the influence of management regime on dry matter digestibility, litter mass loss,
267 CWM and CWV of traits of green plant material. The normality of the distribution of residues was
268 verified for each model. When management regime effect was detected, Tukey tests were used to
269 discriminate among them. Spearman correlations were calculated to test relationships between dry
270 matter digestibility, litter mass loss, CWM and CWV of the different traits.

271 We performed principal components analysis (PCA) using the ade4 R package (Dray &
272 Dufour, 2007) to determine the relationships among CWM and CWV across communities. We
273 tested differences between management regimes using one-way analysis of variance (ANOVA),
274 followed by a Tukey test.

275 To quantify the respective role of CWM and CWV leaf traits on dry matter digestibility and
276 litter decomposition, we performed multiple regressions. We used a stepwise approach to select the
277 best model and we based this on the corrected Akaike information criterion (package glmulti,
278 function glmulti). We tested the variance inflation factor (VIF) (package car, function vif) in order
279 to avoid collinearity between variables. We considered variables presenting VIF <5 in the model

280 (Kutner et al., 2004). If collinearity between variables was high, we used loading of species on PCA
281 axis 1, 2 and 3 in the regressions instead of individual traits. We calculated the partial η^2 (package
282 heplots, function etasq) to provide a measure of the relative importance of each variable
283 representing the proportion of the total variability attributable to a given factor. After selection of
284 variables (the AIC criterion was used), we checked and confirmed the homoscedasticity and
285 normality of the residuals of each best model.

286

287 **Results**

288 *Management effects on community digestibility, litter mass loss and community functional structure*

289 Communities in the high grazing and fertility regime (G+F) were dominated by grass species (89.2
290 %), and especially by *Bromopsis erecta* representing by average a proportion of 69.9 % ($F=5.57^*$)
291 (Appendix 2). The dominance by grasses was less pronounced in the moderate grazing and
292 unfertilized regime (GU) (61.9 %) and the ungrazed and unfertilized regime (UU) (65.5 %), where
293 *B. erecta* was co-dominant (23.9 % and 36.5 % respectively) with *Festuca christiani-bernardii*
294 (32.6 % and 24.2 % respectively) (Appendix 2). There were slight, but non-significant differences
295 ($F=2.01^{ns}$) in species richness among management regimes: 13.8 ± 0.9 , 12.6 ± 1.06 and 10.2 ± 0.77
296 species per m^2 in the G+F, GU and UU regimes, respectively. No significant differences in growth
297 form proportions were found among management regimes: the three communities presented the
298 same proportion in tussocks (80.2%, 67.2% and 78.2% in the G+F, GU and UU regimes,
299 respectively; $F_{management}=2.57^{ns}$), rosettes (3.54%, 5.21% and 3.55% in the G+F, GU and UU
300 regimes respectively; $F_{management}=0.43^{ns}$) and extensive and stemmed-herbs (16.3%, 27.6% and
301 18.3% in the G+F, GU and UU regimes, respectively; $F_{management}=1.38^{ns}$).

302 Our data showed a large variation in dry matter digestibility (322-615 $mg\ g^{-1}$) and litter mass
303 loss (16.2-45.5 $mg\ g^{-1}$) across the 24 communities (Fig. 1), associated to variation in species
304 composition across the different management regimes: dry matter digestibility and litter
305 decomposition were higher in the G+F treatment as compared to the GU and UU treatments in

306 which these were not significantly different ($F_{\text{management}} = 22.5^{***}$ for digestibility and $F_{\text{management}} =$
307 19.2^{***} for litter mass loss). Digestibility was lower in the UU treatment (not significantly), but
308 this is not the case for decomposability.

309 The management regime also influenced the functional structure of the communities:
310 community weighted means of leaf dry matter content (CWM LDMC) (range 277-488 mg g⁻¹) and
311 of leaf neutral detergent fibre content (CWM LNDF) (range 50.7-72.8%) were lower. Community
312 weighted mean of leaf nitrogen content (CWM LNC) (range 7.1-17.2 mg g⁻¹) was higher in the G+F
313 treatment than in the GU or UU treatments (Fig. 2a, 2b, 2c). Community weighed variances of leaf
314 dry matter content (CWV LDMC) and of leaf neutral detergent fibre content (CWV LNDF) were
315 higher in the GU treatment (Fig. 2d and 2e), whereas community weighed variance of leaf nitrogen
316 content (CWV LNC) did not vary significantly among treatments (Fig. 2f).

317

318 *Covariation of indicators of community functional structure*

319 The first axis of the PCA accounted for nearly 49.35% of total inertia, while the second axis
320 accounted for 36.64 % (Fig. 3a). Axis 1 was determined by CWM LDMC and CWM LNDF
321 opposed to CWM LNC. Communities in high grazing intensity and fertilisation regime (G+F) were
322 composed of species with high LNC and low LDMC and LNDF whereas the opposite pattern was
323 found in communities with moderate and no grazing. Loadings of the communities varied
324 significantly on axis 1 according to management regime, discriminating the G+F regime from the
325 two others ($F_{\text{axis1}} = 21.21^{***}$, Fig. 3b). The second axis opposed CWV LNC, CWV LNDF and
326 CWV LNDF to CWM LNDF. Communities presenting high traits variability were opposed to
327 communities composed by species with high values of LNDF (Fig. 3b). Loadings of the
328 communities in the second PCA axis did not vary with management regime.

329

330 *Links between the dry matter digestibility, litter mass loss and community functional structure*

331 A strong positive correlation was found between dry matter digestibility and litter mass loss
332 measured at the community level (Fig. 1, $r=0.80^{***}$). Dry matter digestibility and litter mass loss
333 were both negatively related to CWM LDMC and positively related to CWM LNC (Table 1, Fig.4a,
334 4d). Additionally, digestibility was negatively related to CWM LNDF (Table 1, Fig.4b), while the
335 relationship was not significant with decomposability (Table 1, Fig. 4e). Our results showed a
336 negative relationship between CWV LDMC the two processes (Table 1). Additionally, CWV
337 LNDF was negatively correlated to litter mass loss (Table 1). Both dry matter digestibility and litter
338 mass loss were negatively correlated with the loadings of the first axis of the PCA ($r=-0.9^{***}$ for
339 digestibility and $r=-0.79^{***}$ for litter mass loss, Appendix 3a, 3c) but not with the loading of the
340 second axis (Appendix 3b, 3d).

341 342 *Relative influence of CWM and CWV traits on digestibility and litter mass loss*

343 We used multiple model evaluation to compare the respective role of different community
344 functional parameters (CWM and CWV) on dry matter digestibility and litter decomposition
345 (Appendix 4). Due to the high collinearity between variables, we choose to first consider models
346 with the PCA loadings. Multiple regression models indicated that loadings of the first PCA axis
347 (88.16% relative importance) and loadings of the second axis (11.84% relative importance) were
348 the main contributors to the dry mass digestibility, but only the loading of the first axis were
349 significant (Table 2). For litter mass loss, the multiple regression model showed that only the
350 loading of the first axis were retained (Table 2). This results indicate that litter decomposition was
351 mainly driven by communities weighted means.

352 353 **Discussion**

354 *Effects of management practices on digestibility and decomposability*

355 Our results support the hypothesized effect of management regimes on dry matter digestibility and
356 litter decomposition. Fertilization combined with more intense grazing in the G+F regime induced

357 higher dry matter digestibility and litter decomposability than those in the GU and UU regimes. No
358 difference in dry matter digestibility and decomposability was found between the GU and UU
359 regimes. This can be the consequence of the comparable nutrient availability in these two latter
360 regimes (see Bumb et al. 2018 for more details on the nitrogen and phosphorous nutrient index),
361 and suggests a weak effect of grazing, which remains relatively low in the GU regime, on the two
362 processes. The same responses of community digestibility and litter mass loss on G+F and GU
363 regimes were also found at the species levels for leaf and stems Bumb et al. (2018).

364 In the studied communities, digestibility decreased with the decrease of disturbance
365 intensity. This finding is in accordance with previous studies in other species-rich grasslands (e.g.
366 Louault et al., 2005; Ansquer et al., 2008; Henkin et al., 2011, Gardarin et al. 2014).

367 Litter mass loss showed the same pattern of variation as digestibility. More precisely, we
368 also found that litter decomposability was significantly higher under high grazing pressure and
369 nutrient availability. If the effect of grazing on litter quality has been demonstrated in previous
370 studies (e.g. Wang et al., 2018), the effect of fertilization on litter decomposition (and the combined
371 effect of these two factors) is not clearly demonstrated. Nutrient availability can have either
372 positive, negative or neutral effects on litter decomposition (Wardle et al., 2004; Knorr et al., 2005;
373 Hobbie, 1992; Riggs et al., 2015; Kazakou et al., 2009). Grazing can affect decomposition by
374 altering either the quantity of resources returned to the soil (plant litter production), or the quality of
375 the resources (especially the quantity of nutrients returned to the soil as dung and urine), or through
376 changes in the composition of plant communities (Bardgett & Wardle, 2003). Only this latter effect
377 was considered in our study, as litter decomposability was measured in microcosms where soil
378 conditions and decomposers communities were homogenous between litter samples. We
379 demonstrated that fertile habitats which support high herbivory, corresponding to the G+F regime,
380 are susceptible to cause positive feedbacks in ecosystems because communities of such habitats are
381 more digestible and produce litter that decomposes faster. In infertile habitats with low grazing
382 intensity corresponding to GU regime, positive feedbacks can also occur, as communities of such

383 infertile habitats have more persistent and less digestible organs, and produce recalcitrant litters
384 with low decomposition.

385

386 *Effects of management practices on functional structure of the communities*

387 Intensive grazing and nutrient availability impact communities composition and affect functioning
388 of rangelands by altering species richness and species abundances (Semmartin et al., 2008; Wu &
389 Baldin, 2009). In the studied permanent grasslands, the G+F treatment was dominated by *B. erecta*
390 species, whereas the GU and UU regimes were co-dominated by *B. erecta* and *F. christiani-*
391 *bernardii*. Regarding plant life forms, our results showed that management regimes did not filter
392 species according to their life forms, in contrast with finding of previous studies indicating that
393 grazing favors prostrate over erect plants and rosette architecture over tussock architecture (Diaz et
394 al. 2007). In the same permanent grasslands, Garnier et al. (2018) found that in spite of changes in
395 species abundance, over a 28-year period, in response to increased fertilization and grazing
396 pressure, species richness remained similar in the three management regimes. This suggests that the
397 higher grazing intensity could be supported at this higher resource level without altering species
398 number (Cingolani et al., 2005). Our results showed that changes in species composition induced
399 changes in the functional structure of communities expressed by community weighted mean
400 (CWM) and community weighed variance (CWV) of traits. Increased nutrient availability
401 combined with more intense grazing in the G+F regime induced an increase in CWM LNC and a
402 decrease in CWM LDMC and CWM LNDF. This indicates that management intensification leads to
403 the exclusion of species with high LDMC, while species with opposite trait values either tolerate or
404 benefit from the new conditions created by the high nutrient availability and grazing pressure. In
405 addition, in a previous study conducted in the same grasslands changes in trait values in the same
406 direction were observed at the intraspecific level: fertilization consistently induced an increase in
407 LNC and a decrease in LNDF and LDMC in four species found at both G+F and GU regimes
408 (Bumb et al., 2018).

409 In addition to changes in CWM values, community weighted variances of traits (CWV)
410 were also modified according to management regimes: communities in the G+F regimes were less
411 functionally diversified, with lower CWV LDMC and lower CWV LNDF. The observed lower
412 functional divergence under high grazing pressure and nutrient availability was also found in
413 different rangelands (for a review see Garnier et al., 2016). GU communities presented the higher
414 values of CWV for LDMC and LNDF, recalling the intermediate disturbance hypothesis stating that
415 species diversity would be highest at a moderate intensity of disturbance (Connell, 1978; Huston,
416 1979). Our data showed that there exists a hump-shaped relationship between CWM LDMC and
417 CWV LDMC and a negative relationship between CWM LNDF and CWV LNDF values. Dias et al.
418 (2013) suggested that CWM and different functional diversity indices generally showed a hump-
419 shaped relationship. This means that more extreme CWM values are having lower CWV values.
420 Our results confirmed this pattern only for LDMC trait values showing that grazed and fertilized
421 communities had lower CWM and thus CWV LDMC values and in the contrary moderate grazed
422 and unfertilized communities presented higher CWM and CWV LDMC values. This relationship
423 can be explained by the fact that when CWM values approach the lower bounds of the trait range,
424 functional diversity will decrease because only species with similar trait values (low LDMC in the
425 case of G+F management regime) will be present, leading to a hump-shaped relationship between
426 CWM and functional diversity index. So, due to the non-independence between CWM and CWV
427 trait values in our study, it seems more appropriate to consider the PCA axis and no single trait
428 values for explaining the trait effects on the studied processes.

429

430 *Relative importance of dominance and complementarity hypothesis*

431 The originality of our study is the scaling of the ‘afterlife effect’ hypothesis from the species to the
432 community level. To our knowledge, only White et al. (2004) had previously shown a significant
433 relationship between dry matter digestibility and litter mass loss among communities. This result is
434 in agreement with previous studies conducted at the species level, which showed significant

435 relationships between palatability and decomposability on the one hand (Grime et al., 1996;
436 Cornelissen et al., 1999, Schädler et al., 2003; Kurokawa et al., 2010) and digestibility and
437 decomposability on the other hand (Cornelissen et al., 2004; Bumb et al., 2018). The underlying
438 explanation of this finding is the fact that both dry mass digestibility and litter decomposability are
439 driven by the same traits.

440 Community dry matter digestibility was mainly predicted by CWM (loading of the first axis
441 of PCA) and especially CWM LDMC (Appendix 2). This result is in agreement with the dominance
442 hypothesis and confirms previous results on green leaves linking directly digestibility with CWM
443 LDMC (Andueza et al., 2010; Gardarin et al., 2014). In particular, Gardarin et al. (2014)
444 demonstrated that LDMC had the most consistent effects on digestibility, within and among sites.
445 Accordingly, in our study LDMC was the only significant trait retained in the regression analysis.
446 Our results showed that more digestible communities tended to have low weighted variance of
447 traits, but this result even if it was retained by the model selection it was not significant. This
448 pattern was previously found when productivity in the same rangelands was related to weighted
449 variance of LDMC (Chollet et al., 2014). Negative LDMC diversity effects on dry matter
450 digestibility suggests that dominance by species with low LDMC values, rather than a set of
451 coexisting species with diverse LDMC, results in higher dry matter digestibility.

452 Leaf litter mass loss was strongly related to CWM trait values, lending further support to the
453 mass-ratio hypothesis, suggesting that mixed-species litter decomposition is predominantly driven
454 by the litter quality of the most abundant species (Grime, 1998; Laughlin et al., 2011). Litter
455 decomposition was negatively correlated to CWM LDMC as previously found in old-field
456 communities (Garnier et al., 2004; Cortez et al., 2007) and in disturbed herbaceous communities
457 (Quested et al., 2007; Fortunel et al., 2009; Pakeman, 2011). Communities from GU and UU
458 regimes produced a litter mixture that was less appealing to detritivores due to dilution of essential
459 nutrients and increasing content of more recalcitrant compounds. Community litter decomposability
460 was also negatively correlated to CWM LNDF, in accordance with previous findings at the species

461 level in old-fields (Kazakou et al., 2007) and in the same rangelands (Bumb et al., 2018). In terms
462 of chemical composition, high LNDF values correspond to leaves rich in (hemi)cellulose, insoluble
463 sugars and lignin (Poorter and Bergkotte, 1992). Our results confirmed that high concentrations of
464 lignin and other carbon-rich compounds, particularly when invested in fibres, strengthen living
465 leaves and considerably affect decomposition rates. Litter mass loss was positively correlated to
466 CWM LNC which is consistent with previous studies (Santiago, 2007; Cornwell et al., 2008;
467 Fortunel et al., 2009; Bakker et al., 2011). Decomposers prefer nitrogen-rich leaves as nitrogen is an
468 essential and limiting element for their metabolism.

469 Functional diversity did not affect litter mass loss. Even if we found that an increased
470 variance in LDMC can induce a decrease in litter decomposability, this effect was mainly due to the
471 GU communities, which are the more diverse communities in terms of species and also trait values.
472 Our results do not agree with the ‘synergistic effects’ of biodiversity on litter mass loss which
473 suggest that the common bacterial community could process similar litter species more efficiently,
474 as previously found by Chapman & Koch (2007). While several mechanisms have been postulated
475 to explain the positive effect of litter mixtures on litter mass loss (cf. e.g. Wardle et al., 1997), other
476 studies found that functional diversity had no significant or negative effects on litter mixture
477 decomposition (for exemple Frainer et al., 2015; Tardif & Shipley, 2015).

478

479 **Conclusion**

480 In agreement with our hypothesis, intensively managed regimes induced changes in the functional
481 composition of communities with highly digestible species producing leaves more decomposable
482 than those found in less intensive regimes. In these regimes, communities were composed of less
483 digestible plants producing litter with high amounts of non-labile compounds which decompose
484 slowly. We found a close relationship between digestibility and decomposability, validating the
485 “afterlife effect” hypothesis at the community level. These two ecosystem properties were more

486 tightly related to community-weighted leaf traits than to their variance, which further supports the
487 dominance (Grime, 1998) rather than the complementarity hypothesis (Petchey & Gaston 2006).

488

489 **Authors contributions**

490 **Elena Kazakou:** Conceptualization (equal); methodology (equal); project administration (lead);
491 funding acquisition (lead); formal analysis (equal); writing–original draft (equal); writing–review
492 and editing (lead).

493 **Iris Bumb:** Data curation (lead); formal analysis (equal); methodology (equal); writing–original
494 draft (equal).

495 **Eric Garnier:** Conceptualization (equal); methodology (equal); writing–review and editing (equal).

496

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507

508 **References à vérifier**

509 Aerts, R. & Chapin, F.S. (1980) The Mineral Nutrition of Wild Plants. *Annual Review of Ecology*
510 *and Systematics*, 11 (1), 233–60. <https://doi.org/10.1146/annurev.es.11.110180.001313>.

511 Al Haj Khaled, R., Duru, M., Decruyenaere, V., Jouany, C. & Cruz, P. (2006) Using Leaf Traits to

- 512 Rank Native Grasses According to Their Nutritive Value. *Rangeland Ecology &*
513 *Management*, 59 (6), 648–54. <https://doi.org/10.2111/05-031R2.1>.
- 514 Andueza, D., Cruz, P., Farruggia, A., Baumont, R., Picard, F. & Michalet-Doreau, B. (2010)
515 Nutritive Value of Two Meadows and Relationships with Some Vegetation Traits. *Grass*
516 *and Forage Science*, 65 (3), 325–34. <https://doi.org/10.1111/j.1365-2494.2010.00750.x>.
- 517 Ansquer, P., Duru, M., Theau, J.P. & Cruz, P. (2008) Functional Traits as Indicators of Fodder
518 Provision over a Short Time Scale in Species-Rich Grasslands. *Annals of Botany*, 103 (1),
519 117–26. <https://doi.org/10.1093/aob/mcn215>.
- 520 Aufrère, J., Baumont, R., Delaby, L., Peccatte, J.R., Andrieu, J., & Dulphy, J.P. (2007) Prévion de
521 La Digestibilité Des Fourrages Par La Méthode Pepsine-Cellulase. *Le Point Sur Les*
522 *Équations Proposées*. INRA Productions Animales 20 (129–136).
- 523 Bakker, M.A., Carreño-Rocabado, G. & Poorter, L. (2011) Leaf Economics Traits Predict Litter
524 Decomposition of Tropical Plants and Differ among Land Use Types. *Functional Ecology*,
525 25 (3), 473–83. <https://doi.org/10.1111/j.1365-2435.2010.01802.x>.
- 526 Bardgett, R.D. & Wardle, D.A. (2003) Herbivore-mediated linkages between aboveground and
527 belowground communities. *Ecology*, 84 (9), 2258–68. <https://doi.org/10.1890/02-0274>.
- 528 Berendse, F. (1994) Litter Decomposability - A Neglected Component of Plant Fitness. *Journal of*
529 *Ecology*, 82 (1), 187–90. <https://doi.org/10.2307/2261398>.
- 530 Bernard, C. (1996) *Flore Des Causses Hautes Terres, Gorges, Valées et Vallons* (Aveyron, Lozère,
531 Hérault et Gard). Société Botanique du Centre-Ouest. Vol. 14. Saint-Sulpice-de-Royan.
- 532 Bruinenberg, M.H. Bruinenberg, H. Valk, H. Korevaar, Struik, P.C. (2002). Factors affecting
533 digestibility of temperate forages from semi-natural grasslands: A review. *Grass and Forage*
534 *Science*, 57, 292-301, <https://doi.org/10.1046/j.1365-2494.2002.00327.x>
- 535 Bullock, J., Aronson, J. Newton, A., Pywell, R. & Benayas, J. (2011) Restoration of ecosystem
536 services and biodiversity: Conflicts and opportunities. *Trends in Ecology & Evolution*, 26,
537 541-549. <https://doi.org/10.1016/j.tree.2011.06.011>.

- 538 Bumb, I., Garnier, E., Bastianelli, D., Richarte, J., Bonnal, L. & Kazakou, E. (2016) Influence of
539 management regime and harvest date on the forage quality of rangelands plants: the
540 importance of dry matter content, *AoB PLANTS*, 8, 045,
541 <https://doi.org/10.1093/aobpla/plw045>
- 542 Bumb, I., Garnier, E., Coq, S., Nahmani, J., Del Rey Granada, M., Gimenez, G. & Kazakou E
543 (2018) Traits Determining the Digestibility–Decomposability Relationships in Species from
544 Mediterranean Rangelands. *Annals of Botany*, 121 (3), 459–69.
545 <https://doi.org/10.1093/aob/mcx175>.
- 546 Chapin III, Matson, S.F, Mooney, P.A. (2002). *Principles of Terrestrial Ecosystem Ecology*.
547 <https://doi.org/10.1007/978-1-4419-9504-9>.
- 548 Chapman, S.K. & Koch, G.W. (2007) What Type of Diversity Yields Synergy during Mixed Litter
549 Decomposition in a Natural Forest Ecosystem? *Plant and Soil*, 299 (1), 153–62.
550 <https://doi.org/10.1007/s11104-007-9372-8>.
- 551 Chollet, S., Rambal, S., Fayolle, A., Hubert, D., Foulquié, D. & Garnier E (2014) Combined Effects
552 of Climate, Resource Availability, and Plant Traits on Biomass Produced in a Mediterranean
553 Rangeland. *Ecology*, 95 (3), 737–48. <https://doi.org/10.1890/13-0751.1>.
- 554 Cingolani, A.M., Noy-Meir, I. & Díaz S (2005) Grazing effects on rangeland diversity: a synthesis
555 of contemporary models. *Ecological Applications*, 15 (2), 757–73.
556 <https://doi.org/10.1890/03-5272>.
- 557 Connell, J.H. (1978) Diversity in Tropical Rain Forests and Coral Reefs. *Science*, 199 (4335), 1302.
558 <https://doi.org/10.1126/science.199.4335.1302>.
- 559 Cornelissen, J.H.C., Pérez-Harguindeguy, N., Díaz, S., Marzano B., Cabido, M., Verdardini, F. &
560 Cerabolini B. (1999) Leaf Structure and Defence Control Litter Decomposition Rate across
561 Species and Life Forms in Regional Floras on Two Continents. *New Phytologist*, 143 (1),
562 191–200. <https://doi.org/10.1046/j.1469-8137.1999.00430.x>.
- 563 Cornelissen, J.H.C., Quested, H., Gwynn, D., Van Longtestijn, R.S.P., De Beus, A.H.,

564 Kondratchuk, A., Callaghan TV, Aerts R (2004) Leaf Digestibility and Litter
565 Decomposability Are Related in a Wide Range of Subarctic Plant Species and Types.
566 *Functional Ecology*, 18 (6), 779–86. <https://doi.org/10.1111/j.0269-8463.2004.00900.x>.

567 Cornwell, W., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O.,
568 Hobbie, S.E., et al. (2008) Plant Species Traits Are the Predominant Control on Litter
569 Decomposition Rates within Biomes Worldwide. *Ecology Letters*, 11 (10), 1065–71.
570 <https://doi.org/10.1111/j.1461-0248.2008.01219.x>.

571 Cortez, J., Garnier, E. & Pérez-Harguindeguy, N. 2007. Plant Traits, Litter Quality and
572 Decomposition in a Mediterranean Old-Field Succession. *Plant and Soil*, 296, 19.
573 <https://doi.org/10.1007/s11104-007-9285-6>.

574 Dias, A.T.C., Berg, M.P., de Bello, F., Van Oosten, A.R., Bílá, K. and Moretti, M. (2013), An
575 experimental framework to identify community functional components driving ecosystem
576 processes and services delivery. *J Ecol*, 101: 29-37. [https://doi.org/10.1111/1365-](https://doi.org/10.1111/1365-2745.12024)
577 [2745.12024](https://doi.org/10.1111/1365-2745.12024)

578 Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K. & Robson, T.M. (2007) Incorporating
579 Plant Functional Diversity Effects in Ecosystem Service Assessments. *Proceedings of the*
580 *National Academy of Sciences*, 104 (52), 20684. <https://doi.org/10.1073/pnas.0704716104>.

581 Duru, M., Cruz, P., Al Haj Khaled, R., Ducourtieux, C. & Theau, J.P. (2008) Relevance of Plant
582 Functional Types Based on Leaf Dry Matter Content for Assessing Digestibility of Native
583 Grass Species and Species-Rich Grassland Communities in Spring. *Agronomy Journal*, 100
584 (6), 1622–30. <https://doi.org/10.2134/agronj2008.0003>.

585 Dray, S., & Dufour, A.B. (2007) The ade4 Package: Implementing the Duality Diagram for
586 Ecologists. *Journal of Statistical Software*, 22(4), 1–20.
587 <https://doi.org/10.18637/jss.v022.i04>

588 Fortunel, C., Garnier, E., Joffre, R., Kazakou, E., Quested, H., Grigulis, K., Lavorel, S., et al. (2009)
589 Leaf Traits Capture the Effects of Land Use Changes and Climate on Litter

- 590 Decomposability of Grasslands across Europe. *Ecology*, 90 (3), 598–611.
591 <https://doi.org/10.1890/08-0418.1>.
- 592 Frainer, A., Moretti, M.S., Xu, W. & Gessner, M.O. (2015) No Evidence for Leaf-Trait
593 Dissimilarity Effects on Litter Decomposition, Fungal Decomposers, and Nutrient
594 Dynamics. *Ecology*, 96 (2), 550–61. <https://doi.org/10.1890/14-1151.1>.
- 595 Gardarin, A., Garnier, E., Carrère, P., Cruz, P., Andueza, D., Bonis, A., Colace, M.P., et al (2014)
596 Plant Trait–Digestibility Relationships across Management and Climate Gradients in
597 Permanent Grasslands. *Journal of Applied Ecology*, 51 (5), 1207–17.
598 <https://doi.org/10.1111/1365-2664.12293>.
- 599 Garnier, E., Shipley, B., Roumet, C. & Laurent, G. (2001) A standardized protocol for the
600 determination of specific leaf area and leaf dry matter content. *Functional Ecology*, 15, 688–
601 695. <https://doi.org/10.1046/j.0269-8463.2001.00563.x>
- 602 Garnier, E., Navas, M.L. & Grigulis K (2016) *Plant Functional Diversity. Organism Traits,*
603 *Community Structure, and Ecosystem Properties*. Oxford: Oxford university Press.
- 604 Garnier, E., Cortez, J., Billès, G., Navas, M.L., Roumet, C., Debussche, M., Laurent G et al. (2004)
605 Plant Funcional Markers Capture Ecosystem Properties during Secondary Succession.
606 *Ecology*, 85 (9), 2630–37. <https://doi.org/10.1890/03-0799>.
- 607 Garnier, E., Fayolle, A., Navas, M.L., Damgaard, D., Cruz, P., Hubert, D., Richarte, J., Autran, P.,
608 Leurent, C. & Violle, C. (2018) Plant Demographic and Functional Responses to
609 Management Intensification: A Long-Term Study in a Mediterranean Rangeland. *Journal of*
610 *Ecology*, 106 (4), 1363–76. <https://doi.org/10.1111/1365-2745.12996>.
- 611 Gessner, M.O., Swan, C.M., Dang, C.K/, McKie, B.G., Bardgett, R.D., Wall, D.H., Hättenschwiler,
612 S. (2010). Diversity meets decomposition. *Trends Ecol Evol.*, 25(6), 372-80. doi:
613 10.1016/j.tree.2010.01.010
- 614 Grime, J.P., Cornelissen, J.H.C., Thompson, K. & Hodgson, J.G. (1996) Evidence of a Causal
615 Connection between Anti-Herbivore Defence and the Decomposition Rate of Leaves. *Oikos*,

616 77 (3), 489–94. <https://doi.org/10.2307/3545938>.

617 Grime, J.P. (1998) Benefits of Plant Diversity to Ecosystems: Immediate, Filter and Founder
618 Effects. *Journal of Ecology*, 86 (6), 902–10. [https://doi.org/10.1046/j.1365-](https://doi.org/10.1046/j.1365-2745.1998.00306.x)
619 2745.1998.00306.x.

620 Hättenschwiler, S., Tiunov, A.V., Scheu, S. (2005). Biodiversity and Litter Decomposition in
621 Terrestrial Ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 36, 191–
622 218. [https://doi: 10.1146/annurev.ecolsys.36.112904.151932](https://doi.org/10.1146/annurev.ecolsys.36.112904.151932)

623 Habel, J., Dengler, J., Janišová, M., Török, P., Wellstein, C. & Wiezik, M. (2013) European
624 grassland ecosystems: Threatened hotspots of biodiversity. *Biodiversity and Conservation*,
625 22. [https://doi.org/ 10.1007/s10531-013-0537-x](https://doi.org/10.1007/s10531-013-0537-x).

626 Hellström, K., Huhta, A.-P., Rautio, P., Tuomi, J., Oksanen, J. & Laine, K. (2003) Use of sheep
627 grazing in the restoration of semi-natural meadows in northern Finland. *Applied Vegetation*
628 *Science*, 6, 45-52. [https://doi.org/ 10.1111/j.1654-109x.2003.tb00563.x](https://doi.org/10.1111/j.1654-109x.2003.tb00563.x).

629 Henkin, Z., Ungar, E.D., Dvash, L., Perevolotsky, M., Yehuda, Y., Sternberg, M., Voet, H. &
630 Landau, S.Y. (2011) Effects of Cattle Grazing on Herbage Quality in a Herbaceous
631 Mediterranean Rangeland. *Grass and Forage Science*, 66 (4), 516–25.
632 <https://doi.org/10.1111/j.1365-2494.2011.00808.x>.

633 Herms, D.A., Mattson, W.J.(1992). The Dilemma of Plants: To Grow or Defend. *The Quarterly*
634 *Review of Biology* 67 (1992), 283 - 335. <https://doi.org/10.1086/417659>

635 Hobbie, S.E. (1992) Effects of Plant Species on Nutrient Cycling. *Trends in Ecology & Evolution*, 7
636 (10), 336–39. [https://doi.org/10.1016/0169-5347\(92\)90126-V](https://doi.org/10.1016/0169-5347(92)90126-V).

637 Huston, M. (1979) A General Hypothesis of Species Diversity. *The American Naturalist*, 113 (1),
638 81–101. <https://doi.org/10.1086/283366>

639 Kahmen, S. & Poschlod, P. (2004) Plant functional trait responses to grassland succession over 25
640 years. *Journal of Vegetation Science*, 15, 21-32. [https://doi.org/10.1111/j.1654-](https://doi.org/10.1111/j.1654-1103.2004.tb02233.x)
641 1103.2004.tb02233.x

- 642 Kazakou, E., Vile, D., Shipley, B., Gallet, C. & Garnier, E. (2006) Co-Variations in Litter
643 Decomposition, Leaf Traits and Plant Growth in Species from a Mediterranean Old-Field
644 Succession. *Functional Ecology*, 20 (1), 21–30. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2435.2006.01080.x)
645 2435.2006.01080.x.
- 646 Kazakou, E., Violle, C., Roumet, C., Pintor, C., Gimenez, O. & Garnier, E. (2009) Litter Quality
647 and Decomposability of Species from a Mediterranean Succession Depend on Leaf Traits
648 but Not on Nitrogen Supply. *Annals of Botany*, 104 (6), 1151–61.
649 <https://doi.org/10.1093/aob/mcp202>.
- 650 Knorr, M., Frey, S.D. & Curtis, P.S. (2005) Nitrogen additions and litter decomposition: a meta-
651 analysis. *Ecology*, 86 (12), 3252–57. <https://doi.org/10.1890/05-0150>.
- 652 Kutner, M.H., Neter, J., Nachtsheim, C.J. & Li, W. (2004) *Applied linear statistical models*, 5th
653 Edition. McGraw- Hill Irwin, Boston.
- 654 Kurokawa, H., Peltzer, D.A. & Wardle, D.A. (2010) Plant Traits, Leaf Palatability and Litter
655 Decomposability for Co-Occurring Woody Species Differing in Invasion Status and
656 Nitrogen Fixation Ability. *Functional Ecology*, 24 (3), 513–23.
657 <https://doi.org/10.1111/j.1365-2435.2009.01676.x>.
- 658 Laughlin, D.C., Fulé, P.Z., Huffman, D.W., Crouse, J. & Laliberté, E. (2011) Climatic Constraints
659 on Trait-Based Forest Assembly. *Journal of Ecology*, 99 (6), 1489–99.
660 <https://doi.org/10.1111/j.1365-2745.2011.01885.x>.
- 661 Lemaire, G., Hodgson, J.G. & Chabbi, A. (2011) *Introduction: Food Security and Environmental*
662 *Impacts-Challenge for Grassland Sciences*. CABI Publishing.
- 663 Louault, F., Pillar, V.D., Aufrère, J., Garnier, E. & Soussana, J.-F. (2005) Plant Traits and
664 Functional Types in Response to Reduced Disturbance in a Semi-Natural Grassland.
665 *Journal of Vegetation Science*, 16 (2), 151–60. [https://doi.org/10.1111/j.1654-](https://doi.org/10.1111/j.1654-1103.2005.tb02350.x)
666 1103.2005.tb02350.x.
- 667 Mason, N.W.H., Peltzer, D.A., Richardson, S.J., Belling- Ham, P.J. & Allen, R.B. (2010). Stand

668 development moderates effects of ungulate exclusion on foliar traits in the forests of New
669 Zealand. *Journal of Ecology*, 98(6), 1422–1433. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2745.2010.01714.x)
670 [2745.2010.01714.x](https://doi.org/10.1111/j.1365-2745.2010.01714.x)

671 Mokany, K., Ash, J. & Roxburgh, S. (2008) Functional identity is more important than diversity in
672 influencing ecosystem processes in a temperate native grassland. *Journal of Ecology*, 96,
673 884–893. <https://doi.org/10.1111/j.1365-2745.2008.01395.x>.

674 Molenat, G., Foulquie, D., Autran, P., Bouix, J., Hubert, D., Jacquin, M., Boucquier, F. & Bibe, B.
675 (2005) *Pour Un Élevage Ovin Allaitant performant et Durable Sur Parcours : Un Système*
676 *Expérimental sur Le Causse Du Larzac*. Inra Production Animal 18 (5): 323–38.

677 Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H. & Bellwood DR (2013) A Functional
678 Approach Reveals Community Responses to Disturbances. *Trends in Ecology & Evolution*,
679 28 (3), 167–77. <https://doi.org/10.1016/j.tree.2012.10.004>.

680 Riggs, C.E., Hobbie, S.E., Cavender-Bares, J., Savage, J.A. & Wei, X. (2015) Contrasting effects
681 of plant species traits and moisture on the decomposition of multiple litter fractions. *Oecologia*, 179
682 (2), 573–584. <https://doi.org/10.1007/s00442-015-3352-0>

683 R Development Core Team 2013 A language and environment for statistical computing. R
684 Foundation for Statistical Computing, Vienna, Austria

685 Pakeman, R.J. (2011) Functional Diversity Indices Reveal the Impacts of Land Use Intensification
686 on Plant Community Assembly. *Journal of Ecology*, 99 (5), 1143–51.
687 <https://doi.org/10.1111/j.1365-2745.2011.01853.x>.

688 Pavlů, V., Hejcman, M., Pavlů, L., Gaisler, J. & Nežerková, P. (2006). Effect of continuous grazing
689 on forage quality, quantity and animal performance. *Agriculture, Ecosystems &*
690 *Environment*, 113 (1–4), 349–355. <https://doi.org/10.1016/j.agee.2005.10.010>

691 Peco, B., Carmona, P., Pablos, I., Azcárate, F. (2012). Effects of grazing abandonment on functional
692 and taxonomic diversity of Mediterranean grasslands. *Agriculture Ecosystems &*
693 *Environment*; 152; 27–32. <https://doi.org/10.1016/j.agee.2012.02.009>.

- 694 Pérez-Harguindeguy, N., Díaz, S., Cornelissen, J.H.C., Vendramini, F., Cabido, M. & Castellanos,
695 A. (2000) Chemistry and Toughness Predict Leaf Litter Decomposition Rates over a Wide
696 Spectrum of Functional Types and Taxa in Central Argentina P. *Plant and Soil*, 218, 21-30.
697 <https://doi.org/10.1023/A:1014981715532>.
- 698 Petchey, O. & Gaston, K.J. (2006) Functional Diversity: Back to Basics and Looking Forward.
699 *Ecology Letters*, 9 (6), 741–58. <https://doi.org/10.1111/j.1461-0248.2006.00924.x>.
- 700 Pontes, L., Soussana, J.F., Loualt, F., Andueza, D., Carrère, P. (2007) Leaf Traits Affect the Above-
701 Ground Productivity and Quality of Pasture Grasses. *Functional Ecology*, 21 (5), 844–53.
702 <https://doi.org/10.1111/j.1365-2435.2007.01316.x>.
- 703 Porre, R.J., van der Werf, W., De Deyn, G.B., Stomph, T.J., Hoffland, E. (2020) Is litter
704 decomposition enhanced in species mixtures? A meta-analysis. *Soil Biol Biochem*, 145,
705 107791. <https://doi.org/10.1016/j.soilbio.2020.107791>
- 706 Poorter, H., Bergkotte, M. (1992) Chemical composition of 24 wild species differing in relative
707 growth rate. *Plant, Cell and Environment*, 15, 221-229.
- 708 Quested, H., Eriksson, O., Fortunel, C. & Garnier, E. (2007) Plant Traits Relate to Whole-
709 Community Litter Quality and Decomposition Following Land Use Change. *Functional*
710 *Ecology*, 21 (6), 1016–26. <https://doi.org/10.1111/j.1365-2435.2007.01324.x>.
- 711 Quétier, F., Thébault, A. & Lavorel, S. (2007) Plant traits in a state and transition framework as
712 markers of ecosystem response to land use change. *Ecological Monographs*, 77 (1), 33–52.
713 <https://doi.org/10.1890/06-0054>.
- 714 Santiago, L.S. (2007) Extending the leaf economics spectrum to decomposition: evidence for a
715 tropical forest. *Ecology*, 88 (5), 1126–31. <https://doi.org/10.1890/06-1841>.
- 716 Sasaki, T., Okayasu, T., Jamsran, U. & Takeuchi, K. (2008) Threshold changes in vegetation along a
717 grazing gradient in Mongolian rangelands. *Journal of Ecology*, 96, 145-154.
718 <https://doi.org/10.1111/j.1365-2745.2007.01315.x>
- 719 Schädler, M., Gertraud, J., Auge, H. & Brandl, R. (2003) Palatability, Decomposition and Insect

- 720 Herbivory: Patterns in a Successional Old-Field Plant Community. *Oikos*, 103 (1), 121–32.
721 <https://doi.org/10.1034/j.1600-0706.2003.12659.x>.
- 722 Schumacher, J. & Roscher, C. (2009) Differential effects of functional traits on aboveground
723 biomass in semi-natural grasslands. *Oikos*, 118, 1659-1668. <https://doi.org/10.1111/j.1600-0706.2009.17711.x>
- 725 Semmarti, M., Garibaldi, L.A. & Chaneton, E.J. (2008) Grazing History Effects on Above- and
726 below-Ground Litter Decomposition and Nutrient Cycling in Two Co-Occurring Grasses.
727 *Plant and Soil*, 303 (1), 177–89. <https://doi.org/10.1007/s11104-007-9497-9>.
- 728 Tardif, A. & Shipley, B. (2015) The Relationship between Functional Dispersion of Mixed-Species
729 Leaf Litter Mixtures and Species Interactions during Decomposition. *Oikos*, 124 (8), 1050–
730 57. <https://doi.org/10.1111/oik.01686>.
- 731 Taylor, B. & Parkinson, D. (1988) A new microcosm approach to litter decomposition studies.
732 *Canadian Journal of Botany*, 66, 1933-1939. <https://doi.org/10.1139/b88-265>
- 733 Van Soest, P.J., Robertson, J.B. & Lewis, B.A. (1991) Methods for Dietary Fiber, Neutral Detergent
734 Fiber, and Nonstarch Polysaccharides in Relation to Animal Nutrition. *Journal of Dairy
735 Science*, 74 (10), 3583–97. [https://doi.org/10.3168/jds.S0022-0302\(91\)78551-2](https://doi.org/10.3168/jds.S0022-0302(91)78551-2).
- 736 Wang, L., Gan, Y., Wiesmeier, M., Zhao, G., Zhang, R., Han, G., Kadambot, H.M.S. & Fujiang, H.
737 (2018) Grazing Exclusion—An Effective Approach for Naturally Restoring Degraded
738 Grasslands in Northern China. *Land Degradation & Development*, 29 (12), 4439–56.
739 <https://doi.org/10.1002/ldr.3191>.
- 740 Wardle, D.A., Bonner, K.I. & Barker, G.M. (2002) Linkages between Plant Litter Decomposition,
741 Litter Quality, and Vegetation Responses to Herbivores. *Functional Ecology*, 16 (5), 585–
742 95. <https://doi.org/10.1046/j.1365-2435.2002.00659.x>.
- 743 Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H. & Wall, D.H.
744 (2004) Ecological Linkages Between Aboveground and Belowground Biota. *Science*, 304
745 (5677), 1629. <https://doi.org/10.1126/science.1094875>.

- 746 Wardle, D.A., Zackrisson, O., Hörnberg, G. & Gallet, C. (1997) The Influence of Island Area on
747 Ecosystem Properties. *Science*, 277 (5330), 1296.
748 <https://doi.org/10.1126/science.277.5330.1296>.
- 749 White, T.A., Barker, D.J. & Moore, K.J. (2004) Vegetation Diversity, Growth, Quality and
750 Decomposition in Managed Grasslands. *Agriculture, Ecosystems & Environment*, 101 (1),
751 73–84. [https://doi.org/10.1016/S0167-8809\(03\)00169-5](https://doi.org/10.1016/S0167-8809(03)00169-5).
- 752 Wu, J. & Baldwin, M. (2009) Herbivory-Induced Signalling in Plants: Perception and Action.
753 *Plant, Cell & Environment*, 32 (9), 1161–74. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-3040.2009.01943.x)
754 [3040.2009.01943.x](https://doi.org/10.1111/j.1365-3040.2009.01943.x).
- 755

Table 1. Relationships between the Dry Matter Digestibility or Litter Mass Loss measured at the community level and Community Weighted Means (CWM) and Community Weighted Variance (CWV) of the Leaf Dry Matter Content (LDMC), Leaf Neutral Detergent Fibre content (LNDF) and Leaf Nitrogen Content (LNC). r represents the Pearson or Spearman correlations.

| | | Dry mass Digestibility | Litter mass loss |
|------|-----|------------------------|---------------------|
| | | r | r |
| LDMC | CWM | -0.93*** | -0.79*** |
| | CWV | -0.44* | -0.43*** |
| LNDF | CWM | -0.62** | -0.26 ^{ns} |
| | CWV | -0.12 ^{ns} | -0.52** |
| LNC | CWM | 0.92*** | 0.74*** |
| | CWV | -0.18 ^{ns} | -0.40 ^{ns} |

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, not significant.

Table 2. Effects of the loadings of the first (PCA1) and the second (PCA2) PCA axes on Dry Matter Digestibility and Litter Mass Loss. The table shows Std. Est., standardised beta estimates, Std. Err., standardised errors, *t* values from multiple linear regression models, and with their relative importance in dry matter digestibility or decomposability variation (%). The R^2 / R^2 adjusted results shown are from best model after traits selection.

| Dry mass Digestibility | | | | | |
|-------------------------------|------------------|------------------|-----------------|----------|----------------------------|
| <i>Predictors</i> | <i>Std. Est.</i> | <i>Std.Err.</i> | <i>t</i> | <i>p</i> | <i>Relative importance</i> |
| PCA1 | -0.89 | 0.09 | -9.917 | <0.001 | 88.16 |
| PCA2 | 0.46 | 0.08 | 1.616 | ns | 11.84 |
| R^2 / Adjusted R^2 | | | 0.8279 / 0.8114 | | |
| Litter mass loss | | | | | |
| <i>Predictors</i> | <i>Std. est.</i> | <i>Std. err.</i> | <i>t</i> | <i>p</i> | |
| PCA1 | -0.703 | 0.151 | -4.636 | <0.001 | |
| R^2 / Adjusted R^2 | | | 0.494 / 0.471 | | |

The full model were :

Digest ~ 1 + PCA1 + PCA2

Decomp ~ 1 + PCA1 + PCA2

Figure 1. Relationship between Dry Matter Digestibility (DMD) and Litter Mass Loss measured at the community level. Each point represents one plot (9 plots for the G+F and GU treatments and 6 plots for the UU treatment). Colors represent management regime: G+F, open white symbols; GU, grey symbols; UU, black symbols. The r value is Spearman correlation coefficient between the two properties. $***P < 0.001$. Box plots show the distribution of dry matter digestibility (right panel) and decomposability (top panel) for communities of the three management regimes. Different letters indicate significant differences among management regimes (post hoc Student–Newman–Keuls test). G+F: increased grazing and fertility regime, GU: moderate grazing and unfertilized regime, UU: suppression of grazing and unfertilized regime.

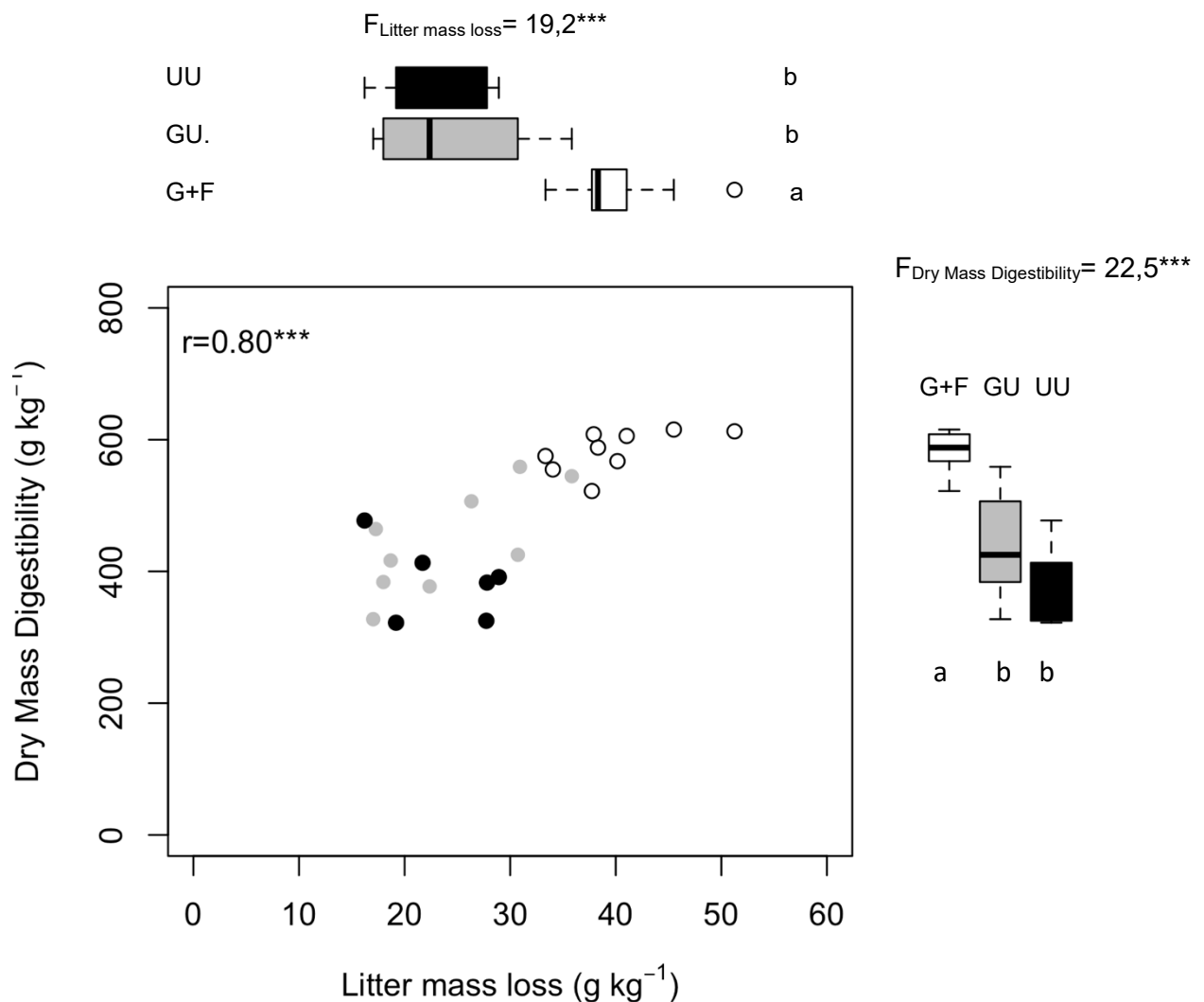
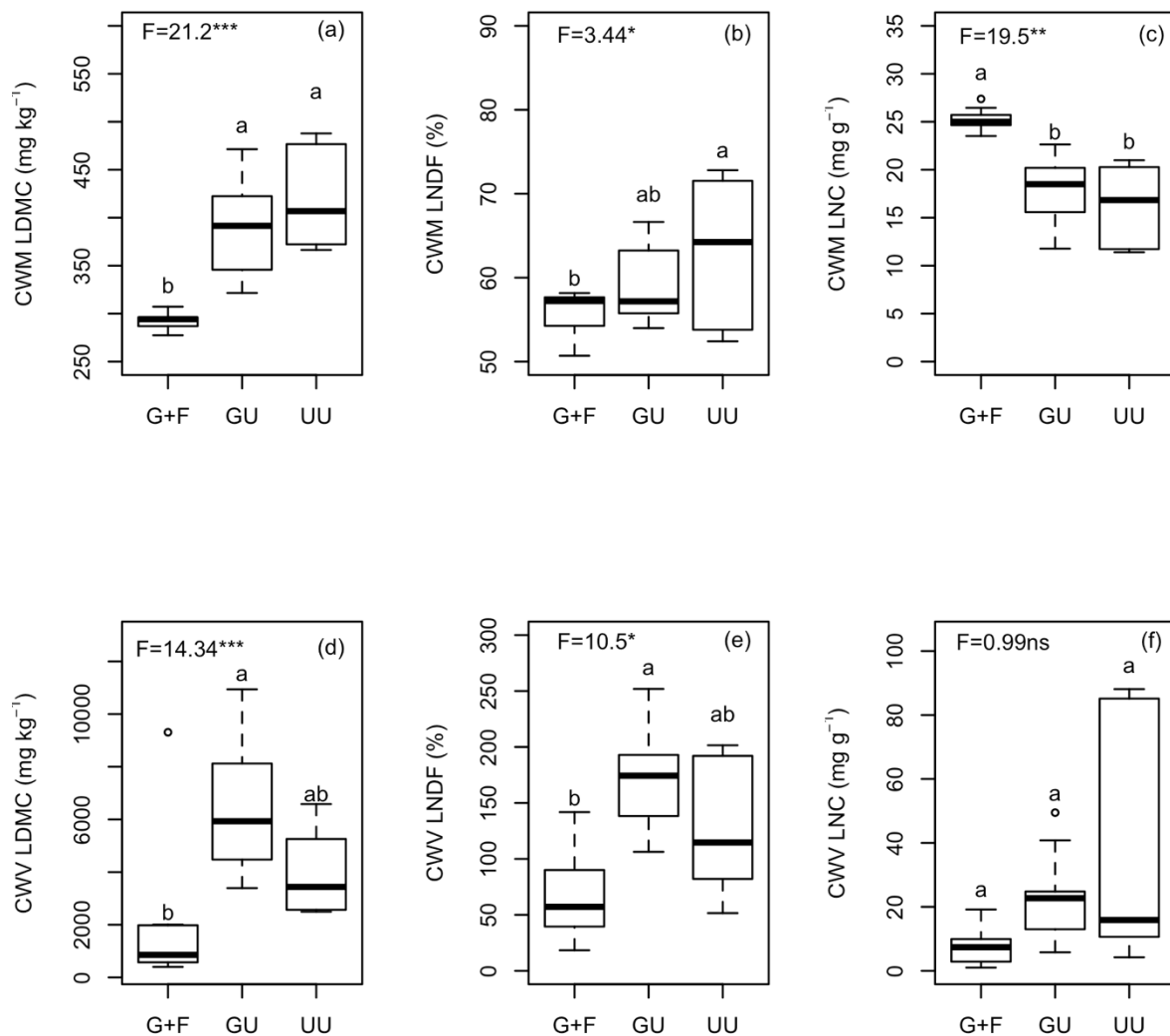


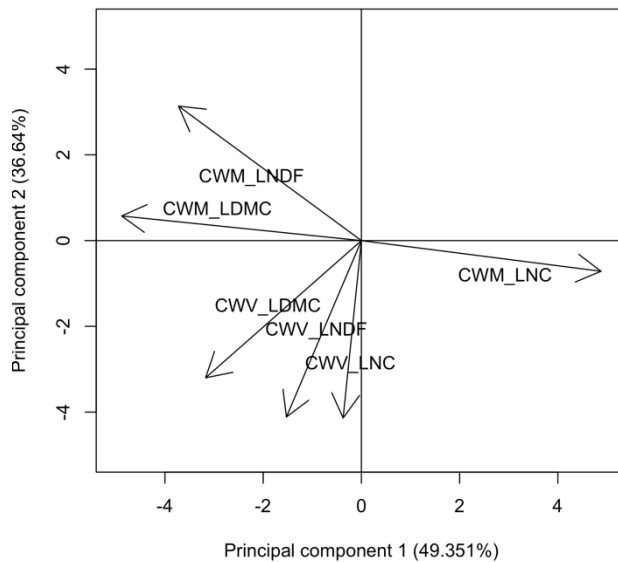
Figure 2. Effect of management regimes on the (a) Community Weighted Means of Leaf Dry Matter Content, (CWM LDMC, mg g^{-1}), (b) Community Weighted Means of Leaf Detergent Fibre (CWM LNDF, %), (c) Community Weighted Means of Leaf nitrogen Content, (CWM LNC, mg g^{-1}), (d) Community Weighted Variance of Leaf Dry Matter Content (CWV LDMC, mg g^{-1}), (e) Community Weighted Variance of Leaf Detergent Fibre (CWV LNDF, %), (f) Community Weighted Variance of Leaf Nitrogen Content (CWV LNC, mg g^{-1}). F-values for ANOVA testing the effect of management practices are indicated, with significance level: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, not significant. Different letters indicate significant differences among management regimes (post hoc Student–Newman–Keuls test). G+F: increased grazing and fertility regime, GU: moderate grazing and unfertilized regime, UU: suppression of grazing and unfertilized regime.



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Figure 3. Projection of (a) variables; (b) communities on the first two axes of a Principal Component Analysis. Confidence ellipses were drawn with the R package FactoMineR. Principal Components were scaled prior to analysis. CWM LDMC: Community Weighted Mean of Leaf Dry Matter Content, CWM LNDF: Community Weighted Means of Leaf Detergent Fibre, CWM LNC: Community Weighted Means of Leaf Nitrogen Content, CWV LDMC: Community Weighted Variance of Leaf Dry Matter Content, CWV LNDF: Community Weighted Variance of Leaf Detergent Fibre, CWV LNC: Community Weighted Variance of Leaf Nitrogen Content. G+F: increased grazing and fertility regime, GU: moderate grazing and unfertilized regime, UU: suppression of grazing and unfertilized regime.

(a)



(b)

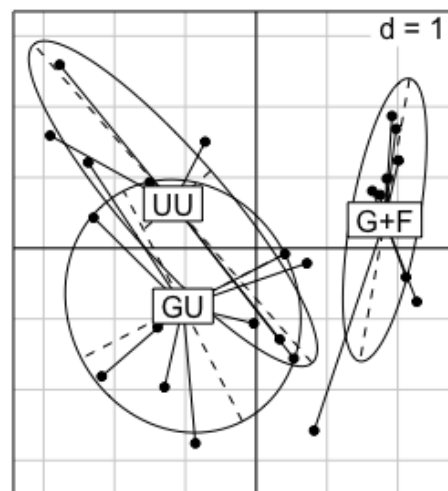
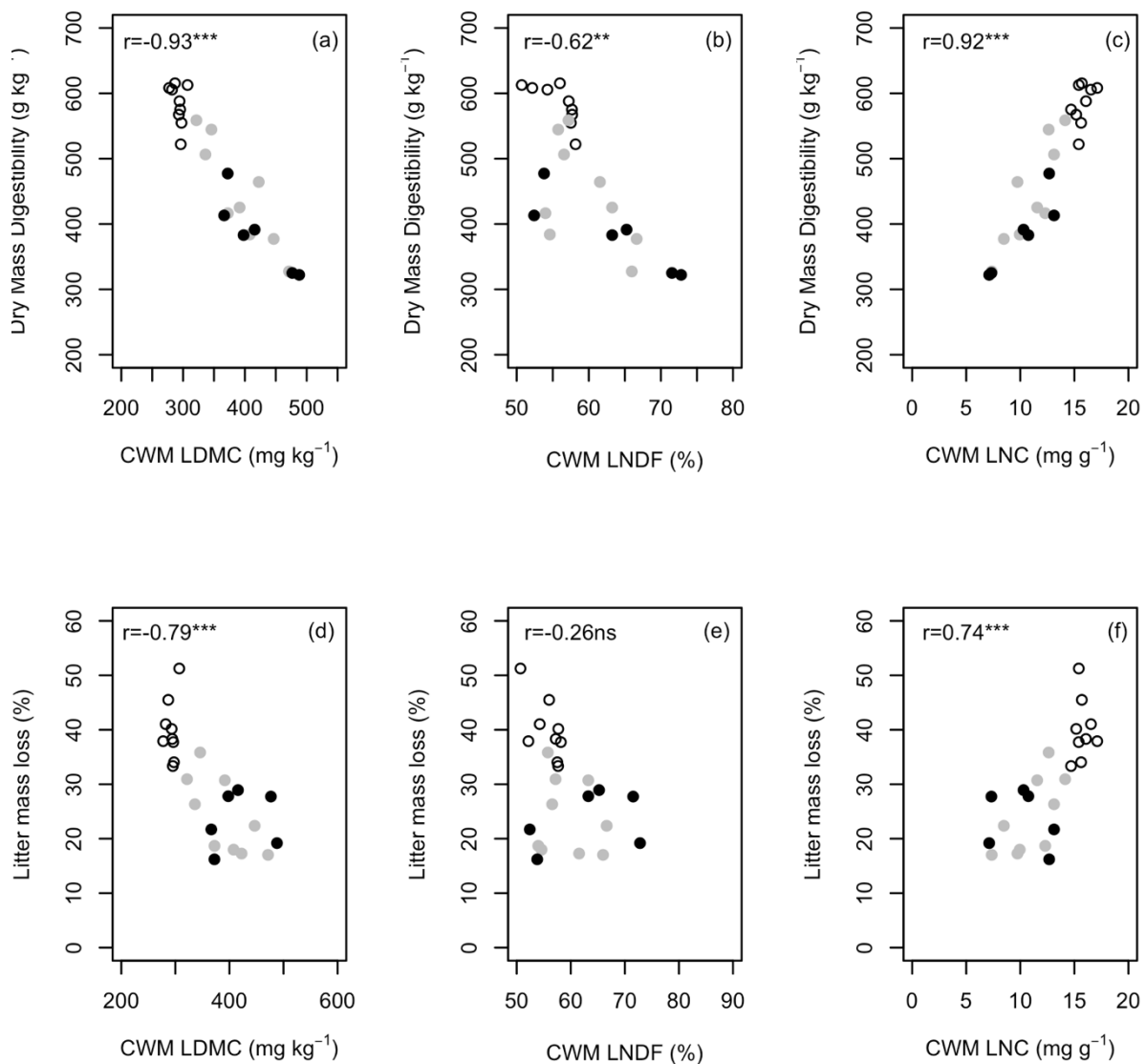


Figure 4. Relationships between Dry Mass Digestibility and (a) Community Weighed Mean of Leaf Dry Matter Content (CWM LDMC), (b) Community Weighed Mean of Leaf Detergent Fibre (CWM LNDF), (c) Community Weighed Mean of Leaf Nitrogen Content (CWM LNC). Relationships between Litter Mass Loss and (d) Community Weighed Mean of Leaf Dry Matter Content, (e) Community Weighed Mean of Leaf Detergent Fibre and (f) Community Weighed Mean of Leaf Nitrogen Content. Colors represent management regime: open symbols for the G+F, shaded symbols for the GU and full symbols for the UU regime. The r value is Person or Spearman correlation coefficients. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, not significant. G+F: increased grazing and fertility regime, GU: moderate grazing and unfertilized regime, UU: suppression of grazing and unfertilized regime.



Appendix 1. List of species studied, with abbreviation, taxonomic group, growth form (Pérez-Harguindeguy et al. 2013) and location in each management regime. G+F: increased grazing and fertility regime, GU: moderate grazing and unfertilized regime, UU: suppression of grazing and unfertilized regime. No shaded cases correspond to traits measured in 2013 and published in Bumb et al., 2018.

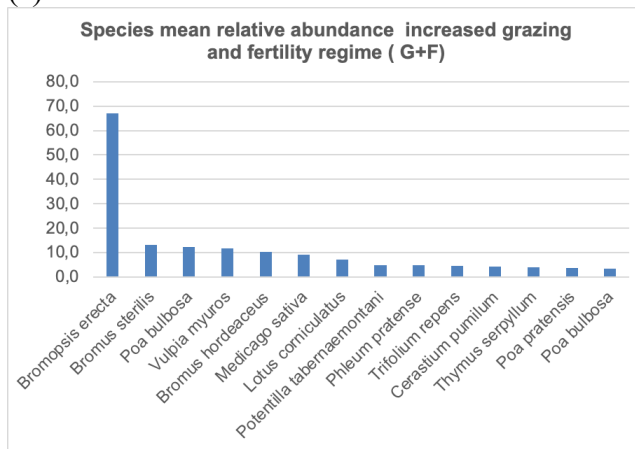
| Species | Taxonomic group | Growth form | G+F | GU | UU |
|--------------------------------------|-----------------|----------------------------|-----|----|----|
| <i>Anthyllis vulneraria</i> | Fabaceae | Rosette | | x | x |
| <i>Aphyllantes monspeliensis</i> | Asparagaceae | Tussock | | | x |
| <i>Brachypodium pinnatum</i> | Poaceae | Tussock | | x | |
| <i>Bromopsis erecta</i> | Poaceae | Tussock | x | x | x |
| <i>Bromus hordeaceus</i> | Poaceae | Tussock | x | | |
| <i>Bromus sterilis</i> | Poaceae | Tussock | x | | |
| <i>Capsella bursa-pastoris</i> | Brassicaceae | Rosette | x | | |
| <i>Carex humilis</i> | Cyperaceae | Tussock | | x | x |
| <i>Coronilla minima</i> | Fabaceae | Extensive and stemmed herb | | x | |
| <i>Erodium cicutarium</i> | Geraniaceae | Rosette | x | | |
| <i>Festuca christianii-bernardii</i> | Poaceae | Tussock | | x | x |
| <i>Geranium molle</i> | Geraniaceae | Extensive and stemmed herb | x | | |
| <i>Helianthemum apenninum</i> | Cistaceae | Extensive and stemmed herb | | x | |
| <i>Helianthemum canum</i> | Cistaceae | Extensive and stemmed herb | | x | |
| <i>Hippocrepis comosa</i> | Fabaceae | Extensive and stemmed herb | | | x |
| <i>Lotus corniculatus</i> | Fabaceae | Extensive and stemmed herb | x | | |
| <i>Ononis striata</i> | Fabaceae | Extensive and stemmed herb | | x | |
| <i>Pilosella officinarum</i> | Asteraceae | Rosette | x | x | |
| <i>Plantago lanceolata</i> | Plantaginaceae | Rosette | x | | |
| <i>Poa bulbosa</i> | Poaceae | Tussock | x | | |
| <i>Potentilla tabernaemontani</i> | Rosaceae | Extensive and stemmed herb | x | x | |
| <i>Poterium sanguisorba</i> | Rosaceae | Rosette | x | x | |

| | | | | |
|--------------------------|----------------|----------------------------|---|---|
| <i>Stipa pennata</i> | Poaceae | Tussock | x | x |
| <i>Trifolium repens</i> | Fabaceae | Extensive and stemmed herb | x | |
| <i>Veronica arvensis</i> | Plantaginaceae | Extensive and stemmed herb | x | |
| <i>Vulpia myuros</i> | Poaceae | Tussock | x | |

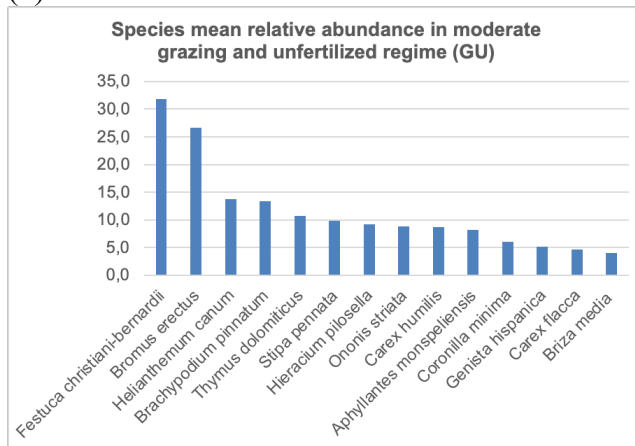
Appendix 2.

Relative contribution of species in the (a) G+F+, (b) GU and (c) UU treatment.

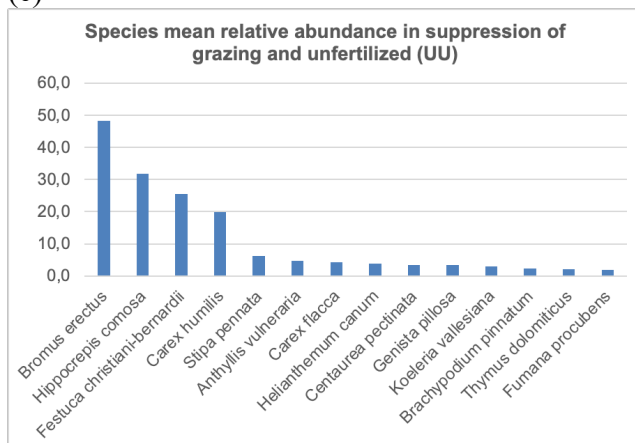
(a)



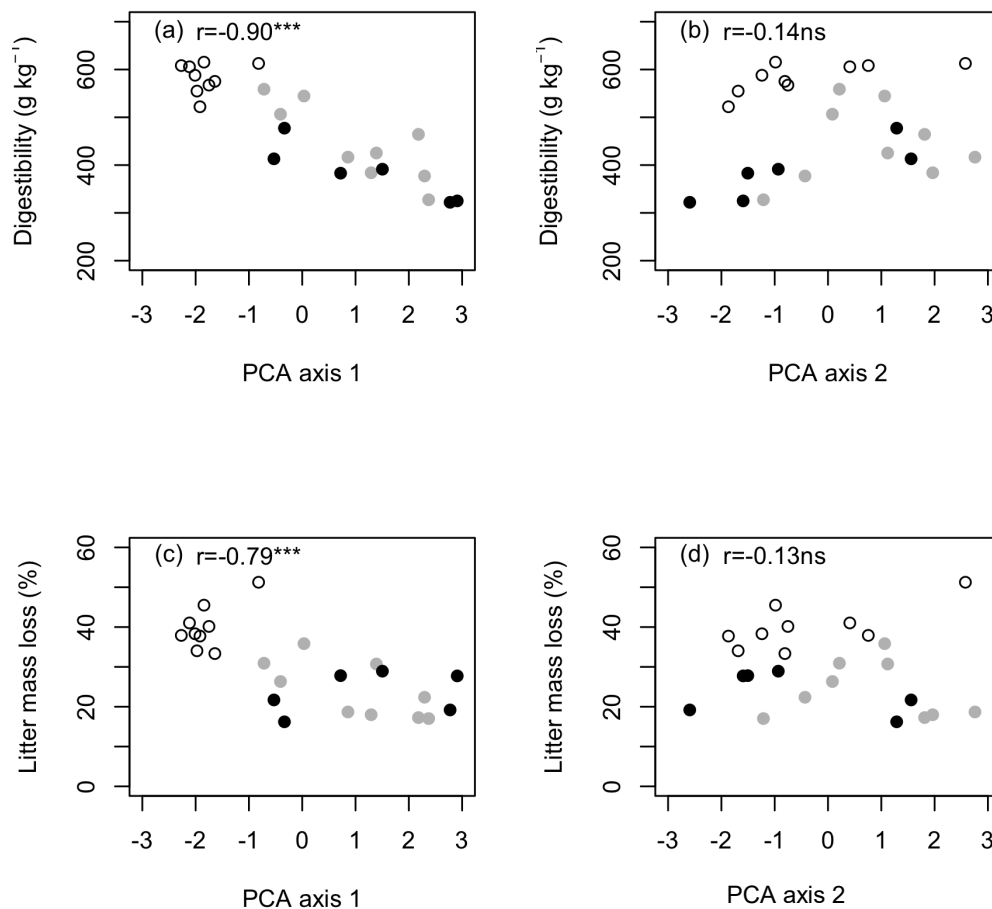
(b)



(c)



Appendix 3. Relationships between (a) Dry Mass Digestibility and (c) Litter Mass Loss with loading axis 1 of the PCA combining Community Weighted Mean of Leaf Dry Matter Content, Community Weighted Mean of Leaf Detergent Fibre opposed to Community Weighted Mean of Leaf Nitrogen Content. Relationships between Dry Mass Digestibility (b) and Litter Mass Loss (d) and loading axis 2 of the PCA combining Community Weighted Variance of Leaf Dry Matter Content, Community Weighted Variance of Leaf Detergent Fibre and Community Weighted Variance of Leaf Nitrogen Content opposed to Community Weighted Mean of Leaf Dry Matter Content. Colors represent management regime: open symbols for the G+F, shaded symbols for the GU and full symbols for the UU regime. The r value is Person or Spearman correlation coefficients. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, not significant. G+F: increased grazing and fertility regime, GU: moderate grazing and unfertilized regime, UU: suppression of grazing and unfertilized regime.



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Appendix 4.

Effects of traits on dry matter digestibility and decomposability. The table shows Std. est., standardised beta estimates, Std. err., standardised errors, t values from multiple linear regression models, and with their relative importance in dry matter digestibility or decomposability variation (%).

The R^2 / R^2 adjusted results shown are from best model after traits selection. CWM LDMC:

Community Weighted Mean of Leaf Dry Matter Content, CWM LNDF: Community Weighted Means of Leaf Detergent Fibre, CWM LNC: Community Weighted Means of Leaf Nitrogen Content, CWV LDMC: Community Weighted Variance of Leaf Dry Matter Content, CWV LNDF: Community Weighted Variance of Leaf Detergent Fibre, CWV LNC: Community Weighted Variance of Leaf Nitrogen Content.

| Dry mass Digestibility | | | | | |
|---------------------------------------|------------------|-----------------|----------|------------------|----------------------------|
| <i>Predictors</i> | <i>Std. Est.</i> | <i>Std.Err.</i> | <i>t</i> | <i>p</i> | Relative importance |
| CWM_LDMC | -0.95 | 0.07 | -13.68 | <0.001 | 100 |
| R^2 / <i>Adjusted R²</i> | 0.895 / 0.890 | | | | |

| Litter mass loss | | | | | |
|---------------------------------------|------------------|------------------|----------|------------------|----------------------------|
| <i>Predictors</i> | <i>Std. est.</i> | <i>Std. err.</i> | <i>t</i> | <i>p</i> | Relative importance |
| CWM_LDMC | -1.45 | 0.25 | -5.79 | <0.001 | 56,15 |
| CWM_LNDF | -0.72 | 0.22 | -3.25 | 0.004 | 31.04 |
| CWV_LDMC | -0.29 | 0.16 | -1.83 | 0.083 | 12.8 |
| R^2 / <i>Adjusted R²</i> | 0.717 / 0.675 | | | | |

The full model were :

Digest ~ CWM_LDMC + CWM_LNC + CWM_LNDF + CWV_LDMC + CWV_LNC + CWV_LNDF

Decomp ~ CWM_LDMC + CWM_LNC + CWM_LNDF + CWV_LDMC + CWV_LNC + CWV_LNDF

Appendix 5

| Treatment | Plot | Digest | Decomp | CWM_ LDMC | CWM_ LNC | CWM_ LNDF | CWV_ LDMC | CWV_ LNC | CWV_ LNDF |
|-----------|------|---------|--------|--------------|-------------|--------------|--------------|-------------|--------------|
| G+F | 1 | 587.975 | 38.315 | 294.259 | 16.071 | 57.217 | 630.998 | 2.803 | 37.232 |
| G+F | 2 | 615.379 | 45.497 | 286.907 | 15.69 | 55.992 | 1979.267 | 0.542 | 77.511 |
| G+F | 3 | 612.676 | 51.251 | 307.224 | 15.409 | 50.695 | 9309.611 | 9.045 | 148.717 |
| G+F | 4 | 605.676 | 41.035 | 282.142 | 16.534 | 54.257 | 1393.33 | 7.438 | 85.669 |
| G+F | 5 | 554.810 | 34.041 | 297.424 | 15.624 | 57.511 | 399.733 | 1.604 | 20.726 |
| G+F | 6 | 522.031 | 37.737 | 296.194 | 15.405 | 58.164 | 524.436 | 1.37 | 9.995 |
| G+F | 7 | 575.174 | 33.344 | 295.283 | 14.697 | 57.658 | 571.635 | 4.687 | 55.41 |
| G+F | 8 | 567.335 | 40.159 | 293.166 | 15.172 | 57.692 | 852.484 | 5.614 | 38.711 |
| G+F | 9 | 608.213 | 37.909 | 277.458 | 17.114 | 52.165 | 2005.167 | 6.303 | 115.729 |
| GU | 10 | 544.552 | 35.834 | 345.798 | 12.624 | 55.752 | 5009.221 | 2.838 | 218.465 |
| GU | 11 | 464.325 | 17.272 | 422.415 | 9.738 | 61.538 | 10690.05 | 1.0 | 145.656 |
| GU | 12 | 383.954 | 17.988 | 407.727 | 9.948 | 54.592 | 7795.93 | 7.29 | 197.668 |
| GU | 13 | 506.431 | 26.326 | 336.159 | 13.119 | 56.562 | 3391.368 | 0.665 | 183.558 |
| GU | 14 | 416.567 | 18.683 | 372.403 | 12.304 | 53.987 | 10940.32 | 9.189 | 184.00 |
| GU | 15 | 327.458 | 17.029 | 471.378 | 7.359 | 65.964 | 4220.187 | 3.164 | 97.588 |
| GU | 16 | 558.773 | 30.926 | 321.526 | 14.148 | 57.183 | 4474.575 | 4.302 | 114.482 |
| GU | 17 | 425.253 | 30.726 | 391.484 | 11.561 | 63.235 | 8122.682 | 8.006 | 149.982 |
| GU | 18 | 377.199 | 22.371 | 446.635 | 8.479 | 66.636 | 5931.852 | 4.897 | 120.264 |
| UU | 19 | 477.282 | 16.210 | 372.233 | 12.673 | 53.795 | 2493.652 | 9.573 | 141.146 |
| UU | 20 | 413.108 | 21.703 | 366.411 | 13.12 | 52.416 | 2567.384 | 9.946 | 148.709 |
| UU | 21 | 391.398 | 28.924 | 415.815 | 10.3 | 65.236 | 6582.757 | 2.86 | 77.322 |
| UU | 22 | 383.040 | 27.803 | 397.885 | 10.749 | 63.241 | 3768.573 | 1.857 | 57.902 |
| UU | 23 | 325.077 | 27.739 | 476.675 | 7.328 | 71.533 | 5256.354 | 3.363 | 82.326 |
| UU | 24 | 322.149 | 19.191 | 487.916 | 7.123 | 72.803 | 3103.881 | 1.536 | 54.532 |