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1 **Forage nutritive value shows synergies with plant diversity**  
2 **in a wide range of semi-natural grassland habitats**

3

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22

23 **Abstract**

24

25 Assessing the relationship between grassland plant diversity and  
26 agronomic value is a major challenge to reconcile nature

27 conservation and agricultural use of extensive grassland habitats.  
28 To do this, multiple facets of forage production must be  
29 considered such as the quantity produced and its nutritive value,  
30 commonly assessed through its digestibility, energy content, and  
31 nutrient content. The aim of this study was to analyse the effects  
32 of plant diversity and functional traits on forage productivity and  
33 nutritive value in a wide set of semi-natural grassland habitats.

34 Forage was sampled in 202 plots located across 68  
35 permanent extensive grasslands in eight regions of France.  
36 Species and functional diversity indices, community-weighted  
37 means (CWM) of plant functional traits, and the relative cover  
38 of main plant functional types (PFT; graminoids, forbs, and  
39 legumes) were used to describe plant communities. Forage  
40 production was evaluated by recording early standing biomass  
41 (SB), and nutritive value parameters, namely digestibility  
42 (DMD), crude protein content (CP), and average mineral content  
43 (MinAv) at the beginning of the vegetation growing season.

44 Species richness was negatively associated with SB and  
45 MinAv. Species evenness was positively correlated with CP,  
46 DMD, and MinAv, while PFT evenness was positively  
47 correlated with CP and DMD. Forage standing biomass  
48 increased with increasing graminoid cover and decreased with  
49 increasing forb cover. A higher legume cover and specific leaf  
50 area CWM as well as a lower leaf dry matter content CWM was  
51 associated with improved forage nutritive value and had no

52 effect on SB. Our results highlight that a better forage nutritive  
53 value can be obtained with a higher plant species evenness in  
54 permanent grassland habitats. Furthermore, in grasslands with an  
55 even distribution of plant functional types, forage nutritive value  
56 may be improved with no loss in early standing biomass.

57

58 **Keywords:** Natura 2000, grassland conservation, LDMC, SLA,  
59 species diversity, functional diversity, forage digestibility,  
60 mineral content, crude protein.

61

62 **1. Introduction**

63

64 Grasslands are the main agricultural land use both on a European  
65 and global scale (Stypinski, 2011; Török et al., 2021). Semi-  
66 natural grasslands are recognized for their heritage values  
67 (Halada et al., 2011), and provide numerous ecosystem services  
68 such as forage production, climate regulation through carbon  
69 sequestration, pollination, water regulation, nutrient cycling, and  
70 provide habitats for biodiversity (Anderson-Teixeira et al., 2012;  
71 Wehn et al., 2018; Bengtsson et al., 2019). All these services  
72 depend on the structural and functional components of grassland  
73 habitats, and could be considered for the structure and function  
74 criteria used to assess their conservation status within the  
75 European Directive 92/43/EEC. Amongst the services provided  
76 by semi-natural grasslands, those related to agronomic and  
77 conservation values deserve particular attention. Agronomic use,  
78 and thus agronomic value, condition the persistence of semi-  
79 natural grasslands, which otherwise would either be converted to  
80 intensive agricultural land uses (often sown grasslands or  
81 croplands), or abandoned and replaced by woody habitats after  
82 natural shrub encroachment (MacDonald et al., 2000. Prévosto  
83 et al., 2006; Henle et al., 2008; Pe'er et al., 2014). This  
84 conversion of temperate grasslands may threaten biodiversity  
85 (Hoekstra et al. 2005) and ecosystem service supply (Vidaller &  
86 Dutoit, 2022). However, forage productivity and nutritive

87 quality are not used in the assessment of conservation status of  
88 Natura 2000 grasslands (Evans & Arvela, 2011, Silva et al.  
89 2019). Considering forage productivity and nutritive value and  
90 investigating to what extent semi-natural grasslands are  
91 agronomically valuable to justify and ensure extensive  
92 traditional agricultural management over the long term is thus of  
93 the utmost importance for conservation. This is especially true  
94 for the many grasslands which are not part of a conservation  
95 scheme and in the many regions where agriculture remains the  
96 main driving factor of rural landscapes. More precisely, we need  
97 to identify the factors that determine forage productivity and  
98 nutritive value, and the relationships between forage production  
99 and plant diversity. As agronomic value and biodiversity may  
100 not vary in the same direction, identifying synergies and trade-  
101 offs, among and between forage nutritive variables, forage  
102 productivity, and species and functional diversity, as well as the  
103 environmental drivers of these relationships is worthwhile for  
104 the conservation of farmed semi-natural grasslands.

105       Assessing forage value is a multifaceted task. The value of  
106 forage is mainly characterised by yield and its nutritional quality,  
107 which can be described by digestibility, net energy, crude  
108 protein, and mineral contents especially those considered to be  
109 essential to animal health (Suttle, 2010; Collins & Newman,  
110 2018).

111 Plant communities through their functional composition  
112 may operate on grassland forage biomass production (Michaud  
113 et al., 2015; Duru et al., 2015). Grasses tend to produce more  
114 biomass than forbs (Michaud et al., 2015) and show better  
115 regrowth capacity after defoliation (Schleip et al., 2013;  
116 Tahmasebi Kohyani et al., 2009). Quantitative functional traits  
117 of plants are also valuable predictors of forage productivity. Leaf  
118 dry matter content (LDMC) has been found to be negatively  
119 correlated with plant growth rate (Wilson et al., 1999; Pontes et  
120 al., 2007). By contrast, vegetation with a high specific leaf area  
121 (SLA) tends to be composed of fast-growing species found in  
122 nutrient-rich habitats (Lavorel & Garnier, 2002; Wright et al.,  
123 2004; Laliberté et al., 2012). This results in a positive correlation  
124 between SLA and above-ground biomass production (Poorter &  
125 de Jong, 1999; Lavorel & Garnier, 2002).

126 Plant functional types and traits may also influence forage  
127 nutritive values (Gardarin et al. 2014; Tasset et al., 2019). It has  
128 already been shown that forage crude protein content varies  
129 between plant functional types, with legumes possessing a  
130 higher protein concentration than grasses, and dicotyledonous  
131 plants containing more digestible tissues than grasses especially  
132 in later development stages (Bruinenberg 2002, Duru et al.,  
133 2010). Forage digestibility has also been shown to be negatively  
134 correlated with LDMC (Pontes et al., 2007; Gardarin et al.,  
135 2014). Forage nutritive value mineral content, although this

136 aspect is often overlooked. Contrasts in functional composition  
137 are meaningful for explaining variations in forage mineral  
138 content, with forbs and legumes more likely to have a higher  
139 individual mineral content than grasses for most minerals  
140 (García-Ciudad et al., 1997; Pirhofer-Walzl et al., 2011; Schlegel  
141 et al., 2016). These contrasts are however not always measured  
142 for all minerals (Schlegel et al., 2016). Manganese, for example,  
143 can be found in higher concentrations in grass-dominated forage  
144 (Spears, 1994). The reason for differences in mineral content  
145 between functional types are not yet well understood, although  
146 they may reflect differences in cation exchange capacities in cell  
147 walls (Haynes, 1980; Marschner, 2011). A positive relationship  
148 is expected between SLA and forage mineral content. This is due  
149 to the combination of a positive relationship between plant  
150 mineral content and plant relative growth rate, and the positive  
151 correlation between SLA and plant growth rate (Poorter &  
152 Bergkotte, 1992; Wright et al., 2004). In general, it seems that  
153 the response of forage biomass production to plant community  
154 composition differs to the response of forage nutritive quality.  
155 This suggests that a negative correlation between biomass  
156 production and certain parameters of forage nutritive quality can  
157 be expected.

158 Forage productivity and nutritive value, and species  
159 diversity are key attributes of grasslands when considering  
160 farming system sustainability from an agroecological



161 perspective (Wezel & Peeters, 2014). The relationship between  
162 plant diversity and biomass production is complex in grasslands.  
163 On the one hand, the most productive grasslands are those which  
164 are intensively managed with fertilisation promoting  
165 competitive species with a consequent reduction of plant  
166 diversity (Tilman, 1982; Plantureux et al., 2005; Gaujour et al.,  
167 2012). On the other hand, it was repeatedly experimentally  
168 shown that the increase in specific and particularly functional  
169 diversity increases plant production (Finn et al., 2013), as a result  
170 of facilitation and species complementarity in the use of  
171 resources (Loreau, 1998; Tilman, et al., 2001; Hector et al.,  
172 2002; Marquard et al., 2009). In studies which disentangle  
173 diversity effects from management effects on semi-natural  
174 grassland productivity, both positive and negative effects of  
175 diversity on production have been reported (Assaf et al., 2011;  
176 Rose & Leuschner, 2012). Grime's humped-back model (1973)  
177 suggests why no simple relationship between species diversity  
178 and primary productivity is expected. This model shows that  
179 diversity decreases both in highly productive systems, due to  
180 competition, and in low-productive systems, because only  
181 species adapted to a high level of stress or disturbance can  
182 survive (Grime, 1973). The positive effect of species richness on  
183 biomass is also essentially obtained in experimental grasslands,  
184 which are immature and simplified. Such results may not be  
185 confirmed by studies in permanent grasslands (Grace et al.,

186 2007) which are, by definition, ancient ecosystems. In such  
187 mature grasslands, which can be counted among the richest plant  
188 communities in the world per unit area (Wilson et al., 2012), the  
189 diversity-production relationship involves a complex web of  
190 multitrophic interactions. The richness-biomass relationship is  
191 likely dependent on the age of the grasslands (Guo, 2007) and it  
192 could be a transitory effect in young ecosystems (Thompson et  
193 al., 2005).

194 Less is known about the effect of species diversity on forage  
195 nutritive value (Baumont et al., 2014; Lü et al., 2021). Negative  
196 effects of species diversity on forage digestibility have been  
197 demonstrated but with possible confounding effects with  
198 management intensity (Schaub et al., 2020). In extensively  
199 managed semi-natural grasslands, a positive correlation between  
200 plant species diversity and plant digestibility and mineral content  
201 was found by Farruggia et al. (2008), probably due to the  
202 presence of diverse and abundant dicotyledonous species. A  
203 similar positive effect of plant diversity was found on vegetation  
204 mineral concentrations (French, 2017) also possibly due to an  
205 increase in the abundance of dicotyledons (Pirhofer-Walzl et al.,  
206 2011). However, relationships between plant diversity and  
207 forage nutritive quality have not been explicitly tested in  
208 empirical studies and among contrasting habitats.

209 Increasing forage yield and nutritive value are the objectives  
210 of management intensification, whether by increasing the

211 frequency of biomass exports or by increasing external inputs  
212 (e.g., fertilisers and pesticides. The effect of management may  
213 be direct by, for example, not allowing plants to flower, with an  
214 increase in stocking density of livestock or mowing frequency  
215 resulting in an increase in forage digestibility (Pavlů et al., 2006;  
216 Pontes et al., 2007; Gardarin et al., 2014). Similarly, soil  
217 characteristics may directly impact forage biomass production  
218 and nutritive value through its capacity to provide nutrients for  
219 plants (Barker & Culman, 2018). However, both management  
220 and soil characteristics may also impact floristic composition  
221 which, as highlighted above, can impact forage productivity and  
222 nutritive quality (Janssens et al., 1998; Rusch et al., 2009;  
223 Gilhaus et al., 2017; Silva et al., 2019). This suggests that the  
224 effects of these factors on forage productivity and quality could  
225 be both direct and indirect by altering vegetation composition.

226       Despite many studies examining relationships between  
227 different descriptors of plant communities, forage productivity,  
228 and nutritive value, none of these studies use a holistic approach  
229 in considering the relationships between both plant traits and  
230 diversity and multiple aspects of forage value, as well as the  
231 influence of environmental and management factors on these  
232 parameters. Our main aim in this study is to identify, synergies  
233 or trade-offs between plant diversity and forage productivity and  
234 nutritive value by testing their relationships across a wide range  
235 of semi-natural grassland habitats in metropolitan France. This

236 choice of sampling sites allows us to see if relationships can be  
237 detected in general across a multitude of different habitats and  
238 environments. To achieve this, we first test for trade-offs or  
239 synergies between forage parameters in (mature) permanent  
240 grasslands, and then determine if the observed relationships were  
241 affected by plant diversity. Secondly, we assess the relationships  
242 between forage parameters and diversity and functional structure  
243 variables. We test how forage parameters vary with functional  
244 composition, taxonomic diversity, and functional diversity.  
245 Finally, we aimed to detect direct and indirect effects of soil  
246 parameters and management intensity on forage quantity and  
247 nutritive value. We hypothesise that the influence of edaphic  
248 conditions and management intensity is mediated by plant  
249 community structure.

250

251

252

## 253 **2. Materials and methods**

254

### 255 *2.1 Study sites*

256

257 Eight study sites representing a wide range of semi-natural  
258 grassland habitat types across France were sampled (Table 1,  
259 map displaying the location of the study sites available in Supp.  
260 info. Fig.1). The sites were AQU: Atlantic dry grasslands located

261 in the Aquitaine region; COT: marshes located in the Cotentin  
262 peninsula; CRA: Mediterranean dry grasslands in the Crau plain;  
263 LOR: mesic grasslands and wet grasslands located in the  
264 Lorraine historical region; POI: marshes and wet grasslands in  
265 the Poitevin natural region; PUY: dry grasslands and heathlands,  
266 and mesic grasslands in the Chaîne des Puys mountain range;  
267 SOM: dry grasslands in the Somme department; VER:  
268 mountainous dry grasslands and heathlands, and mesic  
269 grasslands in the Vercors mountain range. Out of the 202 plots  
270 that were sampled, 172 were located in Natura 2000 sites (for  
271 further site descriptions, see Supp. info. Table 1 and 2).

272

## 273 *2.2 Forage sampling and chemical analysis*

274

275 Sampling was carried out in 2019 apart for plots in CRA which  
276 were sampled in 2020. One to four 10m x 10m sampling plots  
277 were selected in each vegetation unit sampled and five forage  
278 samples were harvested in 20cm x 20cm quadrats in each plot  
279 and their mean values correspond to the *standing biomass* (SB,  
280 g/m<sup>2</sup>). Samples were obtained during the vegetation growth  
281 season and before the beginning of the grazing period as it was  
282 not possible to use exclusion cages in grazed fields to obtain  
283 peak biomass production due to the location and number of  
284 sampling points, and also to abide by the desires of farmers. The  
285 grazing period started generally at the end of spring when the

286 *growing degree days* (GDD) was between 500 and 600 GDD.  
287 Sampling dates were thus fixed as close as possible to 550 GDD.  
288 In COT, where wet grasslands are seasonally flooded, sampling  
289 dates were set between 1000 and 1140 GDD to wait for the end  
290 of flooding. Sampling dates in CRA, where vegetation growth is  
291 limited by drought, were fixed at 210 and 220 GDD to  
292 correspond with the beginning of the grazing season. Plant  
293 biomass was cut at a minimum of 1 cm above ground level in 20  
294 cm x 20 cm quadrats and immediately dried in an oven at 60°C  
295 for at least 48h until a constant mass was obtained, and then  
296 weighted. In some cases, additional forage samples were  
297 collected to obtain at least 40 g of total dry biomass per plot, i.e.,  
298 the quantity required to perform the chemical analyses. Biomass  
299 chemical analyses were performed on samples grinded at 1 mm.  
300 *In vitro dry matter digestibility* (DMD, %), was assessed to  
301 describe forage digestibility (Aufrère et al., 2007; Nozière et al.,  
302 2018). *Crude protein content* (CP, g/kg) was measured using the  
303 Kjeldhal method (NF EN ISO 5983-1). Inductively coupled  
304 plasma optical emission spectrometry was used to measure  
305 contents in *calcium* (Ca, g/kg), *copper* (Cu, mg/kg), *iron* (Fe,  
306 mg/kg), *potassium* (K, g/kg), *magnesium* (Mg, g/kg), *manganese*  
307 (Mn, mg/kg), *sodium* (Na, g/kg), *phosphorus* (P, g/kg) and *zinc*  
308 (Zn, mg/kg) in fodder samples (NF EN 15510 and NF EN ISO  
309 11885).  
310

311

312 2.3. Soil and management data

313

314 The depth of root development in the soil was visually estimated  
315 with soil profiles in each sampling plot (Duchaufour, 1997).

316 Then, three topsoil cores were collected using a manual auger in  
317 the root development layer in each plot. Enough soil was  
318 collected to obtain at least 400g in dry soil mass for each plot.

319 The samples were then immediately dried at room temperature  
320 for 3 to 5 weeks until their mass was stable, then passed through  
321 a 2 mm mesh size sieve before analyses. The following  
322 parameters were measured: soil texture by the pipette method  
323 (NF X 31-107), pH using a glass electrode (NF ISO 10390), CEC  
324 (Meq/100g, Metson method, NF X 31-106), total *nitrogen* (N,  
325 g/kg) and *carbon* (C, g/kg) , and organic C (g/kg) by dry  
326 combustion (NF ISO 13878 and NF ISO 10694; Flash EA 1112,  
327 Thermo Electron, Germany), soluble P ( g/kg, Olsen method, NF  
328 ISO 11263; EON spectrophotometer BioTek Instruments Inc.  
329 USA), and Ca (g/kg), Mg (g/kg), K (g/kg), and Na (g/kg) were  
330 extracted using an ammonium acetate solution and measured by  
331 spectrometry (NF X31-108).

332 Information on grassland management was obtained  
333 from surveys conducted with land owners or managers for the  
334 sampling year. The information includes whether the sites were  
335 grazed, mowed, or both, the herbivore species and the annual

336 stocking rates when grazed, the number of cuts per year when  
337 mown, and whether or not the sites were fertilized. A *land-use*  
338 *intensity index* (LUI) was calculated for each plot as a measure  
339 of grazing intensity, by summing the standardized values of the  
340 number of cuts per year as a measure of mowing intensity and  
341 the annual stocking rate (livestock unit per days of grazing  
342 ha<sup>-1</sup> year<sup>-1</sup>) (Blüthgen et al., 2012). Fertilization intensity was  
343 not used in the equation as either the sites were not fertilized, or  
344 fertilization practices were not known.

345

#### 346 2.4. Plant diversity and traits

347

348 In each sampling plot, the cover of each vascular plant species  
349 was estimated in a 4 m x 4 m quadrat. Trait data was obtained  
350 for species which contributed the most to achieve an 80%  
351 sampling plot cover. Values for *leaf dry matter content* (LDMC),  
352 *specific leaf area* (SLA), were obtained from local databases  
353 when available, or from the TRY database (Kattge et al., 2020).  
354 Community-weighted means were then calculated for LDMC  
355 (LDMC<sub>CWM</sub>) and SLA (SLA<sub>CWM</sub>) in each plot sampled (Garnier  
356 et al., 2004). A categorical *plant functional type* (PFT) variable  
357 was created to differentiate between three plant types:  
358 graminoids (grasses, rushes, and sedges), legumes, and non-N<sub>2</sub>  
359 fixing forbs (hereafter forbs). Percentage covers of each PFT  
360 were calculated for each sampling plot.



361 Three metrics were used to evaluate taxonomic diversity:  
362 species richness, i.e. the number of species occurring in the  
363 4x4m quadrat, Shannon diversity index, and Pielou evenness  
364 index, calculated through species relative abundances.  
365 Functional diversity was described using the functional richness  
366 and functional evenness indices which were calculated for both  
367 LDMC and SLA separately (Mason et al., 2005; Villéger et al.  
368 2008). The functional richness index describes the size of the  
369 functional space, and the functional evenness index estimates the  
370 distribution of abundance in the functional space (Mason et al.,  
371 2005). Additionally, PFT evenness was calculated using the  
372 Pielou evenness index.

373

#### 374 2.5. Data analyses

375

376 Kendall's rank correlation tests were used to detect significant  
377 correlations among variables describing forage productivity and  
378 nutritive value. The tests were performed on the residuals of  
379 generalized linear models of the effect of sampling sites on  
380 forage parameters in order to account for site-dependant effects.  
381 The parameters considered for forage productivity and nutritive  
382 value were SB, DMD, CP, and *average mineral content* (MinAv)  
383 calculated as the average of the standardized macronutrient  
384 values (Ca, K, Mg, Na, P). The effect of diversity on observed  
385 correlations between forage characteristics was tested using a

386 modified bootstrap method to compare the correlation  
387 coefficients at high diversity values and low diversity values  
388 (Wilcox, 2012). For this, diversity variables were transformed  
389 into two-level categorical variables by assigning a high diversity  
390 factor level to values above the median in each sampling site and  
391 low diversity factor level for values below the median. The  
392 bootstrap method was performed on the Kendall correlation  
393 coefficients.

394 Mixed-effects models were fitted to test the effect of  
395 diversity indices, functional traits, and PFT on forage variables.  
396 Sampling sites were added as a random effect in the models to  
397 take into account the nested structure of plots within sites. Each  
398 explanatory variable was fitted individually to assess its effect  
399 on forage quantity and nutritive value. This analytical procedure  
400 was repeated for statistically significant models ( $P < 0.05$ ) with  
401 the inclusion of sampling sites as an interacting term as opposed  
402 to a random effect in generalized linear models to determine if  
403 the observed relationships were stable between sampling sites.  
404 Pairwise comparisons of regressions coefficient were then  
405 performed using a t-test to test differences in the effect of the  
406 explanatory variables between sites. The model estimates, the  
407 distribution families used, and the results of the post-hoc analysis  
408 are given in the supplementary information. Model predictions  
409 were obtained and standardised by dividing each predicted value  
410 by the mean of the response variable for each model. This

411 represented the deviation of predictions from the mean and was  
412 used for graphical presentation of model results. A mineral  
413 content evenness index was calculated using macronutrient  
414 values, however since no significant results was found when  
415 analysing the effects of plant functional traits, plant functional  
416 types, and plant diversity on mineral content evenness, analyses  
417 performed on this parameter have been excluded from the  
418 results.

419 Mixed-effects models were used to detect effects of soil  
420 properties and land-use intensity on forage variables with  
421 sampling sites included as a random effect. A backward stepwise  
422 model selection procedure based on the generalised Akaike  
423 information criterion (GAIC, penalty term  $k = 2.5$ ) was used to  
424 select the most parsimonious model (Rigby & Stasinopoulos,  
425 2005; Zuur et al., 2009). The following variables were included  
426 in the initial model before applying the selection process: C/N  
427 ratio, percentage of clay and fine silt, organic carbon content,  
428 bulk density, pH, mean soil mineral content (the average of the  
429 standardized macronutrient values; Ca, K, Mg, Na, P), and land-  
430 use intensity. The choice of probability distribution type for  
431 mixed-effects models was based on visual assessments of model  
432 residuals using worm plots (van Buuren & Fredriks, 2001). Path  
433 analysis was used to determine if the effects of soil conditions  
434 and land-use intensity on forage were mediated by vegetation  
435 diversity, functional traits, and/or functional types. A backward

436 stepwise selection process was used to select the independent  
437 variables for model inclusion. Statistically significant terms  
438 from the mixed models were retained and were tested separately  
439 in path analysis models for significant relationships with the  
440 dependent and independent variables. Variables leading to  
441 significant results were included in an initial model and a  
442 backward stepwise selection was performed to select the  
443 mediators. Standing biomass was log-transformed to meet the  
444 test assumptions and the square root of CP was used for the same  
445 reason.

446 In all regression analyses, model terms with a p-value  
447 below 0.05 were considered as having a significant effect on the  
448 dependent variable. Analyses were performed on R v.4.1.1 and  
449 the following packages were used: gamlss v. 5.3-4 (Rigby &  
450 Stasinopoulos, 2005) for the multi-level models, piecewiseSEM  
451 v. 2.1.2 (Lefcheck, 2016) for path analysis, and rstatix v. 0.7.0  
452 (Kassambara, 2021) for the correlation analysis. The vegan v.  
453 2.5-7 package (Oksanen et al., 2020) was used to calculate  
454 taxonomic diversity indices and the FD v. 1.0-12 package  
455 (Laliberté et al., 2014) was used to calculate functional diversity  
456 indices and community-weighted means. Graphs were rendered  
457 using the ggplot package v. 3.3.5 (Wickham, 2016) and Inkscape  
458 v. 1.1.1 (Inkscape Project, 2020).

459

460

461

462

463 Table 1: Description of the study sites. Habitat types correspond  
464 to level 2 EUNIS habitat types (Chytrý et al., 2020). Habitats are  
465 classified according to the latest review available for each habitat  
466 type at the time of writing.

467

468

469

470

### 471 **3. Results**

472

#### 473 *3.1. Relationships between forage parameters*

474

475 We first analysed the relationships between forage parameters.

476 A positive correlation was measured between crude protein

477 content (CP) and dry matter digestibility (DMD) ( $\tau = 0.4$ , p-

478 value $<0.001$ ). Average mineral content (MinAv) was positively

479 correlated with CP ( $\tau = 0.37$ , p-value $<0.001$ ) and DMD ( $\tau = 0.62$ ,

480 p-value $<0.001$ ). Standing biomass was not significantly

481 correlated with any of the forage nutritive value variables.

482 Species richness and Shannon index significantly influenced

483 correlations between forage parameters. Greater species richness

484 resulted in a more negative correlation between DMD and SB

485 (high diversity  $\tau$  – low diversity  $\tau = -0.25$ , p-value $<0.05$ ), and

486 MinAv and SB (high diversity  $\tau$  – low diversity  $\tau = -0.22$ , p-  
487 value<0.05). A greater Shannon index also resulted in a more  
488 negative correlation between MinAv and SB (high diversity  $\tau$  –  
489 low diversity  $\tau = -0.25$ , p-value<0.05).

490

491

492 *3.2. Relationships between forage parameters and functional*  
493 *composition, taxonomic diversity, and functional diversity*

494

495 The proportion of each plant functional types (i.e., graminoids,  
496 legumes, and forbs) showed significant relationships with all  
497 forage variables analysed (Fig. 1). Standing biomass increased  
498 with increasing percentage cover of graminoids and decreased  
499 with increasing forb cover. Conversely, DMD decreased with  
500 increasing graminoid cover and increased with increasing forb  
501 and legume covers. Increasing forb and legume covers also led  
502 to an increase in MinAv and CP while legume cover had no  
503 significant effect on SB. The community weighted mean of  
504 specific leaf area ( $SLA_{CWM}$ ) was positively correlated with CP,  
505 DMD, and MinAv, while community weighted mean leaf dry  
506 matter content ( $LDMC_{CWM}$ ) was negatively correlated with the  
507 same forage parameters.

508 Plant community species richness is negatively  
509 correlated with SB and MinAv (Fig. 2). The Shannon index and  
510 species evenness were negatively correlated with SB and

511 positively correlated with MinAv. Species evenness was also  
512 positively correlated with CP and DMD. Plant functional type  
513 evenness was positively correlated with DMD, and MinAv,  
514 while no correlation was found between PFT evenness and CP  
515 and SB (Fig. 3). SLA functional richness was negatively  
516 correlated with SB and DMD and positively correlated with CP.  
517 An increase in functional evenness of SLA was significantly  
518 associated with a decrease in CP, DMD, and MinAv. LDMC  
519 functional richness was negatively correlated with DMD and SB,  
520 and LDMC functional evenness was positively correlated with  
521 DMD and MinAv.

522 A significant site effect was found in five of the eleven models  
523 when including a site effect in models which displayed a  
524 significant effect of diversity or functional traits or types on  
525 DMD (Supp. info. Fig 2, Supp. info. Table 5). For CP, this was  
526 the case in four out of seven models, and for MinAv, for five out  
527 of ten models (Supp. info. Fig 3 and 4, Supp. info. Table 6 and  
528 7). Of the seven models displaying significant relationships  
529 between SB and diversity indices or functional traits, only the  
530 one for the Shannon index significantly differed between sites  
531 (Supp. info. Fig 5, Supp. info. Table 8).

532  
533  
534

535 Figure 1. Effects of plant functional types (a, b, and c), community-  
536 weighted mean of specific leaf area ( $SLA_{CWM}$ , d), and community-  
537 weighted mean of leaf dry matter content ( $LDMC_{CWM}$ , e) on forage  
538 variables. The response variables are represented as the percentage of  
539 deviation of the predicted values from the mean of the response  
540 variable. Statistically significant effects only are plotted ( $P < 0.05$ ).

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546 Figure 2. Effects of species richness (a), Shannon index (b) and species  
547 evenness index (c) on forage variables. The response variables are  
548 represented as the percentage of deviation of the predicted values from  
549 the mean of the response variable. Statistically significant effects only  
550 are plotted ( $P < 0.05$ ).

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553

554 Figure 3. Effects of functional richness and functional evenness of  
555 SLA (a, b), plant functional type (PFT) evenness (c), and functional  
556 richness and functional evenness of LDMC (d, e) on forage variables.  
557 The response variables are represented as the percentage of deviation  
558 of the predicted values from the mean of the response variable.  
559 Statistically significant effects only are plotted ( $P < 0.05$ ).

560



561 3.3. Soil and land use direct and indirect effects on forage  
562 parameters

563

564 Significant effects of abiotic factors on forage parameters were  
565 detected. Soil C/N and pH were negatively correlated with SB,  
566 and soil C/N was also negatively correlated with CP (Table 2).  
567 The effect of pH on SB was mediated by species richness and  
568 forb percentage cover (Fig. 4 a), while the effect of C/N on CP  
569 was partially mediated by percentage graminoid cover,  $SLA_{CWM}$ ,  
570 and  $LDMC_{CWM}$  (Fig. 4 b).

571 Soil average mineral content and LUI had a positive  
572 effect on DMD, CP, and forage MinAv. The effects of soil  
573 average mineral content were partially mediated by graminoid  
574 percentage cover and  $LDMC_{CWM}$  (Fig. 4 b, and Fig. 5 a and b).  
575 For CP, the effect of soil average mineral content was also  
576 partially mediated by  $SLA_{CWM}$  (Fig. 4 b) while for DMD it was  
577 also partially mediated by  $SLA_{CWM}$  and species richness (Fig. 5  
578 a). The effects of LUI on DMD and MinAv were partially  
579 mediated by SLA functional evenness (Fig. 5 a). We found a  
580 negative relationship between soil pH and forage MinAv and  
581 also negative correlations between soil organic C content and  
582 forage DMD and MinAv which were partially mediated by  
583  $LDMC_{CWM}$  and SLA functional evenness (Fig. 5 a and b). Soil  
584 pH had a positive effect on DMD despite being positively

585 correlated with species richness which was in turn negatively  
586 correlated with DMD (Fig. 5 a).

587

588

589 Table 2. Model estimates for the effect of soil properties and land-use  
590 intensity on forage variables. SB: standing biomass, DMD: dry matter  
591 digestibility; CP: crude protein content; MinAv\_f: average mineral  
592 content in forage. C/N: carbon to nitrogen ratio in soil; C\_org: organic  
593 carbon content in soil; MinAv\_s: average mineral content in soil; LUI:  
594 land-use intensity index. \*, \*\*, and \*\*\* indicate  $P<0.05$ ,  $P<0.01$ ,  
595 and  $P<0.001$ , respectively. The Beta distribution (with a logit link), the  
596 Box-Cox t distribution (Rigby & Stasinopoulos, 2006), and the Sinh-  
597 Arcsinh distribution (Jones & Pewsey, 2009) were used.

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614 Fig 4. Path diagrams showing the effect of edaphic factors and land-  
615 use intensity on forage standing biomass (a) and crude protein content  
616 (b) mediated by functional traits, functional types, and diversity  
617 indices.  $R^2_M$  indicates the proportion of variance explained by fixed  
618 effects while  $R^2_C$  indicates the proportion of variance explained by  
619 both fixed and random effects. Blue arrows indicate positive  
620 relationships, red arrows indicate negative relationships, while grey  
621 arrows indicate non-significant relationships. The standardised  
622 regression coefficient for each relationship is indicated above the  
623 arrows. The sizes of the arrows are proportional to the coefficients.  
624  $LDMC_{CWM}$ : community-weighted mean of leaf dry matter content;  
625  $SLA_{CWM}$ : community-weighted mean of specific leaf area. \*, \*\*, and  
626 \*\*\* indicate  $P < 0.05$ ,  $P < 0.01$ , and  $P < 0.001$ , respectively.

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647 Fig 5. Path diagrams showing the effect of edaphic factors and land-

648 use intensity on forage dry matter digestibility (a) and average mineral

649 content (b) mediated by functional traits, functional types, and

650 diversity indices.  $R^2_M$  indicates the proportion of variance explained

651 by fixed effects while  $R^2_C$  indicates the proportion of variance

652 explained by both fixed and random effects. Blue arrows indicate

653 positive relationships, red arrows indicate negative relationships. The

654 standardized regression coefficient for each relationship is indicated

655 above the arrows. The sizes of the arrows are proportional to the

656 coefficients. J: species evenness;  $FE_{vSLA}$ : functional evenness in SLA;

657  $LDMC_{CWM}$ : community-weighted mean of leaf dry matter content;

658  $SLA_{CWM}$ : community-weighted mean of specific leaf area. \*, \*\*, and

659 \*\*\* indicate  $P < 0.05$ ,  $P < 0.01$ , and  $P < 0.001$ , respectively.

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666 **4. Discussion**

667

668 *4.1 Synergies and trade-offs between forage parameters*

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670 Forage agronomic value assessment is based on forage

671 productivity and nutritive value. We showed here that these two

672 aspects of forage production were not correlated in the sampled

673 semi-natural grasslands at the beginning of the grazing season.

674 This offers the possibility of increasing either forage

675 productivity or nutritive value by adapting management

676 practices without impacting the other. It has been demonstrated

677 that management type had a significant effect on forage biomass

678 production but not on forage nutritive quality in mountain

679 grasslands (Loucougaray et al., 2015). A trade-off between

680 forage productivity and forage nutritive value may occur

681 however in species-rich grasslands, since we found a more

682 negative correlation between SB and DMD, and between SB and

683 MinM in plots associated with a higher species richness and

684 Shannon diversity. This suggests that although forage

685 productivity may be lower in species-rich grasslands, forage

686 nutritive value may be greater in these grasslands and can

687 compensate for reduced biomass production. Positive

688 correlations were found amongst parameters associated with  
689 forage nutritive values. This was expected for DMD and CP for  
690 which correlations are commonly reported (Hansen & Lawrence,  
691 2017; Nozière et al., 2018).

692

693

694 *4.2 Relationships between descriptors of plant community and*  
695 *forage parameters*

696

697 General trends in relationships between forage parameters and  
698 plant functional traits and types were measured for extensive  
699 grasslands of conservation interest. The community composition  
700 in plant functional type had an influence on SB with a higher SB  
701 recorded with higher graminoid cover and lower forb cover, as  
702 expected (Michaud et al., 2015). Forage nutritive value  
703 responded positively to the cover of forbs and legumes in plant  
704 communities. For legumes, this result is in line with previous  
705 findings which have demonstrated their higher protein content,  
706 higher energy content, higher digestibility, and higher mineral  
707 content for certain minerals compared to grasses (see review by  
708 Baumont et al., 2016). The greater forage nutritive value of  
709 legumes is probably detected by domestic sheep and cattle as  
710 they show a partial preference for legumes compared to grasses  
711 in their diet (Rutter, 2006). We found that forbs were associated  
712 with high forage mineral contents, as also shown by Pirhofer-

713 Walzl et al. (2011) and Reiné et al. (2020). The different  
714 responses of forage parameters to different PFTs suggests that  
715 an even cover of PFTs may help in jointly increasing forage  
716 biomass production and nutritive value.

717 We did not observe the positive correlation expected  
718 between  $SLA_{CWM}$  and SB nor the expected negative correlation  
719 between  $LDMC_{CWM}$  and SB (Lavorel & Garnier, 2002). This  
720 could be due to the presence of certain tussock perennial grasses  
721 in extensive grasslands which are not consumed by livestock and  
722 subsequently accumulate biomass (Hejmanová et al. 2016;  
723 Massey et al. 2009). It is also possible that these traits are not as  
724 good predictors of early standing biomass as they are of biomass  
725 at a later vegetative stage or their capacity to predict forage  
726 biomass vary between habitat types. The community weighted  
727 means of LDMC and SLA had a negative and positive effect  
728 respectively on CP. Even though the size of the effects varied  
729 between sites, this was mainly due to one site (CRA) in which  
730 the observed effects were particularly strong, and the direction  
731 of the correlation slopes were generally consistent over all  
732 studied sites. Leaf traits are also associated with DMD (Pontes  
733 et al., 2007; Gardarin et al., 2014), and we found that both  
734  $LDMC_{CWM}$  and  $SLA_{CWM}$  were highly correlated, negatively and  
735 positively respectively, with DMD. For grasses, Khaled et al.  
736 (2006) found LDMC to be better at predicting digestibility than  
737 SLA. The correlation of both functional traits with DMD may be

738 due to the presence of forbs and legumes in many of the semi-  
739 natural grasslands we studied, for which SLA was already shown  
740 to be a good predictor for their DMD (Tasset et al., 2019). In  
741 fact,  $SLA_{CWM}$  was a better predictor of DMD in our study since  
742 the relation was more stable between sites than the one observed  
743 between  $LDMC_{CWM}$  and DMD.

744 Positive relationships were observed between both  
745 taxonomic diversity and functional diversity and forage  
746 nutritional quality, supporting the synergy between high plant  
747 diversity and potential for agricultural use through forage  
748 production in semi-natural grasslands of high conservation  
749 value. However, negative relationships were recorded between  
750 taxonomic diversity and standing biomass, which may  
751 classically be explained by the competitive exclusion pressure  
752 exerted by the more productive and competitive species on  
753 others (Grime, 1973; Feßel et al., 2016). The grasslands we  
754 studied may be situated on the declining section of the schematic  
755 unimodal species richness - productivity relationship (Grime,  
756 1973; Rosenzweig & Abramsky, 1993). In support of this  
757 hypothesis, this study was carried out in extensively managed  
758 grasslands and even the plots with the lowest species diversity  
759 may nonetheless have a higher diversity compared to intensively  
760 managed grasslands. It is also possible the negative correlation  
761 between taxonomic diversity and standing biomass can be  
762 explained by the spatial scale at which the study has been



763 conducted. A study taking this spatial effect into account (Gross  
764 et al., 2009) showed that the positive relationship between  
765 biodiversity and production exists in permanent grasslands at  
766 very local scales ( $0.01\text{m}^2$ ) whereas it is not detected at the  
767 community scale ( $>100\text{m}^2$ ), no doubt because at the scale of the  
768 neighbourhood of the plants, complementarity between species  
769 can come into play, while at the plant community level,  
770 production is strongly dependent on environmental  
771 heterogeneity, masking the biodiversity effect.

772         Among the species diversity measures calculated,  
773 species evenness produced the most interesting results since it  
774 was significantly correlated with all forage parameters. The  
775 model outputs demonstrated a trade-off between forage  
776 productivity and forage nutritive quality along a species  
777 evenness gradient.

778         As for functional diversity, the negative effects of SLA  
779 functional richness and LDMC functional richness on standing  
780 biomass suggest that an increase in the occupation of the  
781 functional space led to a decrease in biomass production. This  
782 increase in functional space may be associated with a diversity  
783 of species with diverse resource acquisition capacities but  
784 without highly productive species. Similarly, Chanteloup &  
785 Bonis (2013) found the peaks of standing biomass in fertile  
786 habitats to be negatively correlated with functional diversity  
787 which they interpreted as a dilution of highly productive species

788 that were first recruited in the communities resulting in a  
789 reduction of community production capacity.

790 PFT evenness was correlated with DMD and MinAv  
791 which along with the significant effects of vegetation trait  
792 diversity on DMD, CP, and MinAv further highlights the  
793 importance of traits in determining forage nutritive value. The  
794 effect of species and PFT evenness on forage nutritive value in  
795 our study is linked to the greater presence of forbs and legumes,  
796 as species richness, Shannon index, and species evenness were  
797 positively correlated with legume cover and forb cover which, as  
798 previously discussed, were of higher nutritive value than grasses  
799 in this study. In more evenly distributed communities with  
800 different functional plant types, a large ecological  
801 complementarity effect is obtained, and soil resources can be  
802 exploited more fully by the communities, as suggested by  
803 Picasso (2011) but also as evidenced in overyielding studies  
804 manipulating the diversity of PFT in sown grasslands (Palmborg  
805 et al. 2005; Finn et al. 2013).

806

807 *4.3 Direct and indirect effects of management and soil properties*  
808 *on forage parameters*

809

810

811 Grassland vegetation responds to both environmental factors and  
812 management practices (Delpech, 1982, Gos et al., 2016). In

813 intensive grasslands, biomass production appears mainly driven  
814 by management practices such as the choice of species and  
815 cultivar sown, grazing intensity or cutting frequency, and  
816 fertilisation (Plantureux et al., 2005; Oenema et al., 2014). By  
817 contrast, this study focused on semi-natural grasslands mostly  
818 located in Natura 2000 sites where agricultural practices needed  
819 to fit as much as possible with conservation goals. These semi-  
820 natural grasslands are in general more limited in available soil  
821 resources and their management can be defined as extensive,  
822 with reduced grazing pressure or mowing frequency as well as  
823 no or limited fertilisation input. The range in management  
824 intensity is thus reduced and the effect of environmental factors  
825 such as soil characteristics on grassland vegetation become more  
826 apparent than they are in intensively managed grasslands (Balent  
827 & Stafford Smith, 1991). We found this to be true for SB which  
828 was not correlated with land-use intensity (LUI). However, LUI  
829 did have a direct effect on MinAv and CP, and an indirect effect  
830 on DMD and MinAv via a reduction of SLA evenness. Soil  
831 characteristics had an impact on all forage parameters directly or  
832 indirectly by altering plant diversity and the functional  
833 composition of plant communities. Early standing biomass, CP,  
834 DMD, and MinAv responded to vegetation functional traits and  
835 PFT, and these in turn were correlated with soil fertility and pH  
836 value. Direct effects of soil parameters on CP, DMD, and MinAv  
837 were also detected. Edaphic and management effects on forage

838 parameters mediated by vegetation composition in extensive  
839 grasslands have not been previously studied to our knowledge.  
840 Average mineral soil content influence on forage nutritive value  
841 was associated with a decrease in  $LDMC_{CWM}$  and graminoid  
842 cover and an increase in  $SLA_{CWM}$ . Leaf construction requires the  
843 use of minerals which may explain the correlation measured  
844 between the soil fertility parameters (average soil mineral  
845 content, C/N, organic C content) and  $SLA_{CWM}$  or  $LDMC_{CWM}$   
846 (Wright et al., 2004; Hodgson et al., 2011). The effect of soil pH  
847 on vegetation structure is site-dependent since the sampled  
848 grasslands range from calcareous to acid grasslands.

849

850

851 *4.4 Generalisation of the relationships observed in a variety of*  
852 *habitat types and climatic conditions*

853

854 Although we sampled across different habitat types, our study  
855 design did not allow us to investigate effects of plant community  
856 structure on forage productivity and nutritive value specific to a  
857 study site. However, we were able to show correlations between  
858 forage parameters and descriptors of community structure  
859 among the wide range of habitat type and environmental  
860 conditions sampled. Only the relationship between standing  
861 biomass and species richness varied out of the seven significant  
862 correlations measured between standing biomass and

863 community structure parameters. Relationships between forage  
864 nutritive quality and community structure parameters were less  
865 stable. The correlation between all forage nutritive quality  
866 parameters and  $LDMC_{CWM}$  significantly varied between sites.  
867 However, the relationship between species evenness and DMD  
868 and MinAv was stable across sampled sites. This suggests that  
869 the relationship between standing biomass and forage nutritive  
870 value is driven by species evenness in multiple extensive  
871 grassland habitat types. The forage parameter with the least  
872 stable relationship with community structure parameters across  
873 site was crude protein content (five out of seven significant  
874 relationships). More research is needed to decipher which  
875 parameters among habitat types drive the relationship between  
876 community structure and forage nutritive value.

877

## 878 *5. Conclusion and perspectives*

879

880 Forage production is a key service delivered by grasslands for  
881 farmers. Our work, together with other studies (see review by  
882 Tallwin and Jefferson, 1999, Farruggia et al., 2008), showed  
883 that synergies occurred between plant diversity conservation and  
884 forage nutritional quality in a wide range of semi-natural  
885 grassland types extensively managed in France. Such synergies  
886 may even be expressed in the economic value of forage while

887 considering forage yield and nutritive value in grasslands  
888 (Schaub et al., 2020).

889         This study has demonstrated the importance of plant  
890 functional traits and PFT in determining forage productivity and  
891 nutritive value. Forage production in intensive grasslands tends  
892 to focus on grasses and legumes. Here, we evidenced that non-  
893 fixing forbs play an important role in diversified grasslands for  
894 forage nutritional quality. We also showed that an even  
895 distribution in PFTs may improve forage nutritive value without  
896 reducing biomass production, opening perspectives for the  
897 compatibility of agricultural and conservation values in semi-  
898 natural grasslands. Furthermore, greater species evenness and  
899 especially functional evenness was previously shown to increase  
900 community stability and resistance to external threats  
901 (Hillebrand et al., 2008) and thus show multiple benefits to semi-  
902 natural grasslands. This study highlights the equitability, both at  
903 the species level and at the functional traits and types level, as  
904 key to the analysis of the relationship between biodiversity  
905 conservation and forage production. The idea of considering  
906 nutritive quality in forage evaluation could also be taken further  
907 by analysing the effect on animal health, the diversity of other  
908 taxonomic groups (e.g. birds, insects, and microorganisms), or  
909 the quality of products derived from forage such as meat, milk,  
910 and cheese.

911 Seeking a good compatibility among biodiversity and  
912 forage production is of fundamental importance for high heritage  
913 value grasslands for their sustainable use and management.  
914 Therefore, we recommend integrating forage production  
915 quantity and nutritive value in grasslands conservation status  
916 assessment. This will have two main benefits:

917

918 • To provide managers, conservationist as well as farmers  
919 with the actual nutritive and production values of species-  
920 rich grasslands, offering firm basis for management  
921 choices and then, eventually, limiting underestimation of  
922 their agronomic quality. With such a clear knowledge,  
923 farmers may be enticed to participate in conservation  
924 efforts, as they will be in a position to argue on the related  
925 economic impact or to realise that there is little or no  
926 compromise required between grassland agronomic values  
927 and their conservation efforts (McGinlay et al., 2017).

928

929 • The diagnosis of forage productivity and nutritive value in  
930 evaluating grassland conservation status could help  
931 identify situations which are at risk of land use  
932 abandonment because of poor forage productivity or poor  
933 forage nutritional quality.

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937

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972

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