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

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ABSTRACT

This paper aims in assessing the relationship between grassland plant diversity and agronomic value, which represents a major challenge to reconcile nature conservation and agricultural use of semi-natural grassland habitats. The effects of plant diversity and functional traits were studied on forage nutritive value and early standing biomass in a wide set of semi-natural temperate grassland habitats. Plant communities were described by their species and functional diversity, community-weighted means (CWM) of plant functional traits, and the relative cover of main plant functional types (graminoids, forbs, and legumes). Species richness was found to be negatively associated with early standing biomass and average mineral content. Community evenness, for both species and plant functional types, was positively correlated with digestibility, crude protein content, and average mineral content but negatively with early standing biomass. Early standing biomass was found to increase with increasing graminoid cover and to decrease with increasing forb cover. Forage nutritive value improved with higher legume cover, higher specific leaf area CWM and lower leaf dry matter content CWM, while these functional community characteristics were not found to impact early standing biomass. Our results highlight that a better forage nutritive value can be obtained with a higher plant species evenness in permanent grassland habitats. Furthermore, in grasslands with an even distribution of plant functional types, forage nutritive value may be improved with no loss in early standing biomass.

1. Introduction

Grasslands are the main agricultural land use both on a European and global scale (Stypinski, 2011; Török et al., 2021). Semi-natural grasslands, which are maintained by agricultural practices or conservation management, are recognized for their heritage values (Halada et al., 2011), and provide numerous ecosystem services such as forage production, climate regulation through carbon sequestration, pollination, water regulation, nutrient cycling, and provide habitats for biodiversity (Anderson-Teixeira et al., 2012; Wehn et al., 2018; Bengtsson et al., 2019). All these services depend on the structural and functional

components of grassland habitats, and could be considered for the structure and function criteria used to assess their conservation status within the European Directive 92/43/EEC. This EEC directive has established site networks (Natura 2000 sites) where the semi-natural habitats are recognized as having high conservation values. In this context, management has to respect as much as possible such values while also needing to be socio-economically sustainable. Amongst the services provided by semi-natural grasslands, those related to agronomic and conservation values indeed deserve particular attention. Agronomic use, and thus agronomic value, is a key condition for the persistence of semi-natural grasslands which otherwise would either be converted to

intensive agricultural land uses (often sown grasslands or croplands) or abandoned and replaced by woody habitats after natural shrub encroachment (MacDonald et al., 2000; Prévosto et al., 2006; Henle et al., 2008; Pe'er et al., 2014). This conversion of temperate grasslands may threaten biodiversity (Hoekstra et al., 2005) and ecosystem service supply (Vidaller and Dutoit, 2022). However, forage productivity and nutritive quality are not used in the assessment of conservation status of Natura 2000 grasslands (Evans and Arvela, 2011; Silva et al., 2019). Considering forage production and nutritive value and investigating to what extent semi-natural grasslands are agronomically valuable is thus of the utmost importance for conservation through continuing extensive traditional agricultural management. This is especially true for the many grasslands which are not part of a conservation scheme and in the many regions where agriculture remains the main driving factor of rural landscapes. More precisely, there is a need to identify the factors that determine forage productivity and nutritive value, and the relationships between forage production and plant diversity. As agronomic value and biodiversity may not vary in the same direction, identifying synergies and trade-offs, among and between forage nutritive variables, forage productivity, and species and functional diversity, as well as the environmental drivers of these relationships is worthwhile for the conservation of semi-natural grasslands.

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

Plant communities through their functional composition may operate on grassland forage biomass production (Michaud et al., 2015; Duru et al., 2015). Grasses tend to produce more biomass than forbs (Michaud et al., 2015) and show better regrowth capacity after defoliation (Schleip et al., 2013; Tahmasebi Kohyani et al., 2009). Quantitative functional traits of plants may also be valuable predictors of forage productivity. Leaf dry matter content (LDMC) has been found to be negatively correlated with plant growth rate (Wilson et al., 1999; Pontes et al., 2007). By contrast, vegetation with a high specific leaf area (SLA) tends to be composed of fast-growing species found in nutrient-rich habitats (Lavorel and Garnier, 2002; Wright et al., 2004; Laliberté et al., 2012). This results in a positive correlation between SLA and above-ground biomass production (Poorter and Bergkotte, 1992; Lavorel and Garnier, 2002).

Plant functional types and traits may also influence forage nutritive values (Gardarin et al., 2014; Niu et al., 2016a,b; Tasset et al., 2019). It has already been shown that forage crude protein content varies between plant functional types, with legumes possessing a higher protein content than grasses, and dicotyledonous plants containing more digestible tissues than grasses especially in later development stages (Bruinenberg, 2002; Duru et al., 2010). Forage digestibility has also been shown to be negatively correlated with LDMC (Pontes et al., 2007; Gardarin et al., 2014; Niu et al., 2016a). Contrasts in functional composition are meaningful for explaining variations in forage mineral content, with forbs and legumes more likely to have a higher individual mineral content than grasses for most minerals (García-Ciudad et al., 1997; Pirhofer-Walzl et al., 2011; Schlegel et al., 2016). These contrasts are however not always measured for all minerals (Schlegel et al., 2016). Manganese, for example, can be found in higher concentrations in grass-dominated forage (Spears, 1994). The reason for differences in mineral content between functional types are not yet well understood, although they may reflect differences in cation exchange capacities in cell walls (Haynes, 1980; Marschner, 2011). A positive relationship is expected between SLA and forage mineral content, since a positive relationship between plant mineral content and plant relative growth rate as well as a positive correlation between SLA and plant growth rate were reported (Poorter and Bergkotte, 1992; Wright et al., 2004). The literature cited above indicates that forage biomass production and forage nutritive quality exhibit different responses to plant community

composition. This suggests that some negative correlations are to be expected between biomass production and certain parameters of forage nutritive quality.

Forage productivity and nutritive value, and species diversity are key attributes of grasslands when considering farming system sustainability from an agroecological perspective (Wezel and Peeters, 2014). The relationship between plant diversity and biomass production is complex in grasslands. On the one hand, the most productive grasslands are those which are intensively managed with fertilisation promoting competitive species with a consequent reduction of plant diversity (Tilman, 1982; Plantureux et al., 2005; Gaujour et al., 2012). On the other hand, it was repeatedly experimentally shown that the increase in specific and particularly functional diversity increases plant production (Finn et al., 2013), as a result of facilitation and species complementarity in the use of resources (Loreau, 1998; Tilman et al., 2001; Hector et al., 2002; Marquard et al., 2009). In studies which disentangle diversity effects from management effects on semi-natural grassland productivity, both positive and negative effects of diversity on production have been reported (Assaf et al., 2011; Rose and Leuschner (2012); Grime (1973) suggests why no simple relationship between species diversity and primary productivity is expected. This model shows that diversity decreases both in highly productive systems, due to competition, and in low-productive systems, because only species adapted to a high level of stress or disturbance can survive (Grime, 1973). The positive effect of species richness on biomass is also essentially observed in experimental grasslands (Palmborg et al., 2005; Finn et al., 2013; Husse et al., 2017) which are generally immature and simplified. Such results may not be confirmed by studies in permanent grasslands (Grace et al., 2007) which are, by definition, ancient ecosystems. In such mature grasslands, which can be counted among the richest plant communities in the world per unit area (Wilson et al., 2012), the diversity-production relationship involves a complex web of multitrophic interactions. The richness-biomass relationship is likely dependent on the age of the grasslands (Guo, 2007) and it could be a transitory effect in young ecosystems (Thompson et al., 2005).

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

Increasing forage yield and nutritive value are the objectives of management intensification, whether by increasing the frequency of biomass exports or by increasing external inputs (e.g., fertilisers and pesticides). The effect of management may be direct by, for example, not allowing plants to flower, with an increase in stocking density of live-stock or mowing frequency resulting in an increase in forage digestibility (Pavlů et al., 2006; Pontes et al., 2007; Gardarin et al., 2014). Similarly, soil characteristics may directly impact forage biomass production and nutritive value through its capacity to provide nutrients for plants (Barker and Culman, 2018). However, both management and soil characteristics may also impact species composition which, as highlighted above, can impact forage productivity and nutritive quality (Janssens et al., 1998; Rusch et al., 2009; Gilhaus et al., 2017; Silva et al., 2019). This suggests that the effects of these factors on forage productivity and quality could be both direct and indirect by altering vegetation composition.

Despite many studies examining relationships between different descriptors of plant communities, forage productivity, or nutritive value,

none of these studies consider the relationships between both plant traits and diversity and multiple aspects of forage value, as well as the influence of environmental and management factors on these parameters. Our main aim in this study is to identify synergies or trade-offs between plant diversity and forage quality as well as early standing biomass by testing their relationships across a wide range of semi-natural grassland habitats in metropolitan France. This choice of sampling sites aims to determine whether relationships can be detected in general across a multitude of different habitats and environments. In such a large range of grasslands, climatic effects are expected on forage quantity and quality (Izaurre et al., 2011; Dumont et al., 2015) and such effects need to be taken into account in data analysis and interpretation.

To achieve our study goal, we first tested for trade-offs or synergies between forage parameters in permanent grasslands, and then determined if the observed relationships were affected by plant diversity. Secondly, we assessed the relationships between forage parameters and community diversity and functional structure variables. We tested how forage parameters vary with functional composition, taxonomic diversity, and functional diversity. Finally, we aimed to detect direct and indirect effects of soil parameters and management intensity on forage quality and early standing biomass. We hypothesised that the influence of edaphic conditions and management intensity is mediated by plant community structure.

2. Materials and methods

2.1. Study sites

Eight study sites representing a wide range of semi-natural grassland habitat types across France were sampled (Table 1, map displaying the location of the study sites available in Supp. info. Fig. 1). The sites were AQU: Atlantic dry grasslands located in the Aquitaine region; COT: marshes located in the Cotentin peninsula; CRA: Mediterranean dry grasslands in the Crau plain; LOR: mesic grasslands and wet grasslands located in the Lorraine historical region; POI: marshes and wet grasslands in the Poitevin natural region; PUY: dry grasslands and

Table 1

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

Site	EUNIS habitat type	Geographical feature	Biogeographical region	Number of plots
AQU	(R1) Dry grassland	Hill	Atlantic	11
COT	(R3) Seasonally wet and wet grasslands, (D4) Base-rich fens and calcareous spring mires	Marsh	Atlantic	24
CRA	(R1) Dry grassland	Plain	Mediterranean	30
LOR	(R2) Mesic grasslands, (R3) Seasonally wet and wet grasslands	Plain	Continental	15
POI	(MA2) Littoral biogenic habitat, (R3) Seasonally wet and wet grasslands	Marsh	Atlantic	37
PUY	(R1) Dry grassland, (R2) Mesic grasslands, (S4) Temperate shrub heathland	Mountain	Continental	37
SOM	(R1) Dry grassland,	Hill	Atlantic	27
VER	(R1) Dry grassland, (R2) Mesic grasslands, (S4) Temperate shrub heathland	Mountain	Alpine	21

heathlands, and mesic grasslands in the Chaîne des Puys mountain range; SOM: dry grasslands in the Somme department; VER: mountainous dry grasslands and heathlands, and mesic grasslands in the Vercors mountain range. Out of the 202 plots that were sampled, 172 were located in Natura 2000 sites (for further site descriptions, see Supp. info. Tables 1 and 2).

2.2. Forage sampling and chemical analysis

Plots consisted of 10 m x 10 m quadrats in each vegetation unit sampled. Some of the habitats were represented by several plots in a given site (3–4 plots) while a few others were only represented by 1 or 2 plots per site depending on the site size and habitat rarity. Five forage samples were harvested in 20 cm x 20 cm quadrats in each plot to calculate the mean *standing biomass* (SB, g/m²). In a few cases, additional forage samples were collected to obtain at least 40 g of total dry biomass per plot, i.e., the quantity required to perform the chemical analyses. With the aim of comparing contrasting grassland habitats, we have prioritized a common physiological period for plants evaluated in degree days, which allowed to overcome the problem of variations in grazing or mowing dates specific to local environmental conditions and management habits. Biomass samples were collected during the vegetation growth season in 2019 (apart for CRA which was sampled in 2020) and before the beginning of the grazing period as it was not possible to use exclusion cages in grazed fields during the peak of biomass production due to the remote locations of sites, the large number of sampling points, and also to abide by the desires of farmers. The grazing period started generally at the end of spring when the *growing degree days* (GDD) was between 500 and 600 GDD. Sampling dates were thus fixed as close as possible to 550 GDD. In COT, where wet grasslands are seasonally flooded, sampling dates were set between 1000 and 1140 GDD to wait for the end of flooding. Sampling dates in CRA, where vegetation growth is limited by drought, were fixed at 210 and 220 GDD to correspond with the beginning of the grazing season. Plant biomass was cut at a minimum of 1 cm above ground level in 20 cm x 20 cm quadrats and immediately dried in an oven at 60 °C for at least 48 h until a constant mass was obtained, and then weighted. Biomass chemical analyses were performed on samples grinded at 1 mm. *In vitro dry matter digestibility* (DMD, %) was assessed to describe forage digestibility (Aufrère et al., 2007; Nozière et al., 2018). *Crude protein content* (CP, g/kg) was measured using the Kjeldhal method (NF EN ISO 5983–1). Inductively coupled plasma optical emission spectrometry was used to measure contents in *calcium* (Ca, g/kg), *copper* (Cu, mg/kg), *iron* (Fe, mg/kg), *potassium* (K, g/kg), *magnesium* (Mg, g/kg), *manganese* (Mn, mg/kg), *sodium* (Na, g/kg), *phosphorus* (P, g/kg) and *zinc* (Zn, mg/kg) in fodder samples (NF EN 15510 and NF EN ISO 11885).

2.3. Soil and management data

The depth of root development in the soil was visually estimated using soil profiles in each sampling plot (Duchaufour, 1997). Then, three soil cores were collected using a manual auger, in the A horizon of the soil in each plot, i.e. mineral horizon that formed at the surface of a soil or below a litter-dominated “O” horizon (Jahn et al., 2006). Soil horizons were visually assessed beforehand to distinguish the A horizon from the other soil horizons following FAO 2006 guidelines (Jahn et al., 2006). The depth of the A soil horizon varied from 2 cm to 56 cm depending on sampling location. Such variability probably reflects a mixture of effects due to the large range of parent material, geomorphological context, and land use associated with the studied plots. Enough soil was collected through the entire depth of the A soil horizon, then mixed thoroughly, and aliquoted to obtain at least 400 g in dry soil mass for each plot. The samples were then immediately dried at room temperature for 3–5 weeks until their mass was stable, then passed through a 2 mm mesh size sieve before analyses. The following

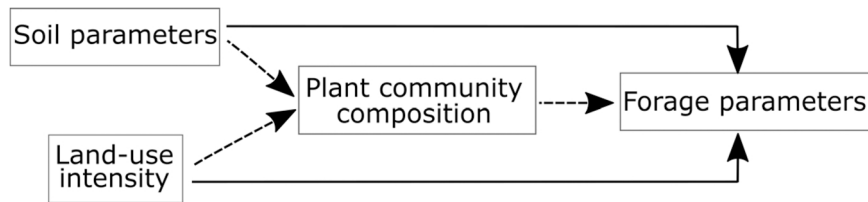


Fig. 1. Theoretical relationships analysed by using piecewise structural equation models. Direct effects of soil parameters and land-use intensity on forage parameters are indicated by solid arrows and indirect effects are indicated by dashed arrows.

parameters were measured: soil texture by the pipette method (NF X 31–107), pH using a glass electrode (NF ISO 10390), the *cation-exchange capacity* (Meq/100 g, Metson method, NF X 31–106), total *nitrogen* (N, g/kg) and *carbon* (C, g/kg), and organic C (g/kg) by dry combustion (NF ISO 13878 and NF ISO 10694; Flash EA 1112, Thermo Electron, Germany), soluble P (g/kg, Olsen method, NF ISO 11263; EON spectrophotometer BioTek Instruments Inc. USA), and Ca (g/kg), Mg (g/kg), K (g/kg), and Na (g/kg) were extracted using an ammonium acetate solution and measured by spectrometry (NF X31–108).

Information on grassland management was obtained from surveys conducted with landowners or managers for the sampling year, and we checked that it closely reflected the management applied for the last 5 years at least. The information includes whether the sites were grazed, mowed, or both, the herbivore species and the annual stocking rates when grazed, the number of cuts per year when mown, and whether or not the sites were fertilised, together with eventual changes in management during the last 5 years. Grasslands whose management changed or was irregular in the last 5 years were omitted from the study to avoid effects associated with mixed management on plant communities and soils. A *land-use intensity index* (LUI) was calculated for each plot as a measure of grazing intensity, by summing the standardised values of the number of cuts per year as a measure of mowing intensity, and the annual stocking rate (livestock unit per days of grazing ha⁻¹ year⁻¹) (Blüthgen et al., 2012). Fertilisation intensity was not used in the equation as the farmers confirmed that the plots were not fertilised.

2.4. Plant diversity and traits

In each sampling plot, the cover of each vascular plant species was estimated in a 4 m x 4 m quadrat. Trait data was obtained for species which contributed the most to achieve an 80% sampling plot cover. Values for *leaf dry matter content* (LDMC) and *specific leaf area* (SLA) were obtained from local databases when available, or from the TRY database (Kattge et al., 2011). Community-weighted means were then calculated for LDMC (LDMC_{CWM}) and SLA (SLA_{CWM}) in each sampling plot (Garnier et al., 2004). A categorical *plant functional type* (PFT) variable was created to differentiate between three plant types: graminoids (grasses, rushes, and sedges), legumes, and non-N₂ fixing forbs (hereafter forbs). Grasses, legumes, and forbs constitute the first level of functional classification in grasslands (Tilman et al., 1997; Reich et al., 2001). In this study we have combined grasses, sedges, rushes in the graminoid category, as they share the characteristic of having very low meristems which gives them good adaptation to defoliation. The legumes differ from the other forbs by their ability to fix atmospheric N₂. Percentage covers of each PFT were calculated for each sampling plot.

Three metrics were used to evaluate taxonomic diversity: species richness, i.e., the number of species occurring in the 4 m x 4 m quadrat, Shannon diversity index, and Pielou evenness index, calculated through species relative abundances based on the species percentage cover and calculated so that their sum reaches 100%. Functional diversity was described using the functional richness and functional evenness indices which were calculated for both LDMC and SLA separately (Mason et al., 2005; Villéger et al., 2008). The functional richness index describes the size of the functional space, and the functional evenness index estimates

the distribution of abundance in the functional space (Mason et al., 2005). Functional richness was calculated as, $FR_{ci} = \frac{SR_{ci}}{R_c}$, where FR_{ci} is the functional richness for the trait c in sampling site i , SR_{ci} is the niche space filled by the species in the sampling site, and R_c is the absolute range of the trait (Mason et al., 2005). The functional evenness is calculated by dividing the trait niche space into many categories and calculating the evenness for the abundance of species in each category (Mason et al., 2005; Villéger et al., 2008). The procedure used is described in detail in Villéger et al. (2008). Additionally, PFT evenness was calculated using the Pielou evenness index.

2.5. Data analyses

Kendall's rank correlation tests were used to detect significant correlations among variables describing forage productivity and nutritive value. We first extracted the effect of sampling sites on the forage variables which include environmental differences between sampling sites. This was accomplished by extracting the residuals from regression models of the effect of sampling sites on each forage parameter. The correlation tests were then performed on the residuals. The parameters considered for forage productivity and nutritive value were SB, DMD, CP, and *average mineral content* (MinAv) calculated as the average of the standardised macronutrient values (Ca, K, Mg, Na, P). The effect of diversity on observed correlations between forage characteristics was tested using a modified bootstrap method to compare the correlation coefficients at high diversity values and low diversity values (Wilcox, 2012). To obtain two groups of similar size, diversity variables were transformed into two-level categorical variables by assigning a high diversity factor level to values above the median in each sampling site and low diversity factor level for values below the median. The bootstrap method was performed on the Kendall correlation coefficients.

Mixed-effects models were fitted to test the effect of diversity indices, functional traits, and PFT on forage variables. Sampling sites were added as a random effect in the models to take into account the nested structure of plots within sites and to control the environmental differences between sites (Bolker et al., 2009). Each explanatory variable was fitted individually to assess its effect on forage quantity and nutritive value. This analytical procedure was repeated for statistically significant models ($P < 0.05$) with the inclusion of sampling sites as an interacting term as opposed to a random effect in generalized linear models to determine if the observed relationships were stable between sampling sites. Pairwise comparisons of regressions coefficient were then performed using a t-test to test differences in the effect of the explanatory variables between sites. The model estimates, the distribution families used, and the results of the post-hoc analysis are given in the [supplementary information](#). Model predictions were obtained and standardised by dividing each predicted value by the mean of the response variable for each model. This represented the deviation of predictions from the mean and was used for graphical presentation of model results. A mineral content evenness index was calculated using macronutrient values. However, since no significant result was found when analysing the effects of plant functional traits, plant functional types, and plant diversity on mineral content evenness, analyses performed on this parameter have been excluded from the results.

Mixed-effects models were used to detect effects of soil properties and land-use intensity on forage variables with sampling sites included as a random effect. A backward stepwise model selection procedure based on the generalised Akaike information criterion (GAIC, penalty term $k = 2.5$) was used to select the most parsimonious model (Rigby and Stasinopoulos, 2005; Zuur et al., 2009). The following variables were included in the initial model before applying the selection process: C/N ratio, percentage of clay and fine silt, organic carbon content, bulk density, pH, mean soil mineral content (the average of the standardized macronutrient values; Ca, K, Mg, Na, P), and land-use intensity. The choice of probability distribution type for mixed-effects models was based on visual assessments of model residuals using worm plots (van Buuren and Fredriks, 2001).

We considered that soil properties and land-use intensity may have a direct impact on forage parameters, but also may indirectly influence forage parameters by altering plant community composition or diversity. Piecewise structural equation models (SEM) were used to determine if the effects of soil conditions and land-use intensity on forage were mediated by vegetation diversity, functional traits, and/or functional types with sampling sites included as a random effect (Shipley, 2000; Fig. 1). A backward stepwise selection process was used to select the independent variables for model inclusion. Statistically significant terms from the mixed models were retained and were tested separately in the SEM for significant relationships with the dependent and independent variables. Variables leading to significant results were included in an initial model and a backward stepwise selection was performed to select the mediators. D-separation tests were used to determine if direct paths should be included or excluded for the soil parameters and land-use intensity index (Shipley, 2000). Global model goodness-of-fit was assessed using Fisher's C test with $P > 0.05$ indicating that no statistically significant paths are missing (Shipley, 2000). Standing biomass was log-transformed to meet the test assumptions and the square root of CP was used for the same reason.

In all regression analyses, model terms with $P > 0.05$ were considered as having a significant effect on the dependent variable. Analyses were performed on R v.4.1.1 and the following packages were used: gamlss v. 5.3–4 (Rigby and Stasinopoulos, 2005) for the multi-level models, piecewiseSEM v. 2.1.2 (Lefcheck, 2016) for the SEM, and rstatix v. 0.7.0 (Kassambara, 2021) for the correlation analysis. The vegan v. 2.5–7 package (Oksanen et al., 2020) was used to calculate taxonomic diversity indices and the FD v. 1.0–12 package (Laliberté et al., 2014) was used to calculate functional diversity indices and community-weighted means. Graphs were rendered using the ggplot package v. 3.3.5 (Wickham, 2016) and Inkscape v. 1.1.1 (Inkscape Project, 2020).

3. Results

3.1. Relationships between forage parameters

We first analysed the relationships between forage parameters. A positive correlation was measured between crude protein content (CP) and dry matter digestibility (DMD) ($\tau = 0.4$, $P < 0.001$). Average mineral content (MinAv) was positively correlated with CP ($\tau = 0.37$, $P < 0.001$) and DMD ($\tau = 0.62$, $P < 0.001$). Standing biomass (SB) was not significantly correlated with any of the forage nutritive value variables. Species richness and Shannon index significantly influenced correlations between forage parameters. Greater species richness resulted in a more negative correlation between DMD and SB (high diversity τ – low diversity $\tau = -0.25$, $P < 0.05$), and MinAv and SB (high diversity τ – low diversity $\tau = -0.22$, $P < 0.05$). A greater Shannon index also resulted in a more negative correlation between MinAv and SB (high diversity τ – low diversity $\tau = -0.25$, $P < 0.05$).

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

The proportion of each plant functional type (i.e., graminoids, legumes, and forbs) showed significant relationships with all forage variables analysed (Fig. 2). Standing biomass increased with increasing percentage cover of graminoids and decreased with increasing forb cover. Conversely, DMD decreased with increasing graminoid cover and increased with increasing forb and legume covers. Increasing forb and legume covers also led to an increase in MinAv and CP while legume cover had no significant effect on SB. The community weighted mean of specific leaf area (SLA_{CWM}) was positively correlated with CP, DMD, and MinAv, while community weighted mean leaf dry matter content ($LDMC_{CWM}$) was negatively correlated with those forage parameters.

Plant community species richness was negatively correlated with SB and MinAv (Fig. 3). The Shannon index and species evenness were negatively correlated with SB and positively correlated with MinAv. Species evenness was also positively correlated with CP and DMD. Plant functional type evenness was positively correlated with DMD, and MinAv, while no correlation was found between PFT evenness and CP and SB (Fig. 4). SLA functional richness was negatively correlated with SB and DMD and positively correlated with CP. An increase in functional evenness of SLA was significantly associated with a decrease in CP, DMD, and MinAv. LDMC functional richness was negatively correlated with DMD and SB, and LDMC functional evenness was positively correlated with DMD and MinAv.

A significant site effect was found in five of the eleven models when sampling site was included as an interaction term instead of a random effect in models which displayed a significant effect of diversity or functional traits or types on DMD (Supp. info. Fig. 2, Supp. info. Table 5). For CP, this was the case in four out of seven models, and for MinAv, for five out of ten models (Supp. info. Figs. 3 and 4, Supp. info. Table 6 and 7). Of the seven models displaying significant relationships between SB and diversity indices or functional traits, only the one for the Shannon index significantly differed between sites (Supp. info. Fig. 5, Supp. info. Table 8).

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

Significant effects of abiotic factors on forage parameters were detected. Soil C/N and pH were negatively correlated with SB, and soil C/N was also negatively correlated with CP (Table 2). The effect of pH on SB was mediated by species richness and forb percentage cover (Fig. 5a), while the effect of C/N on CP was partially mediated by percentage graminoid cover, SLA_{CWM} , and $LDMC_{CWM}$ (Fig. 5b).

Soil average mineral content and LUI had a positive effect on DMD, CP, and forage MinAv. The effects of soil average mineral content were partially mediated by graminoid percentage cover and $LDMC_{CWM}$ (Fig. 5b, and Fig. 6a and b). For CP, the effect of soil average mineral content was also partially mediated by SLA_{CWM} (Fig. 5b) while for DMD it was also partially mediated by SLA_{CWM} and species richness (Fig. 6a). The effects of LUI on DMD and MinAv were partially mediated by SLA functional evenness (Fig. 6a). We found a negative relationship between soil pH and forage MinAv and also negative correlations between soil organic C content and forage DMD and MinAv which were partially mediated by $LDMC_{CWM}$ and SLA functional evenness (Fig. 6a and b). Soil pH had a positive effect on DMD despite being positively correlated with species richness which was in turn negatively correlated with DMD (Fig. 6a).

4. Discussion

4.1. Synergies and trade-offs between forage parameters

Forage agronomic value assessment is usually based on forage productivity and nutritive value (Bruinenberg et al., 2002; Hopkins and

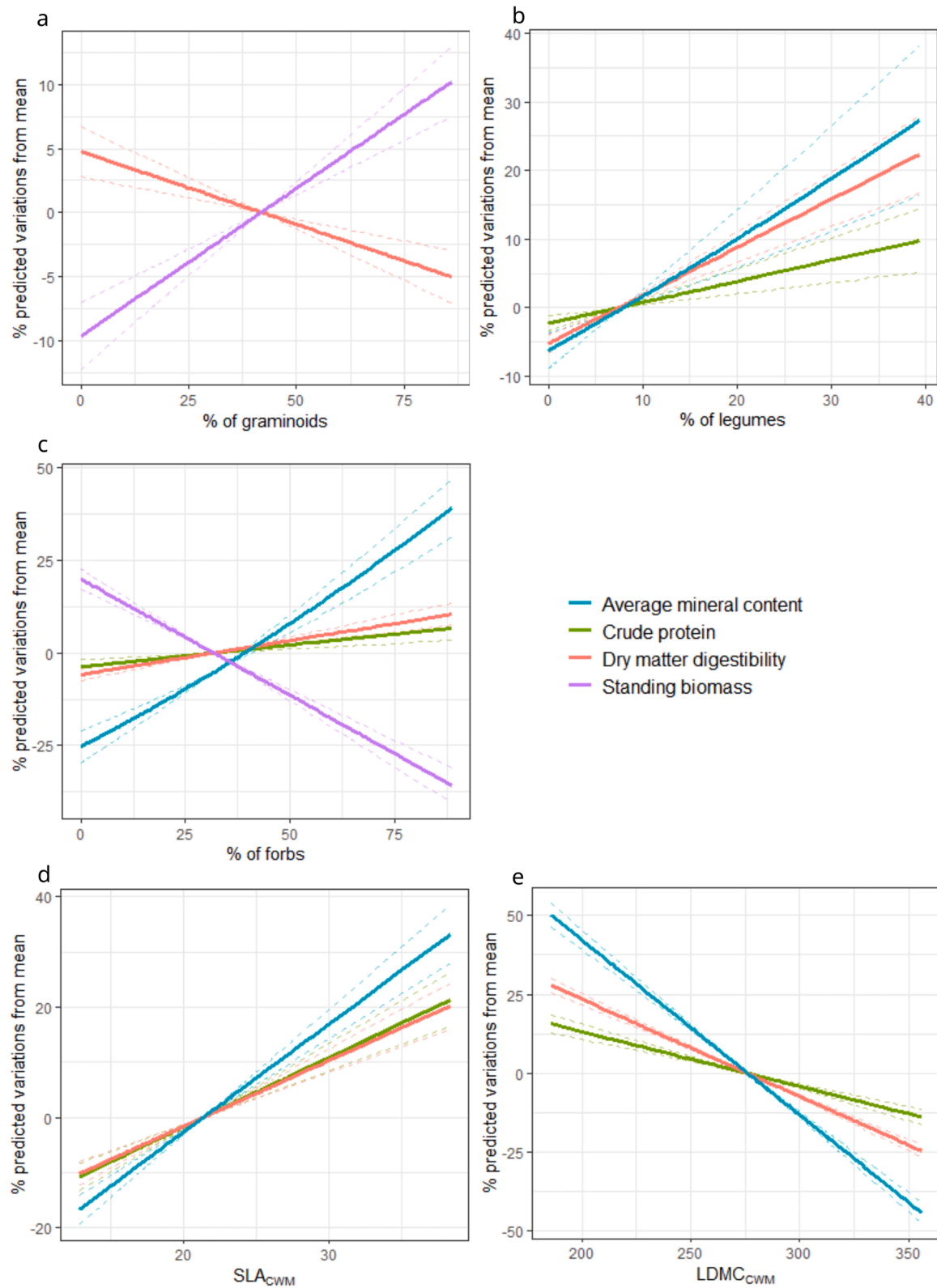


Fig. 2. Effects of plant functional types (a, b, and c), community-weighted mean of specific leaf area (SLA_{CWM} , d), and community-weighted mean of leaf dry matter content ($LDMC_{CWM}$, e) on forage variables. The response variables are represented as the percentage of deviation of the predicted values from the mean of the response variable. Statistically significant effects only are plotted ($P < 0.05$).

Holz, 2006). We showed here that these two aspects of forage production were not correlated at the beginning of the grazing season in a large range of semi-natural grasslands. This offers the possibility of increasing either early standing biomass or forage nutritive value by adapting

management practices without impacting the other parameter. It has been demonstrated that management type had a significant effect on forage biomass production but not on forage nutritive quality in mountain grasslands (Loucougaray et al., 2015). A trade-off between

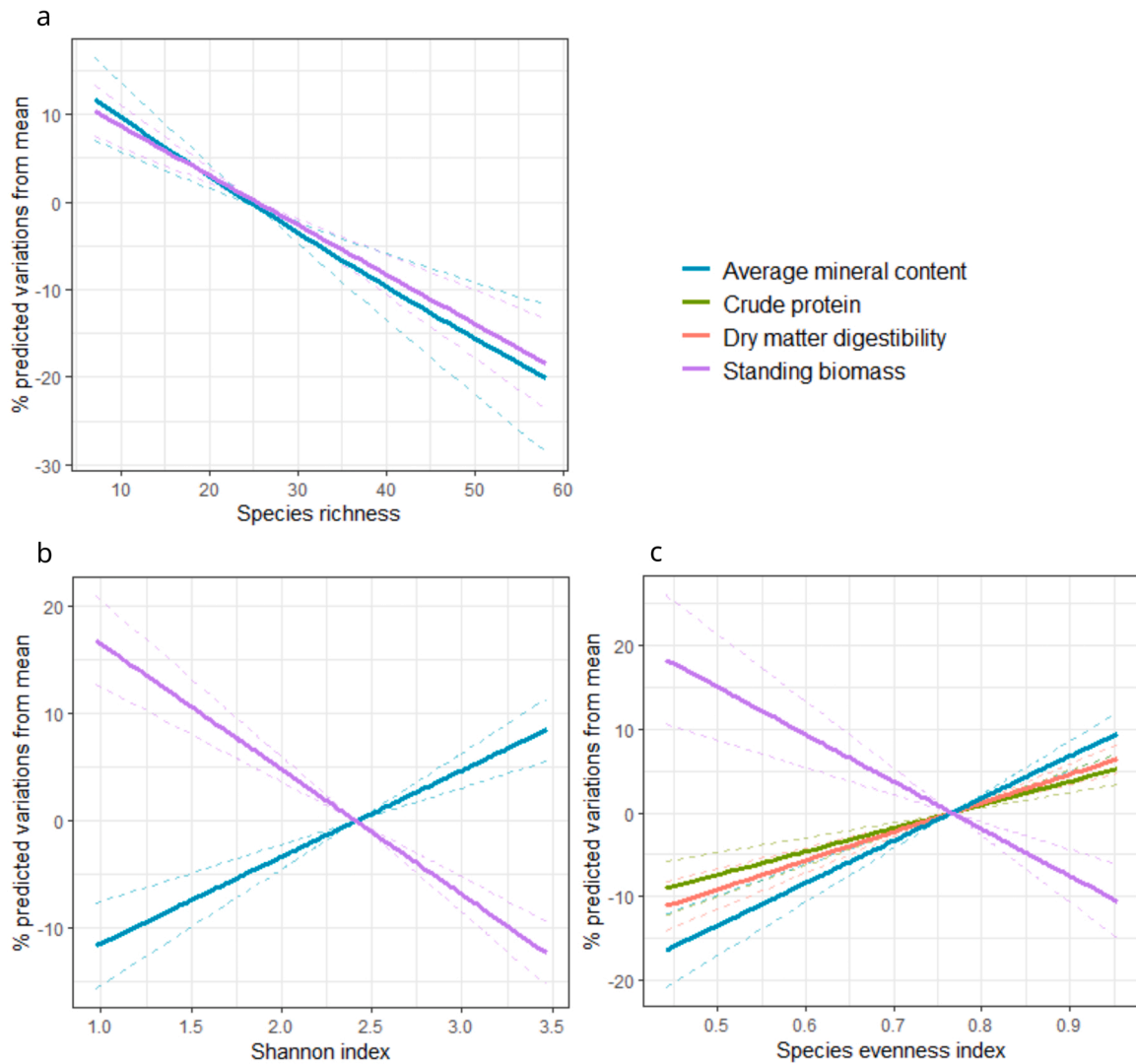


Fig. 3. Effects of species richness (a), Shannon index (b) and species evenness index (c) on forage variables. The response variables are represented as the percentage of deviation of the predicted values from the mean of the response variable. Statistically significant effects only are plotted ($P < 0.05$).

both parameters of the agronomic value may occur however in species-rich grasslands, since we found a more negative correlation between SB and DMD, and between SB and MinM in plots associated with a higher species richness and Shannon diversity. This suggests that although forage early standing biomass may be lower in species-rich grasslands, their forage nutritive value may be greater and can compensate for reduced biomass production. Positive correlations were found amongst parameters associated with forage nutritive values. This was expected for DMD and CP for which correlations are commonly reported (Hansen and Lawrence, 2017; Nozière et al., 2018).

4.2. Relationships between descriptors of plant community and forage parameters

Relationships between forage quality and plant functional composition have often been analysed for productive grasslands. Here, we investigated the general trends in relationships between forage parameters and plant functional traits and types for extensive grasslands of conservation interest. The community composition in plant functional type had an influence on SB with a higher SB recorded with higher graminoid cover and lower forb cover, as expected (Michaud et al., 2015). Forage nutritive value responded positively to the cover of forbs and legumes in plant communities (Fig. 2). For legumes, this result is in

line with previous findings which have demonstrated their higher protein content, higher energy content, higher digestibility, and higher mineral content for certain minerals compared to grasses (see review by Baumont et al., 2016). The greater forage nutritive value of legumes is probably detected by domestic sheep and cattle as they show a preference for legumes compared to grasses in their diet (Rutter, 2006). We found that forbs were associated with high forage mineral contents, as also shown by Pirhofer-Walzl et al. (2011) and Reiné et al. (2020). The different responses of forage parameters to different PFTs suggests that an even cover of PFTs may help in jointly increasing forage biomass production and nutritive value. Those plant community effects are found significant independently of any climatic effects which are known to impact forage quality and quantity (Izaurrealde et al., 2011; Dumont et al., 2015).

We did not observe the positive correlation expected between SLA_{CWM} and SB nor the expected negative correlation between LDMC_{CWM} and SB (Lavorel and Garnier, 2002). This could be due to the presence of certain tussock perennial grasses in extensive grasslands which are not consumed by livestock and subsequently accumulate biomass (Hejcmanová et al., 2016; Massey et al., 2009). It is also possible that these traits are not good predictors of early standing biomass as tussock perennial grasses elaborate most of their biomass at a later vegetative stage. Also, the capacity of these traits to predict forage

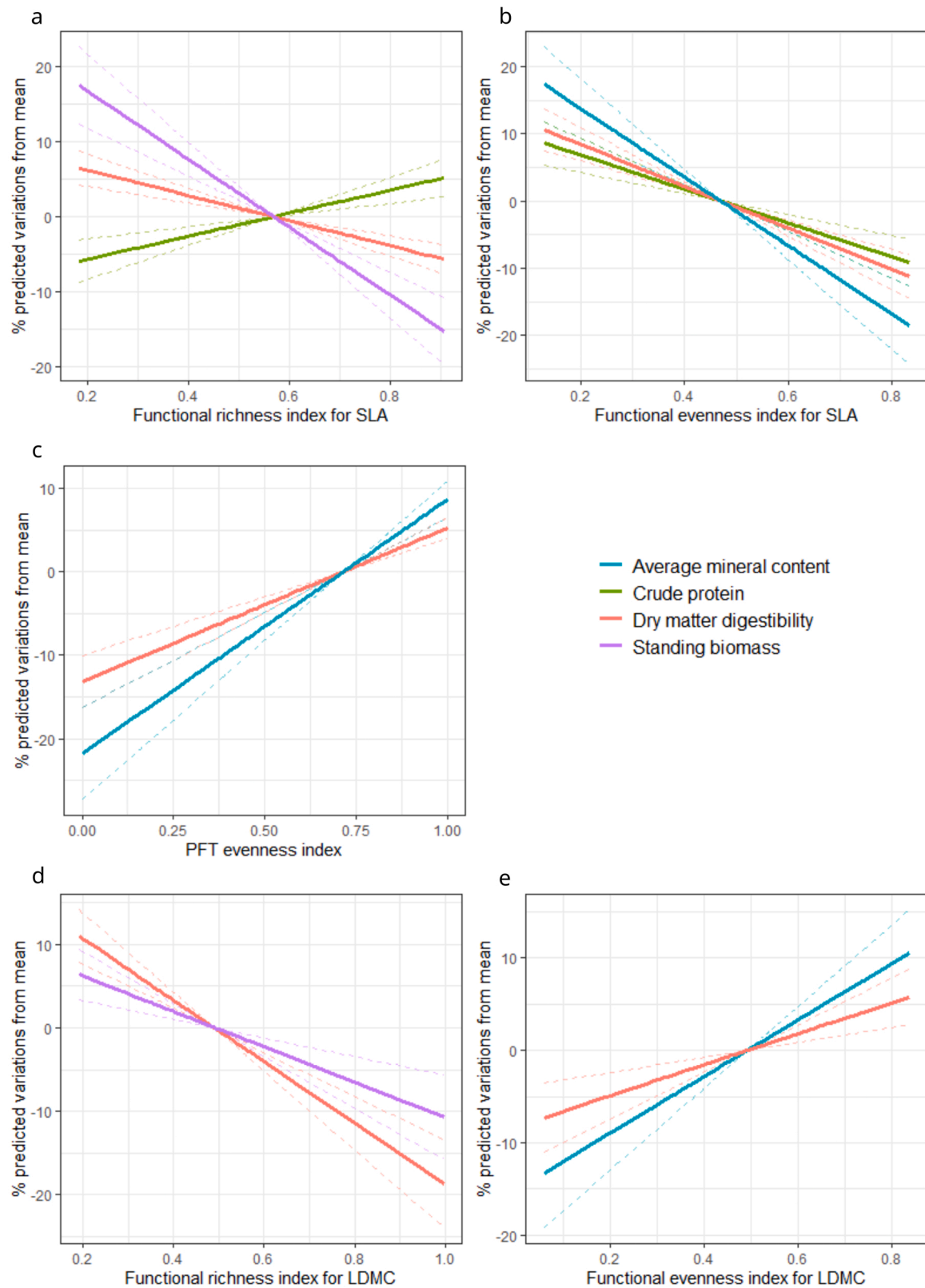


Fig. 4. Effects of functional richness and functional evenness of SLA (a, b), plant functional type (PFT) evenness (c), and functional richness and functional evenness of LDMC (d, e) on forage variables. The response variables are represented as the percentage of deviation of the predicted values from the mean of the response variable. Statistically significant effects only are plotted ($P < 0.05$).

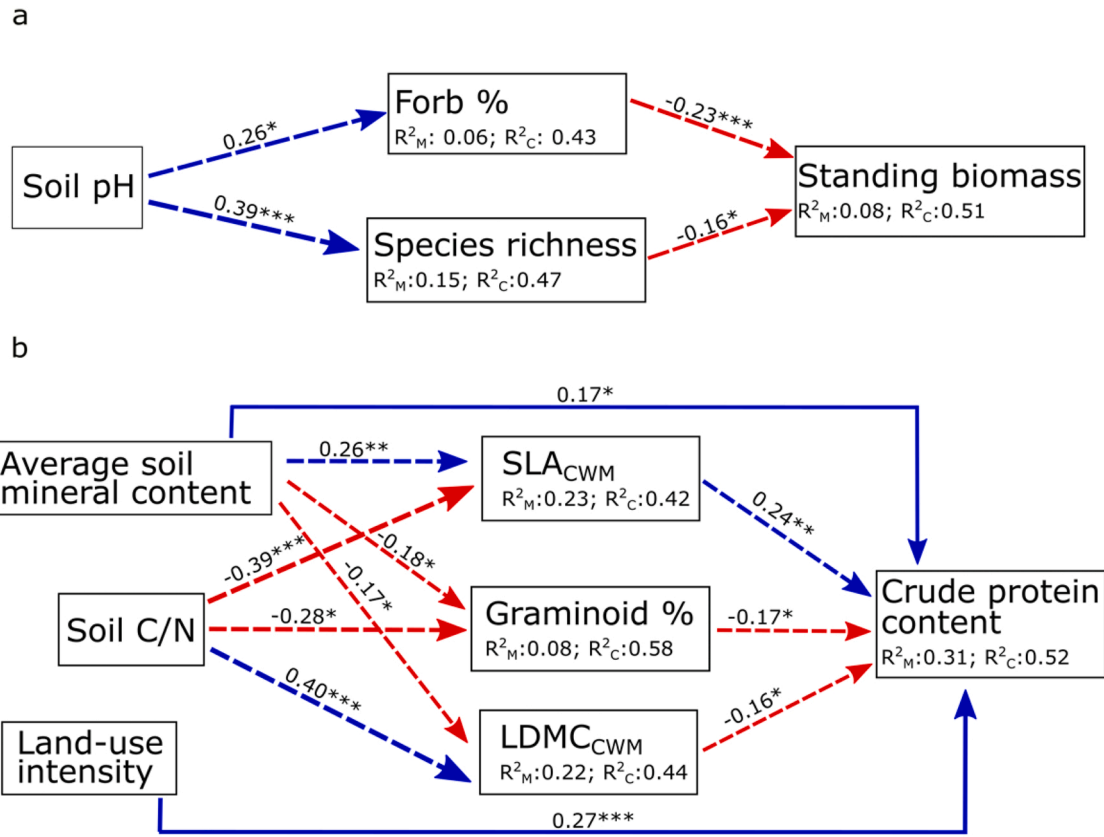


Fig. 5. Path diagrams showing the effect of edaphic factors and land-use intensity on forage standing biomass (Fisher's $C = 2.18$; $P = 0.34$) (a) and crude protein content (Fisher's $C = 2.36$; $P = 0.67$) (b) mediated by functional traits, functional types, and diversity indices. R^2_M indicates the proportion of variance explained by fixed effects while R^2_C indicates the proportion of variance explained by both fixed and random effects. Blue arrows indicate positive relationships, red arrows indicate negative relationships, solid arrows indicate direct effects of soil parameters and land-use intensity, and dashed arrows indicate an indirect effect. The standardised regression coefficient for each relationship is indicated above the arrows. The sizes of the arrows are proportional to the coefficients. $LDMC_{CWM}$: community-weighted mean of leaf dry matter content; SLA_{CWM} : community-weighted mean of specific leaf area. *, **, and *** indicate $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

Table 2

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

	SB	DMD	CP	MinAv.f
Family	Box-Cox t	Sinh-Arcsinh	Box-Cox t	Beta (logit)
Intercept	315.37 (38.09) ***	42.73 (4.01) ***	94.75 (4.20) ***	-0.26 (0.26) ***
C/N	-1.57 (0.57)**		-0.39 (0.14)**	
C.org		-0.09 (0.011) ***		-0.004 (0.0006) ***
MinAv.s		49.73 (6.74) ***	78.90 (13.87) ***	3.00 (0.31)***
pH	-14.01 (6.78)*	1.29 (0.58)*		-0.18 (0.04)***
LUI		1.67 (0.49) ***	9.66 (1.57) ***	0.07 (0.03)*

biomass may vary between habitat types.

The trait values we used come from databases and thus do not take into account the intraspecific trait variation. This is a clear limit of this dataset as Niu et al. (2020) have stressed the importance of intraspecific variations when analysing functional changes along environmental gradients. These variations may even allow to capture functional

changes before plant composition changes (Niu et al., 2016b). Nevertheless, the use of traits from databases such as TRY has been demonstrated as highly relevant when analysing grassland functioning at biogeographical scale (Violle et al., 2015, 2017b). The large scale of this study and the comparison of contrasting habitats allowed the identification of effects of traits and functional diversity on parameters of forage quality. The community weighted means of LDMC and SLA had a negative and positive effect respectively on CP. This was expected as SLA is positively correlated with leaf photosynthesis and high LDMC is associated with an allocation of resources to leaf structural tissues and lower leaf N content (Villar and Merino, 2001; Wright et al., 2004; Poorter et al., 2018). Leaf traits are also associated with DMD (Pontes et al., 2007; Gardarin et al., 2014), and we found that both $LDMC_{CWM}$ and SLA_{CWM} were highly correlated, negatively and positively respectively, with DMD. For grasses, Khaled et al. (2006) found LDMC to be better at predicting digestibility than SLA. The correlation of both functional traits with DMD may be due to the presence of forbs and legumes in many of the semi-natural grasslands we studied, for which SLA was already shown to be a good predictor for their DMD (Tasset et al., 2019). In fact, SLA_{CWM} was a better predictor of DMD in our study since the relation was more stable between sites than the one observed between $LDMC_{CWM}$ and DMD.

Complementarity effects between species may be expected to support the positive relation found between species and functional evenness and forage productivity (see, for example, Oelmann et al., 2021; Komanda et al., 2020; Wang and Yu, 2018) thanks to the diversity of functional strategies of species to acquire resources (Cerabolini et al.,

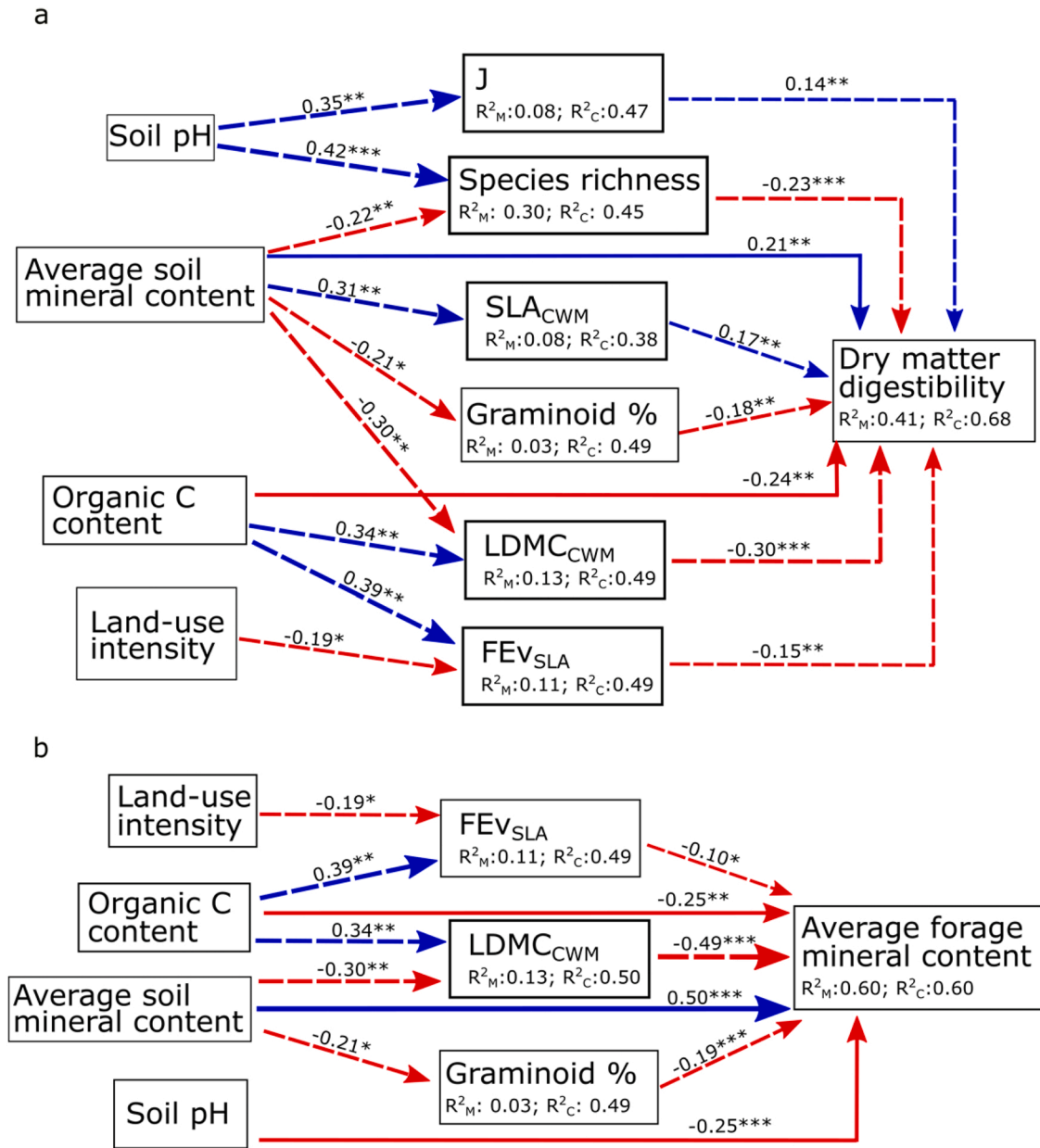


Fig. 6. Path diagrams showing the effect of edaphic factors and land-use intensity on forage dry matter digestibility (Fisher's $C = 21.91$; $P = 0.35$) (a) and average mineral content (Fisher's $C = 10.93$; $P = 0.21$) (b) mediated by functional traits, functional types, and diversity indices. R^2_M indicates the proportion of variance explained by fixed effects while R^2_C indicates the proportion of variance explained by both fixed and random effects. Blue arrows indicate positive relationships, red arrows indicate negative relationships, solid arrows indicate direct effects of soil parameters and land-use intensity, and dashed arrows indicate an indirect effect. The standardized regression coefficient for each relationship is indicated above the arrows. The sizes of the arrows are proportional to the coefficients. J: species evenness; FEV_{SLA} : functional evenness in SLA; $LDMC_{CWM}$: community-weighted mean of leaf dry matter content; SLA_{CWM} : community-weighted mean of specific leaf area. *, **, and *** indicate $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

2010). However, SB pattern which was found to decrease with increasing evenness and species richness does not support here such a complementarity effect.

The negative relationship found between SB pattern and species richness and evenness may reflect the negative impact that increasing standing biomass may have exerted on taxonomic or functional diversity following the competitive exclusion of less competitive species by the more productive and competitive species (Grime, 1973; Feßel et al., 2016). The grasslands we studied may therefore be situated on the declining section of the schematic unimodal species richness - productivity relationship (Grime, 1973; Rosenzweig and Abramsky, 1993). This study was indeed carried out in extensively managed grasslands and even the plots with the lowest species diversity may nonetheless have a

high diversity. It is also possible that the negative correlation between taxonomic diversity and early standing biomass can be explained by the spatial scale at which the study has been conducted. Gross et al. (2009) indeed showed that the positive relationship between biodiversity and production exists in permanent grasslands but at very local scales (0.01 m^2), whereas it is not detected at the community scale ($>100 \text{ m}^2$). Such spatial-dependent effect is probably explained by the fact that complementarity between species can come into play at the scale of the neighbourhood of the plants, while production is probably strongly impacted by environmental heterogeneity at the plant community level, masking the biodiversity effect. Moreover, SB was measured at the beginning of the growth season and the evaluation of the entire season's productivity, which was not possible in this study, could have provided

different results.

Nevertheless, positive relationships were observed between both taxonomic diversity and functional diversity and forage nutritional quality, supporting the synergy between high plant diversity and potential for agricultural use through forage production in semi-natural grasslands of high conservation value. It may be suggested that the positive relation with nutritive value reflects the fact that the more the plant community is balanced the better is the forage quality in particular when approached by synthetic measurements such as average mineral content and digestibility. Conversely, an unbalanced plant community can indeed be dominated by one or few species, which can lead to opposite results depending on the chemical quality of the dominant species (Grime 1998).

As for functional diversity, the negative effects of SLA functional richness and LDMC functional richness on standing biomass suggest that an increase in the occupation of the functional space led to a decrease in biomass production. This increase in functional space may be associated with a diversity of species with diverse resource acquisition capacities but without highly productive species. Similarly, Chanteloup and Bonis (2013) found the peaks of standing biomass in fertile habitats to be negatively correlated with functional diversity which they interpreted as a dilution of highly productive species that were first recruited in the communities resulting in a reduction of community production capacity.

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

4.3. Direct and indirect effects of management and soil properties on forage parameters

Grassland vegetation responds to both environmental factors and management practices (Delpech, 1982; Gos et al., 2016). In intensive grasslands, biomass production appears mainly driven by management practices such as the choice of species and cultivar sown, grazing intensity or cutting frequency, and fertilisation (Plantureux et al., 2005; Oenema et al., 2014). By contrast, this study focused on semi-natural grasslands mostly located in Natura 2000 sites where agricultural practices needed to fit as much as possible with conservation goals. These semi-natural grasslands are in general more limited in available soil resources and their management can be defined as extensive, with reduced grazing pressure or mowing frequency as well as no or limited fertilisation input. The range in management intensity is thus reduced and the effect of environmental factors such as soil characteristics on grassland vegetation become more apparent than they are in intensively managed grasslands (Balent and Stafford Smith, 1991). We found this to be true for SB which was not correlated with land-use intensity (LUI). However, LUI did have a direct effect on MinAv and CP, and an indirect effect on DMD and MinAv via a reduction of SLA evenness. Soil characteristics had an impact on all forage parameters directly or indirectly by altering plant diversity and the functional composition of plant communities. Early standing biomass, CP, DMD, and MinAv responded to vegetation functional traits and PFT, and these in turn were correlated with soil fertility and pH value. Direct effects of soil parameters on CP, DMD, and MinAv were also detected. Edaphic and management effects on forage parameters mediated by vegetation composition in extensive

grasslands have not been previously studied to our knowledge. Average mineral soil content influence on forage nutritive value was associated with a decrease in LDMC_{CWM} and graminoid cover and an increase in SLA_{CWM}. Leaf construction requires the use of minerals which may explain the correlation measured between the soil fertility parameters (average soil mineral content, C/N, organic C content) and SLA_{CWM} or LDMC_{CWM} (Wright et al., 2004; Hodgson et al., 2011). An effect of soil pH was found, as expected, on vegetation composition through filtering the species pool according to species pH tolerance (e.g. Michalcová et al., 2011).

4.4. Generalisation of the relationships observed in a variety of habitat types and climatic conditions

Although we sampled across different habitat types and climatic conditions, our study design did not allow us to investigate effects of plant community structure on forage productivity and nutritive value specific to a study site. However, we were able to show correlations between forage parameters and descriptors of community structure among the wide range of habitat type and environmental conditions sampled. Only the relationship between standing biomass and species richness varied out of the seven significant correlations measured between standing biomass and community structure parameters. Relationships between forage nutritive quality and community structure parameters were less stable. The correlation between all forage nutritive quality parameters and LDMC_{CWM} significantly varied between sites. However, the relationship between species evenness and DMD and MinAv was stable across sampled sites. This suggests that the relationship between standing biomass and forage nutritive value is driven by species evenness in multiple extensive grassland habitat types. The forage parameter with the least stable relationship with community structure parameters across site was crude protein content (five out of seven significant relationships). More research is needed to decipher which parameters among habitat types drive the relationship between community structure and forage nutritive value.

5. Conclusion and perspectives

Forage production is a key service delivered by grasslands for farmers. Our work, together with other studies (see review by Tallwin and Jefferson, 1999; Farruggia et al., 2008), showed that synergies occurred between plant diversity conservation and forage nutritional quality in a wide range of semi-natural grassland types extensively managed in France. Such synergies may even be expressed in the economic value of forage while considering forage yield and nutritive value in grasslands (Schaub et al., 2020).

This study has demonstrated the importance of plant functional traits and PFT in determining forage productivity and nutritive value. Forage production in intensive grasslands tends to focus on grasses and legumes. Here, we evidenced that non-fixing forbs play an important role in diversified grasslands for forage nutritional quality. We also showed that an even distribution in PFTs may improve forage nutritive value without reducing early standing biomass, opening perspectives for the compatibility of agricultural and conservation values in semi-natural grasslands. Furthermore, greater species evenness and especially functional evenness was previously shown to increase community stability and resistance to external threats (Hillebrand et al., 2008) and thus show multiple benefits to semi-natural grasslands. This study highlights that, a well-balanced community regarding the species and functional composition, i.e., communities with high evenness, allows to achieve biodiversity conservation goals while maintaining high forage quality.

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

- To provide managers, conservationists as well as farmers with the actual nutritive and production values of species-rich grasslands, offering firm basis for management choices and then, eventually, limiting underestimation of their agronomic quality. With such a clear knowledge, farmers may be enticed to participate in conservation efforts, as they will be in a position to argue on the related economic impact or to realise that there is little or no compromise required between grassland agronomic values and their conservation efforts (McGinlay et al., 2017).
- The diagnosis of forage productivity and nutritive value in evaluating grassland conservation status could help identify situations which are at risk of land use abandonment because of poor forage productivity or poor forage nutritional quality.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2023.108369](https://doi.org/10.1016/j.agee.2023.108369).

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