



Community leaf dry matter content mediates the impact of mixture composition on forage yield and nutritive value in temporary mountain grasslands

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ABSTRACT

Mountain forage production is increasingly threatened by grassland degradation and limited adaptation to climate change. Regenerating these grasslands with multispecies forage mixtures adapted to altitude and future climatic conditions may enhance the sustainability of livestock systems. We conducted a field study across four mountain grassland sites in Switzerland, experimentally manipulating the dominant species identity (*Dactylis glomerata* and/or *Alopecurus pratensis*) and the proportion of low-abundant species in sown mixtures (0, 15 or 30%), including *Plantago lanceolata*. We measured forage yield, protein and neutral detergent fiber (NDF) over three harvests during the growing season, and quantified specific leaf area (SLA) and leaf dry matter content (LDMC) of all species to characterize community functional strategies. We found that the botanical composition influenced yield and NDF primarily through shifts in community functional traits mostly related to LDMC, whereas it mostly influenced protein concentration through direct effects from legumes. Forage yield was not influenced by the identity of the dominant species but increased with an increasing abundance of *P. lanceolata* at the second harvest in summer. Across the season, forage NDF concentration increased with increasing abundance of the two dominant grasses but decreased with increasing abundance of *P. lanceolata* and legumes. Overall, our findings demonstrate that integrating *P. lanceolata*, a species with low LDMC, into forage mixtures can enhance seasonal stability in forage production through complementarity with dominant grasses and improve forage nutritive value. These results highlight the importance of trait-based species selection for designing resilient forage mixtures adapted to mountain environments.

1. Introduction

Grasslands cover approximately 23% of the Earth's terrestrial surface (MacDougall et al., 2026) and provide important ecosystem functions and services, including high levels of biodiversity and forage production. While permanent grasslands (i.e., maintained for at least five consecutive years and excluded from crop rotation) have been extensively studied (Schils et al., 2022; Zhao, 2023; Zhao et al., 2020; Zhu et al., 2023), temporary grasslands (established by sowing a chosen seed mixture and younger than five years) have received considerably less attention, despite their central role in agricultural systems. These

grasslands represent an important additional source of forage for ruminants and are therefore critical to the functioning and sustainability of livestock production systems (Bengtsson et al., 2019; Peeters, 2009).

In mountain farming systems, grasslands play a particularly crucial role due to important constraints for agricultural production. Indeed, topographical constraints such as steep slopes and fragmented landscapes, combined with harsh climatic conditions, severely limit land-use options for agriculture and increase production costs (Institute for Prospective Technological Studies, 2013). These limitations often render crop cultivation impractical, increasing reliance on grasslands to supply sufficient forage for livestock. Mountain environments also pose

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significant challenges to grassland management due to the higher elevations and lower temperatures that lead to long winters and extended snow cover, and thus to a shortened growing season. Consequently, forage production is largely concentrated from the end of spring to the beginning of autumn, the period during which weather conditions allow active vegetation growth and when biomass is harvested to secure feed supplies for winter, or sometimes directly grazed in the second half of the season when livestock is brought back down from higher elevation alpine pastures. Ensuring stable and reliable forage production is therefore a key requirement for the sustainability of mountain livestock systems.

Maintaining forage production in mountain areas is becoming increasingly challenging under climate change. Indeed, climate change is projected to intensify summer droughts (Calanca, 2007), increasing water stress during the main forage production period, which can reduce grassland productivity (Deléglise et al., 2015; Finn et al., 2018) and increase temporal variability in forage yields (Chang et al., 2017; Graux et al., 2013; Haughey et al., 2018; Luo et al., 2025). Moreover, mountain grasslands are vulnerable to pest damage, notably from voles (*Arvicola* sp.) (Fichet-Calvet et al., 2000; Giraudoux et al., 1997) and white grubs (Hann et al., 2015; Pedrazzini et al., 2023), that feed on plant roots and leaves and cause soil perturbations. Consequently, there is a growing need for resilient grassland mixtures capable of restoring degraded permanent grasslands in mountain regions while remaining adapted to future climatic conditions.

Historically, agricultural intensification has led to the use of low-diversity temporary grasslands dominated by grass species selected for their high yield and nutritive value (Humphreys, 2005), that often require high fertilizer inputs to sustain grassland productivity. Such simplified systems are recognized as being more vulnerable to climatic variability and extreme events, resulting in reduced yield stability and lower resilience under current and future climate conditions (De Keersmaecker et al., 2016; Isbell et al., 2015; Korell et al., 2024). Therefore, improving the resilience and stability of multispecies forage mixtures has become a major challenge for the sustainability of grassland-based livestock systems facing increasing climatic uncertainty. Increasing species richness, particularly through the inclusion of multiple functional groups, has been shown to enhance grassland resistance and resilience to climatic fluctuations (Grange et al., 2021; Lüscher et al., 2022; Tilman et al., 2001), notably by stabilizing forage yields over time (Haughey et al., 2018). Numerous studies have also demonstrated the benefits of including legumes in forage mixtures, such as increased productivity, improved forage quality and enhanced nitrogen-use efficiency (Finn et al., 2013; Lüscher et al., 2014; Nyfeler et al., 2009), as well as increased drought tolerance (Hofer et al., 2016). More recently, attention has also been given to the role of forbs in improving sward productivity and nutritive value (Cong et al., 2018; Jensen et al., 2025; Moloney et al., 2021; O'Malley et al., 2026). Together, these studies support the increased use of legumes and forbs in forage mixtures, though species richness generally remains quite low, with mixtures rarely exceeding six species (Finn et al., 2013; 2018; Cong et al., 2018; Elgersma and Søgaard, 2018; Moloney et al., 2021).

Beyond functional groups, community functional traits may also play an important role in enhancing the performance and temporal stability of temporary grasslands. A functional trait-based approach allows a more mechanistic and general framework to understand how changes in species composition influence ecosystem functioning, particularly biomass production. Functional traits capture differences in species strategies and provide mechanistic links between community composition and ecosystem processes (de Bello et al., 2010; Lavorel and Garnier, 2002). In grasslands, leaf traits such as specific leaf area (SLA) and leaf dry matter content (LDMC) are particularly informative, as they enable measurement of contrasting resource-use strategies along the leaf economics spectrum (Wright et al., 2004) and are closely related to biomass production and forage nutritive value (Blaix et al., 2023; Hanisch et al., 2020; Muraina et al., 2025). At the community level, these traits can be

integrated through community-weighted means (Lavorel et al., 2008) to describe the dominant functional strategy of forage mixtures. Moreover, measures of trait dissimilarity quantify within-community functional diversity and may reflect niche differentiation and complementarity mechanisms that might enhance ecosystem stability (Wagg et al., 2017).

Plant species generally exhibit two contrasting resource-use strategies: acquisitive and conservative. Acquisitive species are characterized by functional traits associated with rapid resource acquisition and high biomass production under favorable conditions, such as high SLA and low LDMC (Mariotte, 2014; Wright et al., 2004). These traits confer strong competitive ability under optimal growth conditions, and such species are generally the main dominant grass species within nutrient-rich grassland communities. Consequently, these dominant grass species largely determine community-weighted trait values and strongly contribute to forage yield during periods of optimal growth (mass ratio theory; Grime, 1998). However, acquisitive strategies may be poorly suited to stressful summer conditions when water and nutrient availability are limited. In contrast, conservative species exhibit low SLA and high LDMC, traits that enhance resource-use efficiency and persistence under less favorable conditions (Grime, 1998; Oram et al., 2021; Walde et al., 2021). Conservative species are generally low-abundance species in nutrient-rich plant communities (also called subordinate species, Mariotte, 2014), often including low competitive grasses, legumes and forbs that rarely become dominant in the long term but contribute to functional diversity. Through mechanisms such as spatial niche differentiation, resource complementarity, and shifts in competitive interactions (Doudová and Douda, 2020), low-abundant species may help buffer seasonal declines in productivity and stabilize ecosystem functioning under changing environmental conditions, particularly during dry periods (Mariotte et al., 2013; Canarini et al., 2026). By compensating for temporary declines in dominant species cover or colonizing gaps created by disturbance, low-abundant species can contribute to maintaining ecosystem functioning (Grime, 1998). However, their contribution to forage yield and nutritive value, as well as their functional role in temporary grassland, remains poorly documented. Indeed, despite extensive research in plant functional ecology, studies addressing the functional structure of grassland communities in an agronomic context remain scarce (Garnier and Navas, 2012). Knowledge of the functional traits and strategies of forage cultivars, that have been selected and bred to increase their productivity and nutritive value, is also lacking. Therefore, a better understanding of how species composition and functional structure influence forage yield and nutritive value throughout the growing season is essential to sustain the productivity of temporary mountain grasslands and to enhance their capacity to adapt to climate change.

In this study, we conducted a field experiment across four mountain grassland sites in Switzerland, manipulating both the identity of the dominant species and the proportion of low-abundant species in forage mixtures. Our objectives were to assess how dominant species identity and low-abundant species relative abundance contribute to shaping community-level functional traits, and to quantify their effects on forage yield and nutritive value throughout the growing season. Specifically, we hypothesized that (i) dominant grass species exhibit traits related to acquisitive strategy, whereas low-abundant species exhibit traits related to conservative strategy (ii) the effects of the mixture composition on forage yield, protein and NDF concentration are mediated by shifts in community-level functional traits, (iii) dominant species are the primary drivers of forage yield and nutritive value in spring, whereas low-abundant species enhance summer forage yield by increasing functional diversity and complementarity with dominant species, relative to mixtures without low-abundant species.

2. Materials and methods

2.1. Study sites

The study was conducted at four mountain grassland sites across Switzerland, spanning four cantons (Uri, Bern, Valais, Ticino), with altitudes ranging from 950 to 1250 m a.s.l., mean annual temperature from 4.6 to 8.6 °C and mean annual precipitation from 843 to 1580 mm (data from 1991 to 2020, MeteoSwiss, Switzerland), which are representative of the wide environmental conditions in mountain grasslands (Table A.1 in Appendices).

2.2. Forage mixture composition

Forage mixtures were created following a factorial design including two drivers of plant community structure: the identity of the dominant species (three levels) and the abundance of low abundant species (three levels), yielding nine different mixture combinations. Species selection was guided by expert knowledge and criteria related to adaptation to mountain conditions, agronomic compatibility, and persistence under local management. Seeding rates and functional group proportions followed Swiss guidelines for the development of standard forage mixtures (e.g., combination of species that provide a fast cover of the ground with slower and long-lasting species, varieties adapted to local conditions and seed density based on species competitiveness indices, Suter and Frick, 2025). Dominant species were high-yielding perennial grasses commonly used in temperate managed grasslands in Switzerland and well adapted to a broad range of climatic conditions. The low-abundant species were selected based on their complementary agro-ecological characteristics with dominant species as well as on their potential persistence under future climatic conditions (e.g., drought, warming). In all mixtures, we aimed to have about 20–25% legumes to promote forage protein but also to reduce the need for fertilizers.

Mixtures were dominated by *Dactylis glomerata* L. or *Alopecurus pratensis* L., or co-dominated by both species. Low-abundant species were *Agrostis capillaris* L., *Festuca rubra* L., *Lotus corniculatus* L. and *Plantago lanceolata* L., which are often included in low proportions in sown mixtures due to their low productivity. These species were sown at variable proportions, i.e. absent (0%) or present at 15% or 30% of expected aboveground biomass in the mixtures, with equal expected proportion of the four species within the low-abundant species-group. The expected proportions of each species were estimated based on the interaction between species-specific seed density and interspecific competition effects (Caputa, 1948). All mixtures were completed with a pool of five common productive species: *Lolium perenne* L., *Phleum pratense* L., *Poa pratensis* L., *Trifolium pratense* L. and *Trifolium repens* L., thus mixture species richness ranged from six to eleven species depending on the treatment combination. More details on mixture seed density and species cultivars are available on Table A.2.

2.3. Experimental design

At each of the four sites, we established four blocks (17 × 7 m) of nine plots (each plot was 1.7 m × 7 m, and plots were separated by 20 cm), corresponding to the nine mixtures, randomized within each block, thus yielding 36 plots per site (144 plots in total). Prior to sowing, the soil was fertilized with manure and tilled with an agricultural tiller up to 10–20 cm depth, following common practices before the establishment of temporary grasslands. Plots were sown in May 2023 using an experimental broadcast-seeder (Hege 80, Hege Saatzuchtmaschinen, Hohebuch, Germany) attached to a small tractor to mimic conventional seeding practices. The distance between the two wheels of the tractor was 1.70 cm (i.e., plot width), thus creating no physical disturbance within the plots and a buffer of 20 cm between each plot (i.e., wheel width). During the year of mixture establishment (2023), plots were weeded to remove common unwanted weeds (e.g. *Rumex acetosa* L.,

Rumex obtusifolius L., *Amaranthus retroflexus* L., *Heracleum sphondylium* L.) and forage was cut twice for maintenance. In 2024, all plots were fertilized with a slow-release organic fertilizer (BiorgaQuick) at a rate of 75 kg N ha⁻¹ yr⁻¹, split into three applications of 25 kg N ha⁻¹, occurring at the beginning of the growing season and following the first two forage harvests.

2.4. Forage yield and nutritive value

In 2024, all mixtures were well established at all sites. The forage of the different mixtures was harvested three times during the growing season, the first in May-June (spring), the second in July-early August (early summer) and the third in late August-October (late summer/early autumn). The timing of the first harvest was based on the phenological stage of grasses, targeting inflorescence heading stage following common agricultural practices. Then, the regrowth period between two cuts varied from six to eight weeks, depending on weather conditions. A fourth harvest was performed at the end of the season (late autumn) on two sites (Ticino and Valais) to remove excess vegetation before winter. This harvest was not included in subsequent analyses. At each harvest, we mowed aboveground plant biomass at around 6–7 cm in a subplot of 1 m × 5 m (area of 5 m²) within each plot and weighed the fresh harvested forage biomass directly in the field (Fig. A.1). A subsample of the harvested forage biomass (about 400 g) was then collected using a metal corer (5 cm diameter), and was immediately stored in a cooling box, then brought to the laboratory, oven-dried at 60°C for 48 h and weighed again to calculate dry matter (DM) content (%) and expressed forage yield in t_{DM} ha⁻¹. The same subsamples were used for forage nutritive value analyses. Samples were ground to < 1 mm particle size using a rotary mill (Brabender, Germany) and analysed for residual DM and neutral detergent fiber (NDF) using near-infrared spectroscopy (Büchi NIRFlex N-500; BÜCHI Labortechnik AG, Switzerland) according to Kragten and Wyss (2014). The N concentration was determined by the Dumas method (ISO 16634-1:2008) and protein was calculated as N × 6.25. Protein (g kg⁻¹) and NDF (g kg⁻¹) of each sample were corrected using residual DM (%) after drying a subsample at 105°C during 3 h.

2.5. Botanical composition

Before each harvest, the botanical composition of each plot was determined by sorting plants at the species level. In each plot, six vegetation subsamples measuring 10 cm × 20 cm were taken at a height of 5 cm above the ground (on the border of the 5 m × 1 m subplots used for forage yield measurements, with three vegetation subsamples on each side, Fig. A.1) and pooled together. Vegetation samples were stored in a cooling box and brought to the laboratory, where they were kept in the fridge at 4°C prior to species sorting. All species sown in the mixtures were sorted at the species level, while the other unsown species were pooled together. The sorted biomass of each plant species for each plot was then oven-dried at 100°C for 24 h and weighed. The relative abundance of each species was estimated by dividing each species biomass by the total biomass of the sorted sample.

2.6. Leaf functional traits

At the three forage harvests, we collected leaves of all the 11 plant species sown in the experiment at the block level and the specific leaf area (SLA) and leaf dry matter content (LDMC) were determined following standardized protocol (Cornelissen et al., 2003). In each block of each site and at each forage harvest, we selected the youngest fully mature and undamaged leaf of five individuals of each species. In total, 2640 leaves were collected (5 leaves × 11 species × 4 blocks × 4 sites × 3 harvests). The leaves were kept in plastic bags containing a piece of paper towel moisturised with deionised water to rehydrate the leaf tissues, stored in a cooling box and brought to the laboratory, where they

were stored at 4°C overnight. Each leaf was scanned (CanoScan LiDE 300, Canon), and the resulting image was analyzed using an image analysis software (ImageJ, [Schneider et al., 2012](#)) to determine the leaf area (cm²). Leaves were then weighed to determine fresh weight (FW) and dried at 60°C for 72 h to determine dry weight (DW). We calculated SLA (cm² g⁻¹) as the leaf surface area (cm²) divided by DW (g), and LDMC (mg g⁻¹) as DW (mg) divided by FW (g).

The five SLA and LDMC values were averaged by block and values at block level were used to calculate the community weighed mean (CWM) of the different mixtures in each block. The CWM of each trait was calculated for each mixture based on the trait value of the species and the relative abundance of the species ([Lavorel et al., 2008](#)) following the equation:

$$CWM_{trait} = \sum_{i=1}^n p_i \times trait_i$$

with p_i the relative abundance of species i , $trait_i$ the trait value of species i and n the number of species.

To further assess functional diversity, we calculated functional dissimilarity (FDis), which quantifies the degree of dispersion of plant functional traits within communities as described by [Laliberté and Legendre \(2010\)](#). This index is based on a principal coordinates analysis (PCoA) performed on a Gower dissimilarity matrix. The FDis was computed as the abundance-weighted mean distance of each species to the community-weighted trait centroid in the multidimensional trait space:

$$FDis_{trait} = \sum_{i=1}^n p_i \times z_i$$

with p_i the relative abundance of species i and z_i the distance of species i to the community-weighted trait centroid. The CWM and FDis of SLA and LDMC were both calculated in R using the 'FD' package ([Laliberté et al., 2014](#)).

2.7. Statistical analyses

Prior to analysis, data exploration was performed to identify potential outliers. Three experimental units (2% of the dataset) presenting extreme values were excluded from subsequent analyses. All analyses were performed using R studio (version 4.4.3; R Core Team, 2025). The differences in yield, protein and NDF among the nine mixtures at the three harvests were tested using linear-mixed effect (lme) model with 'dominant species identity', 'proportion of low-abundant species' and their interaction as fixed factors with 'block' nested into 'site' as random factor using the 'nlme' package. *Post hoc* tests were performed for the models when significant effects were detected (Tukey's test, $P < 0.05$) using the 'emmeans' package (Fig. A.2).

The realized botanical composition differed substantially from the expected composition, especially for low-abundant species (Fig. A.3). *Plantago lanceolata* dominated this group, representing 62% of the low-abundant species biomass, whereas *F. rubra* and *A. capillaris* were nearly absent. We suspect that the high abundance of *P. lanceolata* was partly explained by the weather conditions during the year of sowing, with higher abundance of *P. lanceolata* under drier conditions (see Fig. A.4). Consequently, for the subsequent analyses, we simplified the botanical composition by focusing on the main components that were experimentally manipulated and which structured the realized mixture composition: the abundances of the two dominant grasses (*D. glomerata* and *A. pratensis*), the low-abundant species *P. lanceolata*, and legumes. Legumes were retained because their abundance was partially manipulated through sowing (i.e., *L. corniculatus*) and because they represent a key functional group with well-established effects on forage yield and protein.

The differences in functional traits values (SLA and LDMC) among

A. pratensis, *D. glomerata*, *P. lanceolata* and legumes (i.e., average traits values of *T. pratense*, *T. repens* and *L. corniculatus*) across the harvests were tested using lme models with 'botanical group', 'harvest' and their interactions as fixed factors with 'block' nested into 'site' as random factor. The effects of the different harvests on the botanical composition, community functional traits, forage yield and nutritive value were tested using lme models with 'block' nested into 'site' as random factor. *Post hoc* tests were performed for the models when significant effects were detected.

Since the harvest timing (three harvests) had significant impacts on all variables, results were then analyzed separately for each harvest. The effects of the sites on the botanical composition, forage yield, nutritive value (protein and NDF concentration), and community functional traits at each harvest were assessed using analyses of variance (ANOVAs) based on fitted linear models, with 'site' and 'block' included as explanatory variables (Table A.3). Because our main objective was to evaluate the effects of the botanical composition, particularly the role of the two dominant grasses, legumes and *P. lanceolata* within the mixtures, rather than the variability among sites, we extracted the residuals from these linear models and used these in the following statistical analyses. This procedure allowed us to fully remove site and block effects on all variables. To evaluate the existing linkages between the different variables, we performed a Pearson correlation analysis at the first, second and third harvest. These analyses highlighted the limited autocorrelation among the different variables related to the botanical composition (Fig. A.5) thus allowing to evaluate the relative influence of each botanical group independently.

To investigate the complex relationships among the botanical composition, community functional traits, forage yield and nutritive value, we applied structural equation modeling (SEM) using the lavaan package ([Rosseel, 2012](#)). A path analysis framework was used to quantify the linkages between botanical composition and community functional traits, as well as their respective effects on forage yield, protein and NDF concentration. Using *a priori* knowledge and results from the Pearson correlation analysis, we built a network of causal relationships among all measured variables (Fig. A.6). In order to simplify the SEM, we did not include CWM SLA and FDis SLA, as these variables were not strongly influenced by the botanical composition (Fig. A5). Models were fit using maximum likelihood estimation with robust (Huber-White) standard errors and a scaled test statistic that is asymptotically equal to the Yuan-Bentler test statistic (MLR estimator). Fully standardized parameter estimates (*std.all* function in lavaan) were reported to facilitate comparison of effect sizes. Standardization was performed post-estimation by scaling coefficients according to the variances of the corresponding variables. Models were assessed with a nonsignificant chi-square test ($P > 0.05$), a high comparative fit index (CFI > 0.9), a low root mean square error of approximation (RMSEA < 0.1) and a low standardized root mean square residual (SRMR < 0.05).

The strength of the relationships between botanical composition (X) and forage yield, protein or NDF concentration (Y) was quantified by decomposing total effects into direct and indirect components. Community functional traits (M) were considered as mediating variables between botanical composition and yield. The effect sizes were reported as standardized coefficients. Direct effects corresponded to the standardized path coefficient linking X directly to Y, whereas indirect effects were calculated as the product of the coefficients linking X to M and M to Y, as follows:

$$Indirect_{X \rightarrow Y} = (X \rightarrow M) \times (M \rightarrow Y)$$

In order to further investigate the effects of *P. lanceolata* on yield over the growing season, we selected plots sown either without (0%) or with a high proportion of low-abundance species (30%) and calculated the biomass of *A. pratensis*, *D. glomerata*, *P. lanceolata*, legumes, and other grasses in these plots. The biomass of each species was calculated for each plot at each harvest by multiplying the relative abundance of the species in the plot by the forage yield of the plot. Differences in species

biomass across harvests for *A. pratensis*, *D. glomerata*, legumes, and other grasses were analyzed using lme models, with 'harvest', 'proportion of low-abundant species' and their interaction as fixed factors, and 'block' nested into 'site' as a random factor. We used a generalized lme model fitted with a Tweedie distribution for *P. lanceolata* to account for the zero-inflated nature of the data related to the absence of *P. lanceolata* in most plots with 0% low-abundant species.

3. Results

3.1. Mixture botanical composition

Based on our treatment combination of dominant species identity and abundance of low-abundant species across the four sites, our analysis revealed a wide abundance gradient of *D. glomerata* (0–77%), *A. pratensis* (0–51%), *P. lanceolata* (0–74%) and legumes (1–55%) over the three harvests (Fig. 1), allowing us to accurately determine the effects of these species and botanical group on forage yield, protein and NDF concentration, as well as on community functional traits along the growing season. On average, the cumulative abundance of *A. pratensis*, *D. glomerata*, *P. lanceolata* and legumes represented 39.4%, 49.6% and 51.7% of the mixture's composition for the first, second and third harvest, respectively. Across sites, *A. pratensis* and *D. glomerata* were more abundant and *P. lanceolata* less abundant at the third harvest (Fig. 1). Legumes were more abundant at the 2nd and 3rd harvest. Forage protein concentration increased, whereas forage yield and NDF concentration decreased, following the successive harvests.

3.2. Relative importance of the dominant grasses, legumes and *Plantago lanceolata* on community functional traits and forage yield and nutritive value

The two dominant grasses, *P. lanceolata* and legumes had similarly high SLA values (around $260 \text{ cm}^2 \text{ g}^{-1}$, Fig. 2, non-significant species effect), which were not impacted by the harvest, except for *A. pratensis* for which SLA slightly increased over the season. By contrast, these species consistently differed in their LDMC values across the three harvests (Fig. 2., significant species effect), except at the first harvest where *A. pratensis* and *D. glomerata* had similar LDMC values. Overall, LDMC values were high for *A. pratensis* and *D. glomerata* (around $280 \text{ mg} \cdot \text{g}^{-1}$),

low for *P. lanceolata* (around $120 \text{ mg} \cdot \text{g}^{-1}$) and intermediate for legumes (around $170 \text{ mg} \cdot \text{g}^{-1}$). Both functional traits showed low intraspecific variability across block and sites as indicated by the low standard errors for the trait values for all botanical groups (Fig. 2).

The three SEMs, associated with the three forage harvests (Fig. 3), revealed that the effects of the botanical composition on forage yield, protein and NDF concentration were mainly mediated by both CWM LDMC and FDis LDMC, which had significant and contrasting effects (Fig. 3). The CWM LDMC increased yield at the 3rd harvest (path = 0.30) and NDF concentration at the 1st (path = 0.41), 2nd (path = 0.55) and 3rd (path = 0.52) harvest, while it negatively affected protein concentration at the 2nd harvest (path = -0.56). In contrast, FDis LDMC consistently showed opposite effects to those of CWM LDMC (Fig. 3), except for yield at the 3rd harvest, where the pathway was not significant. At the 1st harvest, FDis LDMC additionally exhibited a negative effect on yield (path = -0.26) and a positive effect on protein concentration (path = 0.23). All other pathways involving CWM LDMC and FDis LDMC were not significant.

The abundance of the two dominant grasses *D. glomerata* and *A. pratensis*, *P. lanceolata* and legumes had contrasting effects on forage yield, protein and NDF concentration along the vegetation season (Fig. 3). Overall, forage yield was more explained by the botanical composition and functional traits at the 1st ($R^2 = 0.34$), rather than the 2nd ($R^2 = 0.10$) or 3rd ($R^2 = 0.05$) harvest. Moreover, forage yield was still mostly impacted by the abundance of *P. lanceolata* (Fig. 4a). At the 1st and 3rd harvest, increasing abundance of *P. lanceolata* reduced forage yield, respectively through an increase in FDis LDMC (Fig. 3a) and a decrease in CWM LDMC (Fig. 3c.). In contrast, at the 2nd harvest, an increasing abundance of *P. lanceolata* had a direct positive impact on forage yield (Fig. 3b, path = 0.53). Additional analysis of the species biomass at the three harvests (Fig. A.7) further explains the negative impact of *P. lanceolata* on forage yield at the first harvest and its positive impact at the second harvest. Indeed, a high abundance of *P. lanceolata* (i.e., 30% low-abundant species treatment) in the mixtures led to a strong decrease in grasses biomass at the first harvest compared to plots where it was nearly absent (i.e., 0% low-abundant species treatment) but this was not observed for the second harvest, where *P. lanceolata* provided additional forage yield without constraining the yield of the other grass species.

An increasing abundance of *D. glomerata* and *A. pratensis* also had

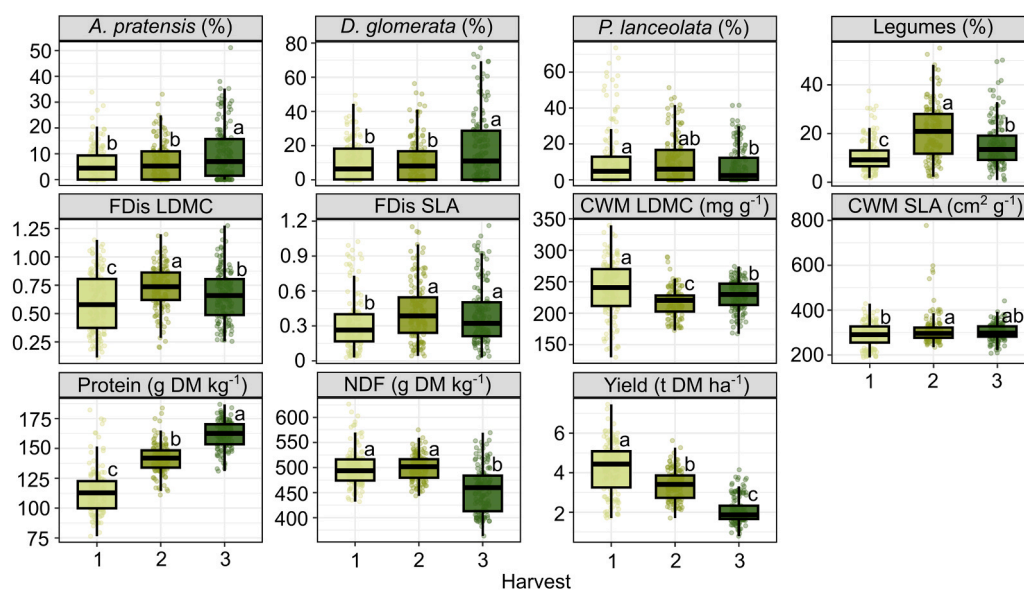


Fig. 1. Range values of the biomass proportion (including the dominant species *A. pratensis* and *D. glomerata*, the low-abundant species *P. lanceolata*, and legumes), community functional traits (CWM and FDis SLA and LDMC), forage yield and nutritive value (protein and NDF) across sites for the first (light green), second (medium green) and third (dark green) harvest. Boxplots sharing a letter are not significantly different from each other ($P > 0.05$).

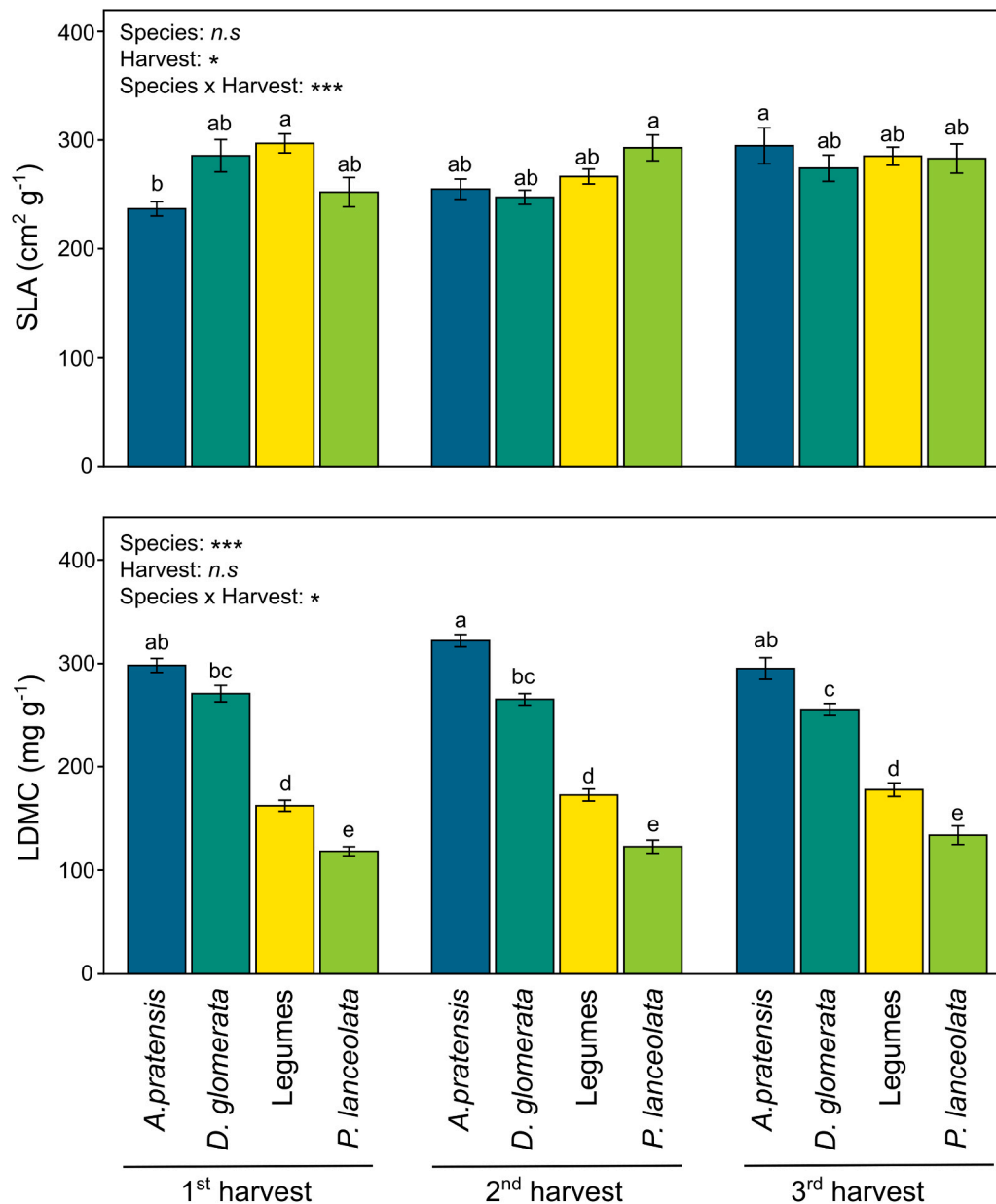


Fig. 2. Specific leaf area (SLA) and leaf dry matter content (LDMC) of the two dominant species *A. pratensis* and *D. glomerata*, the low-abundant species *P. lanceolata* and legumes at each harvest. Bars sharing a letter are not significantly different from each other ($P > 0.05$). n.s, $P > 0.05$; *, $P < 0.05$; *** $P < 0.001$.

slight positive effect on forage yield at the 3rd harvest (Fig. 4a), principally mediated by an increase in CWM LDMC (Fig. 3c), while legumes had a small negative effect at the 1st harvest (Fig. 4a), through an increase in FDis LDMC (Fig. 3a), and a globally positive direct effect at the 3rd harvest (Fig. 4a).

Unlike forage yield, the NDF concentration was strongly influenced by the botanical composition and functional traits of the mixtures at the 1st ($R^2 = 0.59$), 2nd ($R^2 = 0.39$) and 3rd ($R^2 = 0.48$) harvest. Forage NDF concentration was mostly impacted by the abundance of *P. lanceolata*, with a consistent decrease in NDF concentration with increasing *P. lanceolata* abundance at the three harvests (Fig. 4b), principally mediated by a decrease in CWM LDMC (Fig. 3a,b,c; path < -0.40 along the whole growing season) and an increase in FDis LDMC (path > 0.40 along the whole growing season). Forage NDF concentration also decreased with increasing abundance of legumes at the three harvests (Fig. 4b), through an increase in FDis LDMC (Fig. 3a) at the 1st harvest, and a decrease in CWM LDMC (Fig. 3b, c) at the 2nd and 3rd harvests. The abundance of *D. glomerata* and *A. pratensis* also influenced

forage NDF concentration, with an increase in NDF concentration at the three harvests (Fig. 4b), principally mediated by an increase in CWM LDMC (Fig. 3a, b, c), except for *D. glomerata* at the 1st harvest where the pathway was not significant.

Forage protein concentration was partly explained by the botanical composition and functional traits of the mixtures at the 1st ($R^2 = 0.27$), 2nd ($R^2 = 0.20$) and 3rd ($R^2 = 0.23$) harvest. The abundance of *P. lanceolata* was a strong driver of forage protein concentration (Fig. 4c), with negative direct effects (Fig. 3b, c; path < -0.40) starting from the second harvest. Globally, this negative effect at the 2nd harvest was almost entirely compensated by a positive and indirect effect (Fig. 4a) mediated through an increase in FDis LDMC and a decrease in CWM LDMC (Fig. 3b). Overall, the abundance of *D. glomerata* and *A. pratensis* had a positive effect on forage protein concentration at the 1st harvest and a slight negative effect at the 2nd harvest (Fig. 4c).

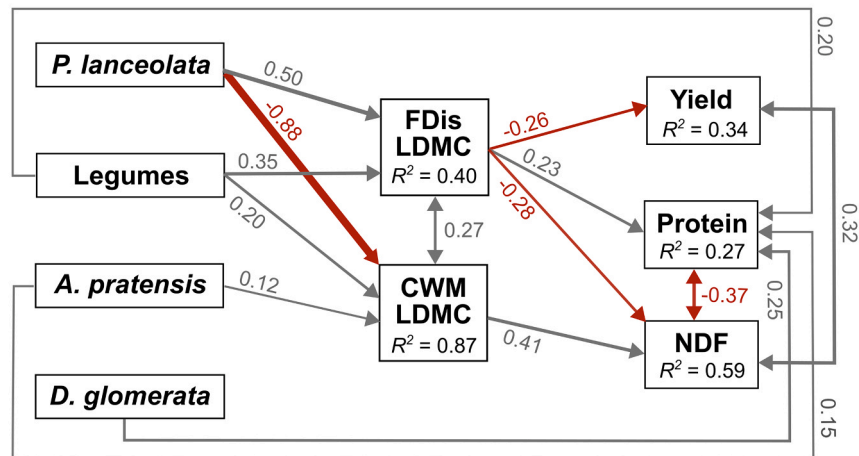
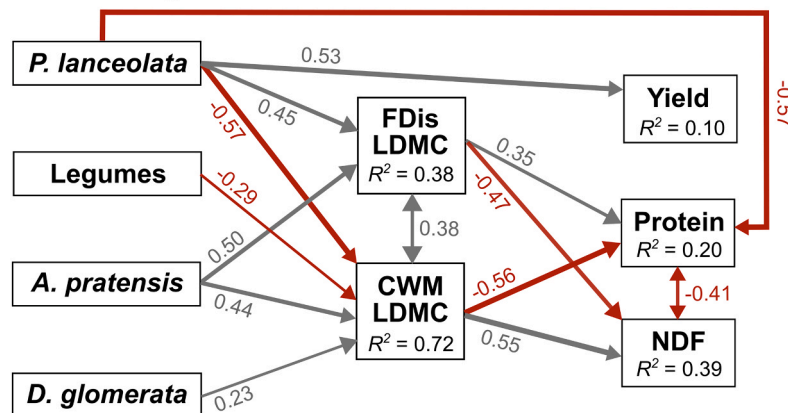
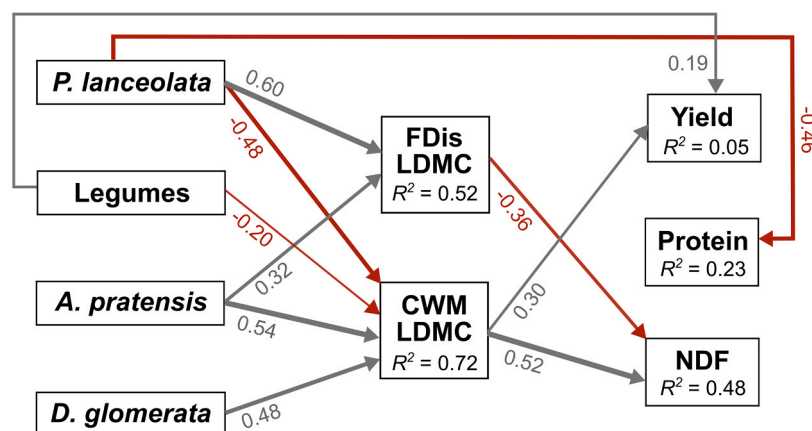
(a) 1st harvest $\chi^2 = 0.22$, $df = 2$, $P = 0.90$, $CFI = 1$, $SRMR < 0.01$, $RMSEA < 0.001$ (b) 2nd harvest $\chi^2 = 0.93$, $df = 2$, $P = 0.63$, $CFI = 1$, $SRMR < 0.01$, $RMSEA < 0.001$ (c) 3rd harvest $\chi^2 = 2.73$, $df = 2$, $P = 0.26$, $CFI = 0.99$, $SRMR = 0.01$, $RMSEA = 0.05$ 

Fig. 3. Structural equation models showing the effects of the botanical composition (*D. glomerata*, *A. pratensis*, *P. lanceolata* and legume abundance) and community functional traits (CWM LDMC and FDis LDMC) on forage yield and nutritive value (protein and NDF) for the first (a), second (b) and third (c) harvest. For clarity, only statistically significant pathways ($P < 0.05$) are shown in the figures. The arrow size is proportional to the path coefficient (numbers next to the arrow, standardized coefficient) and double-headed arrows show covariances. Red is for negative relationships and grey for positive relationships. Square multiple correlations (R^2 values) for the predicted variables are given in the box of the predicted variable.

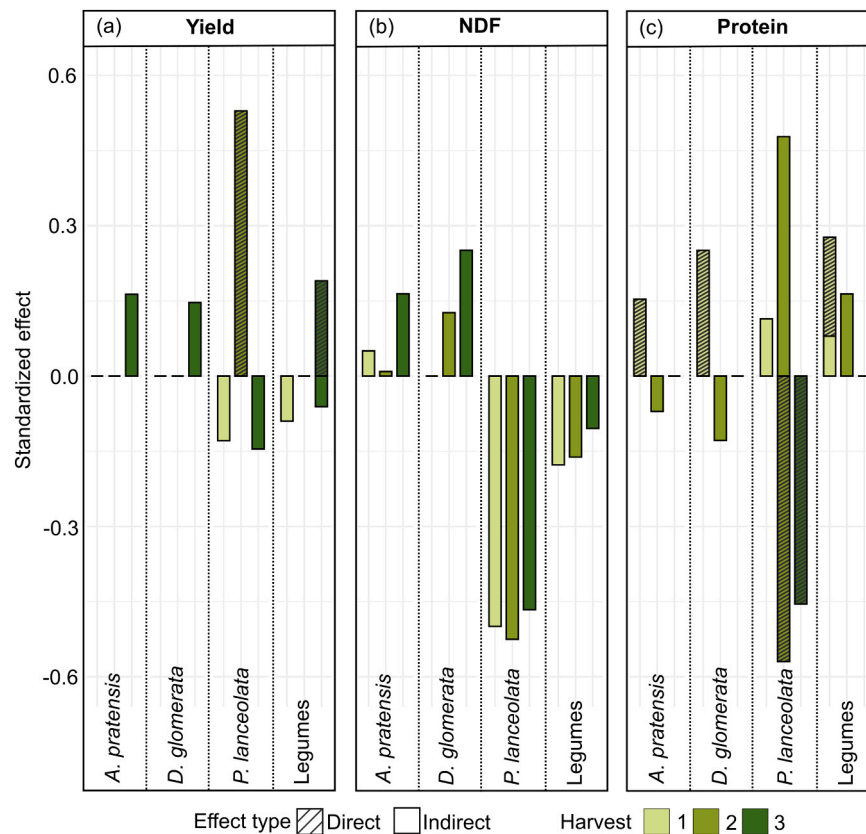


Fig. 4. Summary of the global direct and indirect effects of the botanical composition (*A. pratensis*; *D. glomerata*; *P. lanceolata* and legumes) on forage yield (a), NDF (b) and protein (c) concentration at the first (light green), second (medium green) and third (dark green) harvest, identified through the structural equation modeling. Solid bars represent indirect effects and hatched bars direct effects.

4. Discussion

4.1. Functional strategies of dominant and low-abundant species

Contrary to our first hypothesis, the dominant grass species and low-abundant species did not differ considerably in their functional strategies. Indeed, the dominant grass species, *P. lanceolata* and the legumes had similarly high SLA values, indicative of acquisitive resource-use strategies (Wright et al., 2004). This convergence likely reflects the agronomic context of our study system. Indeed, the species included in our mixtures have been selected and bred partly for high productivity, which may have indirectly favored functional traits associated with rapid growth, such as high SLA, and thus reduced leaf area variance among coexisting plant species, as also demonstrated by Chacón-Labelle et al. (2019). Indeed, cultivars of grassland species, including *D. glomerata* and *T. repens*, have higher SLA values than their corresponding natural ecotypes, consistent with trait shifts driven by selection for enhanced performance (Prieto et al., 2017). In contrast, the same study reported no significant effect of breeding on LDMC, suggesting that this trait has not been subjected to similar indirect selection. This aligns with our results, as dominant grass species, *P. lanceolata* and legumes showed pronounced differences in LDMC, indicating the coexistence of contrasting strategies for this trait, with the dominant species having the highest LDMC values and *P. lanceolata* having the lowest LDMC values (approximately half those of the dominant species). Together, these findings suggest that, in agronomic systems, varietal selection may homogenize certain traits linked to productivity (SLA), while allowing others (LDMC) to remain more functionally differentiated.

4.2. Role of plant community functional traits in shaping forage yield and nutritive value

Our SEM results showed that both botanical composition and community functional traits influenced forage yield and nutritive value throughout the growing season, although the number and strength of significant relationships declined over the season. Consistent with our second hypothesis, most effects of the botanical composition on forage yield, protein and NDF concentration were mediated through shifts in functional traits, with LDMC exerting a stronger influence than SLA, confirming its value as a predictor of biomass production (Breitschwerdt et al., 2019; Smart et al., 2017). Since all species included in our analysis exhibited relatively high SLA values with limited interspecific variation, this likely constrained our ability to detect relationships between SLA and both yield and nutritive value. As a result, SLA may not have been a sufficiently discriminating trait in this context, whereas LDMC exhibited greater interspecific variability and thus stronger potential to explain differences in mixtures functioning. Community-weighted mean LDMC was negatively associated with protein content during the second harvest and positively associated with NDF throughout the growing season. These findings align with previous studies showing that higher LDMC is generally linked to reduced digestibility, arising from lower leaf nitrogen concentration and greater structural fiber concentration (Blaix et al., 2023; Bumb et al., 2016). The functional dissimilarity of LDMC had the opposite effect to community-weighted mean LDMC, with mixtures having a higher variability in LDMC values displaying lower forage yield but higher nutritive value (lower NDF and increased protein concentration). This result highlights the importance of increasing functional trait diversity within forage mixtures by including species with contrasted functional trait values (high and low LDMC) to improve forage nutritive value, as previously demonstrated by Blaix et al. (2023).

4.3. Impact of dominant grasses on forage yield at the spring harvest

Contrary to our third hypothesis, neither *A. pratensis* nor *D. glomerata* exerted a positive effect on yield at the first harvest. Instead, their effects became apparent later in the growing season (i.e. at the third harvest) when their proportion increased in the mixtures. This pattern suggests that other grass species reaching high relative abundances in the mixtures (e.g., *Phleum pratense* and *Lolium perenne*), may have been the primary drivers of yield, particularly at earlier growth stages (see Fig. A.7). For both dominant species at the third harvest, yield effects were largely mediated by shifts in CWM and FDis LDMC. In addition, *A. pratensis* and *D. glomerata* showed a positive effect on NDF throughout the growing season, indicating reduced forage digestibility. This finding is in line with previous studies demonstrating that grasses tend to increase NDF concentration (Dindová et al., 2019; Perotti et al., 2021), with pronounced effects attributed to *D. glomerata* (Verma et al., 2026). Moreover, *A. pratensis* is an early-developing species that reaches advanced phenological stage more rapidly than other species (Pontes et al., 2007), which may explain the higher NDF concentration at harvest, as cell wall content typically increases with herbage maturity (Elgersma and Søgaard, 2018).

4.4. *Plantago lanceolata* enhances summer productivity and reduces fiber concentration across the growing season

Our third hypothesis concerning low-abundant species and their potential to enhance summer yield through complementarity effects could only be partly evaluated, due to their poor establishment or absence in the mixtures. Except for *P. lanceolata*, these species failed to generate a meaningful gradient in biomass proportion across treatments. Such establishment failure of species introduced at low seeding rates has previously been reported in multispecies swards (Shackleton et al., 2024). We believe that their absence or irregularity in establishment may be linked to sowing conditions in the previous year (e.g. weeds abundance or weather conditions), as well as to competitive interactions within the mixtures. More competitive and higher-seeded species, such as productive grasses, may have limited the establishment success of the low competitive species. In contrast, *P. lanceolata*, initially expected to be low-abundant, reached higher abundance than expected and even achieved dominance at certain locations. In this context, the main novelty of our work lies in the assessment of *P. lanceolata* effects on forage production within a relatively high-diverse mixture, whereas previous studies have mainly focused on low-diversity swards, comprising on average no more than six species (Dodd et al., 2025).

Our results indicated that a high abundance of *P. lanceolata* had negative effect on yield at the first harvest in spring, a period when forage production is largely driven by productive grass species. However, at the 2nd harvest in summer, *P. lanceolata* showed a direct positive relationship with yield, consistent with our second hypothesis when considering this species only. The negative effect of *P. lanceolata* on forage yield observed in spring may reflect a reduction in grass yield in mixtures with high *P. lanceolata* abundance compared with mixtures where this species was nearly absent (Fig. A.7). Indeed, the biomass of grasses was generally lower in plots with high *P. lanceolata* abundance at the first harvest, whereas these differences disappeared at the second harvest. Therefore, the positive effect of *P. lanceolata* on forage yield observed in summer appears to result from an additional biomass contribution of *P. lanceolata* (i.e., direct effect), without a corresponding reduction in the biomass of the other species, especially grasses. This seasonal shift is consistent with previous findings highlighting the capacity of *P. lanceolata* to achieve yield dominance during summer conditions (Dodd et al., 2025). The phenological pattern of *P. lanceolata* may therefore contribute to the compensation of the common yield decrease following the first harvest, particularly when the productivity of certain grass species declines (Hamacher et al., 2021; Pontes et al., 2007), showing additional evidence of a stabilizing effect due to species

growth asynchrony (Haughey et al., 2018; Husse et al., 2016). As a result, our results demonstrate that *P. lanceolata* enhanced seasonal yield stability and coupled with its relative resistance to drought (Pol et al., 2021), could also ensure forage production under variable climatic conditions, including dry summers. This pattern is particularly noteworthy because the relatively high abundance of *P. lanceolata* observed early in the season at some locations could be linked to establishment conditions during the sowing year, which was drier than average (Fig. A.4), thereby reinforcing evidence of its drought tolerance. Moreover, although this study did not directly test this mechanism, we speculate that this pattern may indicate not only strong resistance to water limitation but also a high capacity for successful establishment under dry conditions, potentially facilitating the establishment of other species during the early stages of community assembly. Importantly, *P. lanceolata* also persisted into 2024, a year characterized by comparatively wet conditions (Table A.4), especially during summer. This persistence across contrasting climatic contexts highlights the ecological plasticity of *P. lanceolata* and marks its capacity to establish, grow, and maintain populations under a broad range of environmental conditions (Villellas et al., 2021).

In contrast to yield responses, the effect of *P. lanceolata* on NDF concentration was more consistent across the growing season. Its presence was negatively associated with NDF concentration, suggesting an improvement in forage digestibility, while grasses tended to increase forage NDF concentration. This difference between grasses and forbs regarding forage nutritive value has been shown in Wu et al. (2025), where forbs showed higher protein concentration and lower NDF than grass-dominated grasslands, even though these observations remain species dependent. For *P. lanceolata* specifically, this pattern can be explained by its lower LDMC compared to grasses, which results in reduced concentrations of structural fibers (Al Haj Khaled et al., 2005; Dodd et al., 2025). This was indeed confirmed in our study since *P. lanceolata* leaves had much lower LDMC (122 mg g^{-1} across site and harvest) than those of *D. glomerata* (261 mg g^{-1}) and *A. pratensis* (311 mg g^{-1}), thus decreasing community-weighted mean LDMC while increasing the community functional dissimilarity of LDMC, both of which decreased forage NDF concentration and increased protein concentration. However, previous studies also showed that *P. lanceolata* exhibits higher acid detergent lignin (ADL) concentration than many other forage species (Elgersma et al., 2014), which increases with plant maturity (Kara et al., 2018) and could be related to the increase in flowering stem proportion at later phenological stages (Cougnon et al., 2025; Lee et al., 2015; Merino et al., 2024). As ADL represents the least digestible fiber fraction, these observations from other studies should temper the interpretation of its positive effects on NDF and the overall digestibility of mixtures. At the same time, this also highlights the importance of selecting *P. lanceolata* varieties that have a lower stem/leaf ratio, as this greatly varies among genotypes (Cougnon et al., 2025).

4.5. Legumes as the main contributor of crude protein concentration

Among the botanical variables considered, the relative abundance of legumes was the only one exhibiting a consistent and positive effect on crude protein concentration. This finding is in line with previous studies reporting higher CP concentration in mixed swards when legumes are abundant (Dindová et al., 2019; Jensen et al., 2025). Although the present study revealed a relatively small and negative effect of legumes on yield, several studies have shown that legumes can enhance productivity when introduced into grass-dominated mixtures (Finn et al., 2013). This contrast may be partly attributable to the experimental design, as all mixtures included legumes, even though their realized abundance was sometimes very low in certain plots. Consequently, the absence of a clear non-legume baseline may have constrained our ability to detect positive effects of legumes on productivity. Legume proportion reached up to 55% in some of our mixtures, which lies at the upper end of the range generally considered optimal for maximizing the benefits of

mixed swards (30–50%; Lüscher et al., 2014). Because relatively high legume sowing rates were applied, a substantial legume proportion was expected from the beginning of the experiment. Accordingly, nitrogen fertilization was set at approximately 60–70% of the recommended rate for Swiss grasslands (Huguenin-Elie et al., 2017). This adjustment was based on evidence showing that mixtures with high legume abundance can sustain yields comparable to those of highly productive and fertilized grass swards, while requiring lower nitrogen inputs (Nyfeler et al., 2009; Trumpp et al., 2025). Consistent with this expectation, yields across all mixtures were satisfactory (on average 9.7 t ha⁻¹ annual yield across mixtures and sites) and fell within the range typically reported for this type of grassland, despite being fertilized at lower nitrogen rates. Therefore, a high abundance of legumes can reduce dependence on nitrogen fertilizers, thereby lowering production costs and mitigating environmental impacts such as nitrate leaching and greenhouse gas emissions, which reinforces their role as a key component of agroecological grassland mixtures that aim to reconcile productivity, feed quality and environmental sustainability (Lüscher et al., 2014). In this study, we included a broader range of legume species, notably increasing the abundance of *L. corniculatus* (reaching up to 7.5% of the expected biomass proportion in the mixtures). Given the interspecific variation in legumes characteristics, particularly in terms of secondary compounds (Hamacher et al., 2021; Ramírez-Restrepo and Barry, 2005) and tolerance to environmental stress (Komainda et al., 2019), further investigation on the role of legume diversity is necessary and could provide valuable insights into the functioning and optimization of temporary grasslands.

5. Conclusion

Our study demonstrates that plant community functional traits provide a reliable framework for understanding and predicting forage yield and nutritive value in temporary mountain grasslands. Across the growing season, CWM and FDis LDMC emerged as key drivers of forage production, mediating most of the effects of the botanical composition on forage yield and nutritive value. Seasonal dynamics were influenced by both the dominant grasses (*D. glomerata* and *A. pratensis*, high LDMC species), which increased protein concentration in spring and NDF concentration along the whole growing season, whereas the forb *P. lanceolata* (low LDMC species) contributed to yield in summer and reduced NDF concentration along the growing season, thereby improving seasonal yield stability and forage digestibility. Legumes played a central role in sustaining high protein concentration and allowed reduced nitrogen fertilization, reinforcing their potential for low-input mountain grassland systems. Overall, our findings emphasize that integrating functional trait-based approaches with strategic species composition can enhance resilience, resource-use efficiency and environmental performance of temporary mountain mixtures under variable climatic conditions. As a next step and to better assess mixtures suitability to predicted mountain climatic conditions, further research should investigate how these mixtures respond to severe summer drought and determine whether the observed benefits for seasonal yield stability extend in the long term. Future studies should also aim to disentangle more precisely the functional contribution of individual species to community resilience, productivity and forage nutritive value under contrasting climatic conditions.

CRedit authorship contribution statement

Emilie Roinel: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Mas-similiano Probo:** Writing – review & editing, Supervision, Methodology, Conceptualization. **David Frund:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Marlyse Raemy:** Writing – review & editing, Methodology. **Eric Allan:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization.

Pierre Mariotte: Writing – original draft, Validation, Supervision, Project administration, Methodology, Investigation, Conceptualization.

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.

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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.2026.110758.

Data availability

Data is available online: <https://doi.org/10.5281/zenodo.22042753>

References

- Al Haj Khaled, R., Duru, M., Theau, J.P., Plantureux, S., Cruz, P., 2005. Variation in leaf traits through seasons and N-availability levels and its consequences for ranking grassland species. *J. Veg. Sci.* 16, 391–398. <https://doi.org/10.1111/j.1654-1103.2005.tb02378.x>.
- Bengtsson, J., Bullock, J.M., Egoh, B., Everson, C., Everson, T., O'Connor, T., O'Farrell, P. J., Smith, H.G., Lindborg, R., 2019. Grasslands more important for ecosystem services than you might think. *Ecosphere* 10, e02582. <https://doi.org/10.1002/ecs2.2582>.
- Blaix, C., Chabrierie, O., Alard, D., Catterou, M., Diquelou, S., Dutoit, T., Lacoux, J., Loucougaray, G., Michelot-Antalik, A., Pacé, M., Tardif, A., Lemauiel-Lavenant, S., Bonis, A., 2023. Forage nutritive value shows synergies with plant diversity in a wide range of semi-natural grassland habitats. *Agric. Ecosyst. Environ.* 347, 108369. <https://doi.org/10.1016/j.agee.2023.108369>.
- Breitschwerdt, E., Jandt, U., Bruelheide, H., 2019. Trait–performance relationships of grassland plant species differ between common garden and field conditions. *Ecol. Evol.* 9, 1691–1701. <https://doi.org/10.1002/ecs3.4818>.
- Bumb, L., Garnier, E., Bastianelli, D., Richarte, J., Bonnal, L., Kazakou, E., 2016. Influence of management regime and harvest date on the forage quality of rangelands plants: the importance of dry matter content. *AoB PLANTS* 8, plw045. <https://doi.org/10.1093/aobpla/plw045>.
- Calanca, P., 2007. Climate change and drought occurrence in the Alpine region: How severe are becoming the extremes? *Glob. Planet. Change* 57, 151–160. <https://doi.org/10.1016/j.gloplacha.2006.11.001>.
- Canarini, A., Mariotte, P., Carrillo, Y., Ochoa-Hueso, R., Bougoure, J., Vasileiadis, S., Anderson, I.C., Dijkstra, F.A., Richter, A., Toju, H., Donner, E., Power, S.A., Drigo, B., 2026. Enhanced below-ground functioning is associated with higher plant resistance against drought: Implications for ecosystem functions. *Journal of Ecology* 114 (3), e70289. <https://doi.org/10.1111/1365-2745.70289>. <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.70289>.
- Caputa, J., 1948. Untersuchungen über die Entwicklung einiger Gräser und Kleearten in Reinsaat und Mischung: ein Beitrag zur Konkurrenz- und Saatmengenfrage. *ETH Zur.* <https://doi.org/10.3929/ETHZ-A-000110637>.
- Chacón-Labela, J., García Palacios, P., Matesanz, S., Schöb, C., Milla, R., 2019. Plant domestication disrupts biodiversity effects across major crop types. *Ecol. Lett.* 22, 1472–1482. <https://doi.org/10.1111/ele.13336>.
- Chang, J., Ciais, P., Viovy, N., Soussana, J.-F., Klumpp, K., Sultan, B., 2017. Future productivity and phenology changes in European grasslands for different warming levels: implications for grassland management and carbon balance. *Carbon Balance Manag.* 12, 11. <https://doi.org/10.1186/s13021-017-0079-8>.
- Cong, W.-F., Suter, M., Lüscher, A., Eriksen, J., 2018. Species interactions between forbs and grass-clover contribute to yield gains and weed suppression in forage grassland mixtures. *Agric. Ecosyst. Environ.* 268, 154–161. <https://doi.org/10.1016/j.agee.2018.09.019>.

- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G., Poorter, H., 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust. J. Bot.* 51, 335–380. <https://doi.org/10.1071/BT02124>.
- Cougnon, M., Komainda, M., Ebert, C., Isselstein, J., Grelier, M., 2025. Flower stem proportion and digestibility of contrasting plantain (*Plantago lanceolata* L.) genotypes. In: EGF Symposium 2025 - Proceedings. Wageningen Academic, pp. 94–97. <https://doi.org/10.1163/9789004751163.019>.
- de Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J.H.C., Bardgett, R.D., Berg, M.P., Cipriotti, P., Feld, C.K., Hering, D., Martins da Silva, P., Potts, S.G., Sandin, L., Sousa, J.P., Storkey, J., Wardle, D.A., Harrison, P.A., 2010. Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodivers. Conserv.* 19, 2873–2893. <https://doi.org/10.1007/s10531-010-9850-9>.
- De Keersmaecker, W., van Rooijen, N., Lhermitte, S., Tits, L., Schaminée, J., Coppin, P., Honnay, O., Somers, B., 2016. Species-rich semi-natural grasslands have a higher resistance but a lower resilience than intensively managed agricultural grasslands in response to climate anomalies. *J. Appl. Ecol.* 53, 430–439. <https://doi.org/10.1111/1365-2664.12595>.
- Deléglise, C., Meisser, M., Mosimann, E., Spiegelberger, T., Signarbieux, C., Jeangros, B., Buttler, A., 2015. Drought-induced shifts in plants traits, yields and nutritive value under realistic grazing and mowing managements in a mountain grassland. *Agric. Ecosyst. Environ.* 213, 94–104. <https://doi.org/10.1016/j.agee.2015.07.020>.
- Dindová, A., Hakl, J., Hrevašová, Z., Nerušil, P., 2019. Relationships between long-term fertilization management and forage nutritive value in grasslands. *Agric. Ecosyst. Environ.* 279, 139–148. <https://doi.org/10.1016/j.agee.2019.01.011>.
- Dodd, M.B., Pinxterhuis, I.B., Judson, H.G., 2025. Narrow-leaved plantain (*Plantago lanceolata* L.): A review of research on forage management within temperate grazing systems. *Grassl. Res.* 4, 41–56. <https://doi.org/10.1002/glr2.12107>.
- Doudová, J., Douda, J., 2020. Along with intraspecific functional trait variation, individual performance is key to resolving community assembly processes. *Funct. Ecol.* 34, 2362–2374. <https://doi.org/10.1111/1365-2435.13646>.
- Elgersma, A., Søgaard, K., 2018. Changes in nutritive value and herbage yield during extended growth intervals in grass-legume mixtures: effects of species, maturity at harvest, and relationships between productivity and components of feed quality. *Grass Forage Sci.* 73, 78–93. <https://doi.org/10.1111/gfs.12287>.
- Elgersma, A., Søgaard, K., Jensen, S.K., 2014. Herbage dry-matter production and forage quality of three legumes and four non-leguminous forbs grown in single-species stands. *Grass Forage Sci.* 69, 705–716. <https://doi.org/10.1111/gfs.12104>.
- Fichet-Calvet, E., Pradier, B., Quéré, J.P., Giraudoux, P., Delattre, P., 2000. Landscape composition and vole outbreaks: evidence from an eight year study of *Arvicola terrestris*. *Ecography* 23, 659–668. <https://doi.org/10.1111/j.1600-0587.2000.tb00309.x>.
- Finn, J.A., Kirwan, L., Connolly, J., Sebastià, M.T., Helgadottir, A., Baadshaug, O.H., Bélanger, G., Black, A., Brophy, C., Collins, R.P., Cop, J., Dalmannsdóttir, S., Delgado, I., Elgersma, A., Fothergill, M., Frankow-Lindberg, B.E., Ghesquiere, A., Golinska, B., Golinski, P., Grieu, P., Gustavsson, A.-M., Höglind, M., Huguenin-Elie, O., Jørgensen, M., Kadziuliene, Z., Kurki, P., Llurba, R., Lunnan, T., Porqueddu, C., Suter, M., Thumm, U., Lüscher, A., 2013. Ecosystem function enhanced by combining four functional types of plant species in intensively managed grassland mixtures: a 3-year continental-scale field experiment. *J. Appl. Ecol.* 50, 365–375. <https://doi.org/10.1111/1365-2664.12041>.
- Finn, J.A., Suter, M., Haughey, E., Hofer, D., Lüscher, A., 2018. Greater gains in annual yields from increased plant diversity than losses from experimental drought in two temperate grasslands. *Agric. Ecosyst. Environ.* 258, 149–153. <https://doi.org/10.1016/j.agee.2018.02.014>.
- Garnier, E., Navas, M.-L., 2012. A trait-based approach to comparative functional plant ecology: concepts, methods and applications for agroecology. A review. *Agron. Sustain. Dev.* 32, 365–399. <https://doi.org/10.1007/s13593-011-0036-y>.
- Giraudoux, P., Delattre, P., Habert, M., Quéré, J.P., Deblay, S., Defaut, R., Duhamel, R., Moissenet, M.F., Salvi, D., Truchetet, D., 1997. Population dynamics of fossorial water vole (*Arvicola terrestris* scherman): a land use and landscape perspective. *Agric. Ecosyst. Environ.* 66, 47–60. [https://doi.org/10.1016/S0167-8809\(97\)80706-2](https://doi.org/10.1016/S0167-8809(97)80706-2).
- Grange, G., Finn, J.A., Brophy, C., 2021. Plant diversity enhanced yield and mitigated drought impacts in intensively managed grassland communities. *J. Appl. Ecol.* 58, 1864–1875. <https://doi.org/10.1111/1365-2664.13894>.
- Graux, A.-I., Bellocchi, G., Lardy, R., Soussana, J.-F., 2013. Ensemble modelling of climate change risks and opportunities for managed grasslands in France. *Agric. For. Meteorol.* 170, 114–131. <https://doi.org/10.1016/j.agrformet.2012.06.010>.
- Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* 86, 902–910. <https://doi.org/10.1046/j.1365-2745.1998.00306.x>.
- Hamacher, M., Malisch, C.S., Reinsch, T., Taube, F., Loges, R., 2021. Evaluation of yield formation and nutritive value of forage legumes and herbs with potential for diverse grasslands due to their concentration in plant specialized metabolites. *Eur. J. Agron.* 128, 126307. <https://doi.org/10.1016/j.eja.2021.126307>.
- Hanisch, M., Schweiger, O., Cord, A.F., Volk, M., Knapp, S., 2020. Plant functional traits shape multiple ecosystem services, their trade-offs and synergies in grasslands. *J. Appl. Ecol.* 57, 1535–1550. <https://doi.org/10.1111/1365-2664.13644>.
- Hann, P., Trška, C., Wechselberger, K.F., Eitzinger, J., Kromp, B., 2015. Phyllopertha horticola (Coleoptera: Scarabaeidae) larvae in eastern Austrian mountainous grasslands and the associated damage risk related to soil, topography and management. *SpringerPlus* 4, 139. <https://doi.org/10.1186/s40064-015-0918-6>.
- Haughey, E., Suter, M., Hofer, D., Hoekstra, N.J., McElwain, J.C., Lüscher, A., Finn, J.A., 2018. Higher species richness enhances yield stability in intensively managed grasslands with experimental disturbance. *Sci. Rep.* 8, 15047. <https://doi.org/10.1038/s41598-018-33262-9>.
- Hofer, D., Suter, M., Haughey, E., Finn, J.A., Hoekstra, N.J., Buchmann, N., Lüscher, A., 2016. Yield of temperate forage grassland species is either largely resistant or resilient to experimental summer drought. *J. Appl. Ecol.* 53, 1023–1034. <https://doi.org/10.1111/1365-2664.12694>.
- Huguenin-Elie, O., Mosimann, E., Schlegel, P., Lüscher, A., Kessler, W., 2017. 9/ Fertilisation des herbages: Principes de fertilisation des cultures agricoles en Suisse (PRIF). *Rech. Agron. Suisse* 8, 1–22.
- Humphreys, M.O., 2005. Genetic improvement of forage crops – past, present and future. *J. Agric. Sci.* 143, 441–448. <https://doi.org/10.1017/S0021859605005599>.
- Hushe, S., Huguenin-Elie, O., Buchmann, N., Lüscher, A., 2016. Larger yields of mixtures than monocultures of cultivated grassland species match with asynchrony in shoot growth among species but not with increased light interception. *Field Crops Res.* 194, 1–11. <https://doi.org/10.1016/j.fcr.2016.04.021>.
- Institute for Prospective Technological Studies (Joint Research Centre), Gomez y Paloma, Sergio, Guri, Fatmir, Santini, Fabien, 2013. Labelling of agricultural and food products of mountain farming. Publications Office of the European Union.
- Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer, T. M., Bonin, C., Bruelheide, H., de Luca, E., Ebeling, A., Griffin, J.N., Guo, Q., Hautier, Y., Hector, A., Jentsch, A., Kreyling, J., Lanta, V., Manning, P., Meyer, S.T., Mori, A.S., Naeem, S., Niklaus, P.A., Polley, H.W., Reich, P.B., Roscher, C., Seabloom, E.W., Smith, M.D., Thakur, M.P., Tilman, D., Tracy, B.F., van der Putten, W.H., van Ruijven, J., Weigelt, A., Weisser, W.W., Wilsey, B., Eisenhauer, N., 2015. Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature* 526, 574–577. <https://doi.org/10.1038/nature15374>.
- Jensen, J.L., Malisch, C.S., Thers, H., Eriksen, J., 2025. Adding forbs and legumes to a grass-clover mixture suppressed weeds and maintained herbage yield and crude protein content across slurry application rates. *Eur. J. Agron.* 164, 127458. <https://doi.org/10.1016/j.eja.2024.127458>.
- Kara, K., Ozkaya, S., Baytok, E., Güclu, B., Aktuğ, E., Erbas, S., 2018. Effect of phenological stage on nutrient composition, in vitro fermentation and gas production kinetics of *Plantago lanceolata* herbage. *Vet. Med. (Praha)* 63. <https://doi.org/10.17221/2/2017-vetmed>.
- Komainda, M., Küchenmeister, K., Küchenmeister, F., Breitsameter, L., Wrage-Mönig, N., Kayser, M., Isselstein, J., 2019. Forage legumes for future dry climates: Lower relative biomass losses of minor forage legumes compared to *Trifolium repens* under conditions of periodic drought stress. *J. Agron. Crop. Sci.* 205, 460–469. <https://doi.org/10.1111/jac.12337>.
- Korell, L., Andzejak, M., Berger, S., Durka, W., Haider, S., Hensen, I., Herion, Y., Höfner, J., Kindermann, L., Klotz, S., Knight, T.M., Linstädter, A., Madaj, A.-M., Merbach, I., Michalski, S., Plos, C., Roscher, C., Schädler, M., Welk, E., Auge, H., 2024. Land use modulates resistance of grasslands against future climate and inter-annual climate variability in a large field experiment. *Glob. Change Biol.* 30, e17418. <https://doi.org/10.1111/gcb.17418>.
- Kragten, S.A., Wyss, U., 2014. Futtermittel im Nah-Infrarotlicht (NIRS). *Agrar. Schweiz*.
- Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91, 299–305. <https://doi.org/10.1890/08-2244.1>.
- Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.* 16, 545–556. <https://doi.org/10.1046/j.1365-2435.2002.00664.x>.
- Lavorel, S., Grigulis, K., McIntyre, S., Williams, N.S.G., Garden, D., Dorrough, J., Berman, S., Quélet, F., Thébaud, A., Bonis, A., 2008. Assessing functional diversity in the field – methodology matters! *Funct. Ecol.* 22, 134–147. <https://doi.org/10.1111/j.1365-2435.2007.01339.x>.
- Lee, J.M., Hemmingson, N.R., Minnee, E.M.K., Clark, C.E.F., 2015. Management strategies for chicory (*Cichorium intybus*) and plantain (*Plantago lanceolata*): impact on dry matter yield, nutritive characteristics and plant density. *Crop. Pasture Sci.* 66, 168–183. <https://doi.org/10.1071/CP14181>.
- Luo, W., Ishii, N.I., Muraina, T.O., Song, L., Te, N., Griffin-Nolan, R.J., Slette, I.J., Ross, S.R.P.J., Sasaki, T., Rudgers, J.A., Smith, M.D., Knapp, A.K., Collins, S.L., 2025. Extreme Drought Increases the Temporal Variability of Grassland Productivity by Suppressing Dominant Grasses. *Ecol. Lett.* 28, e70127. <https://doi.org/10.1111/ele.70127>.
- Lüscher, A., Barkaoui, K., Finn, J.A., Suter, D., Suter, M., Volaire, F., 2022. Using plant diversity to reduce vulnerability and increase drought resilience of permanent and sown productive grasslands. *Grass Forage Sci.* 77, 235–246. <https://doi.org/10.1111/gfs.12578>.
- Lüscher, A., Mueller-Harvey, I., Soussana, J.F., Rees, R.M., Peyraud, J.L., 2014. Potential of legume-based grassland-livestock systems in Europe: a review. *Grass Forage Sci.* 69, 206–228. <https://doi.org/10.1111/gfs.12124>.
- MacDougall, A.S., Vanzant, B., Sulik, J., Bagchi, S., Naidu, D., Muraina, T.O., Seabloom, E.W., Borer, E.T., Wilfahrt, P., Slette, I., Hierro, J.L., Pearson, D.E., Abedi, M., Akasaka, M., Alberti, J., Aleksanyan, A., Amisu, A.A., Anderson, T.M., Arnillas, C.A., Ayer, M., Bakker, J.D., Basant, S., Basto, S., Biederman, L., Bloodworth, K.J., Boscutti, F., Boughton, E.H., Bruschetti, C.M., Buckley, H.L., Buckley, Y.M., Bugalho, M.N., Caldeira, M.C., Campetella, G., Cannone, N., Carbognani, M., Carbutt, C., Carniello, M.A., Cervellini, M., Chaudhary, T., Chen, Q., Clark, A.T., Cousins, S., Dalle Fratte, M., Day, N.J., Deak, B., Dietrich, J., Dixon, A., Eisenhauer, N., Elgersma, K.J., Eren, O., Eskelinen, A., Estrada, C., Fay, P.A., Fayvush, G., Flynn, K.C., García Meza, D., Gargano, D., Gherardi, L., Girkin, N.T., González, L., Graff, P., Hagenberg, L.W.C., Halbritter, A.H., Havrilchak, N.A., Herdóza, N., Hersch-Green, E., Hopping, K., Jentsch, A., Jimoh, S.O., Kerby, J., Kirkman, K., Knops, J.M.H., Koerner, S.E., Koltz, A., Komatsu, K.J., Koura, B.I., Kruse, S., Laanisto, L., Lannes, L.S., Li, W., Liang, M., Lkhagva, A., López-Olmedo, L.,

- Lorenzo, P., Lortie, C.J., Loydi, A., Luo, W., Macek, P., Malfasi, F., Mariotte, P., Martina, J.P., Martínez-Blancas, A., Martinson, H., Martorell, C., Meave, J.A., Medina-Villar, S., Mganga, K.Z., Monsimét, J., Nerlekar, A.N., Niu, S., Ohlert, T., Oliveras Menor, I., Onatibia, G.R., Ortega, Y.K., Osborne, B., Palpurina, S., Pascual, J., Pennings, S.C., Pérez-García, E., Peri, P.L., Petit Bon, M., Petraglia, A., Pijcke, F., Prober, S.M., Quiroga, R.E., Ramírez, J.I., Reed, S., Rosado, B.H.P., Roscher, C., Rowley, D.W., Sereda, I., Small, D.M., Smith, N.G., Song, Y., Stevens, C., Suarez Jimenez, L.E., te Beest, M., Tedder, M., Terry, R.S., Thornton, K.S., Tian, D., Titcomb, G., Valkó, O., 'Ciska' Veen, G.F., Virtanen, R., Welti, E. A. R., Wheeler, G.R., Wolf, A.A., Wolff, P., Young, A.L., Young, H.S., Zeglin, L.H., Zhu, K., Zong, S., Siewert, M.B., 2026. The global extent of the grassland biome and implications for the terrestrial carbon sink. *Nat. Ecol. Evol.* 10, 246–257. <https://doi.org/10.1038/s41559-025-02955-6>.
- Mariotte, P., 2014. Do subordinate species punch above their weight? Evidence from above- and below-ground. *New. Phytol.* 203, 16–21. <https://doi.org/10.1111/nph.12789>.
- Mariotte, P., Vandenbergh, C., Kardol, P., Hagedorn, F., Buttler, A., 2013. Subordinate plant species enhance community resistance against drought in semi-natural grasslands. *J. Ecol.* 101, 763–773. <https://doi.org/10.1111/1365-2745.12064>.
- Merino, V.M., Aguilar, R.I., Rivero, M.J., Ordóñez, I.P., Piña, L.F., López-Belchí, M.D., Schoebitz, M.I., Noriega, F.A., Pérez, C.I., Cooke, A.S., Guedes, L.M., 2024. Distribution of Non-Structural Carbohydrates and Root Structure of *Plantago lanceolata* L. under Different Defoliation Frequencies and Intensities. *Plants* 13, 2773. <https://doi.org/10.3390/plants13192773>.
- Moloney, T., Sheridan, H., Grant, J., O'Riordan, E.G., O'Kiely, P., 2021. Yield of binary- and multi-species swards relative to single-species swards in intensive silage systems. *Ir. J. Agric. Food Res.* 59, 12–26. <https://doi.org/10.2478/ijaf-2020-0002>.
- Muraina, T.O., Vitra, A., Probo, M., Martina, J.P., Buttler, A., Mariotte, P., 2025. Linking Leaf Economic Traits With Forage Quality Across Temperate Grasslands Under Ambient and Drought Conditions. *Ecol. Evol.* 15, e71569. <https://doi.org/10.1002/ecs3.71569>.
- Nyfelde, D., Huguenin-Elie, O., Suter, M., Frossard, E., Connolly, J., Lüscher, A., 2009. Strong mixture effects among four species in fertilized agricultural grassland led to persistent and consistent transgressive overyielding. *J. Appl. Ecol.* 46, 683–691. <https://doi.org/10.1111/j.1365-2664.2009.01653.x>.
- O'Malley, J., Finn, J.A., Malisch, C.S., Suter, M., Meyer, S.T., Peratoner, G., Thivierge, M.-N., Abalos, D., Adler, P.R., Bezemer, T.M., Black, A.D., Ergon, A., Golińska, B., Grange, G., Hakl, J., Hoekstra, N.J., Huguenin-Elie, O., Jing, J., Jungers, J.M., Lajeunesse, J., Loges, R., Louarn, G., Lüscher, A., Moloney, T., Reynolds, C.K., Sturite, I., Khan, A.S., Vishwakarma, R., Zhang, Y., Zhu, F., Brophy, C., 2026. Multispecies grasslands produce more yield from lower nitrogen inputs across a climatic gradient. *Science* 391 (6781), 179–183. <https://doi.org/10.1126/science.ad7064>. <https://www.science.org/doi/10.1126/science.ad7064>.
- Oram, N.J., Sun, Y., Abalos, D., van Groenigen, J.W., Hartley, S., De Deyn, G.B., 2021. Plant traits of grass and legume species for flood resilience and N2O mitigation. *Funct. Ecol.* 35, 2205–2218. <https://doi.org/10.1111/1365-2435.13873>.
- Pedrazzini, C., Strasser, H., Zemp, N., Holderegger, R., Widmer, F., Enkerli, J., 2023. Spatial and temporal patterns in the population genomics of the European cockchafer *Melolontha melolontha* in the Alpine region. *Evol. Appl.* 16, 1586–1597. <https://doi.org/10.1111/eva.13588>.
- Peeters, A., 2009. Importance, evolution, environmental impact and future challenges of grasslands and grassland-based systems in Europe. *Grassl. Sci.* 55, 113–125. <https://doi.org/10.1111/j.1744-697X.2009.00154.x>.
- Perotti, E., Huguenin-Elie, O., Meisser, M., Dubois, S., Probo, M., Mariotte, P., 2021. Climatic, soil, and vegetation drivers of forage yield and quality differ across the first three growth cycles of intensively managed permanent grasslands. *Eur. J. Agron.* 122, 126194. <https://doi.org/10.1016/j.eja.2020.126194>.
- Pol, M., Schmidtke, K., Lewandowska, S., 2021. *Plantago lanceolata* – An overview of its agronomically and healing valuable features. *Open. Agric.* 6, 479–488. <https://doi.org/10.1515/opag-2021-0035>.
- Pontes, L.S., Carrère, P., Andueza, D., Louault, F., Soussana, J.F., 2007. Seasonal productivity and nutritive value of temperate grasses found in semi-natural pastures in Europe: responses to cutting frequency and N supply. *Grass Forage Sci.* 62, 485–496. <https://doi.org/10.1111/j.1365-2494.2007.00604.x>.
- Prieto, I., Litrico, I., Violle, C., Barre, P., 2017. Five species, many genotypes, broad phenotypic diversity: When agronomy meets functional ecology. *Am. J. Bot.* 104, 62–71. <https://doi.org/10.3732/ajb.1600354>.
- Ramírez-Restrepo, C.A., Barry, T.N., 2005. Alternative temperate forages containing secondary compounds for improving sustainable productivity in grazing ruminants. *Anim. Feed. Sci. Technol.* 120, 179–201. <https://doi.org/10.1016/j.anifeedsci.2005.01.015>.
- Rosseel, Y., 2012. lavaan: An R Package for Structural Equation Modeling. *J. Stat. Softw.* 48, 1–36. <https://doi.org/10.18637/jss.v048.i02>.
- Schils, R.L.M., Bufer, C., Rhymer, C.M., Francksen, R.M., Klaus, V.H., Abdalla, M., Milazzo, F., Lelkei-Kovács, E., Berge, H.T., Bertora, C., Chodkiewicz, A., Dámátrcá, C., Feigenwinter, I., Fernández-Rebollo, P., Ghiasi, S., Hejduk, S., Hiron, M., Janicka, M., Pellaton, R., Smith, K.E., Thorman, R., Vanwalleghem, T., Williams, J., Zavattaro, L., Kampen, J., Derckx, R., Smith, P., Whittingham, M.J., Buchmann, N., Price, J.P.N., 2022. Permanent grasslands in Europe: Land use change and intensification decrease their multifunctionality. *Agric. Ecosyst. Environ.* 330, 107891. <https://doi.org/10.1016/j.agee.2022.107891>.
- Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* 9, 671–675. <https://doi.org/10.1038/nmeth.2089>.
- Shackleton, J., Boland, T.M., Kennedy, J., Grace, C., Beaucarne, G., Kirwan, S.F., Schmidt, O., Sheridan, H., 2024. Annual and seasonal dry matter production, botanical species composition, and nutritive value of multispecies, permanent pasture, and perennial ryegrass swards managed under grazing. *Grass and Forage Science* 79 (4), 630–650. <https://doi.org/10.1111/gfs.12691>. <https://onlinelibrary.wiley.com/doi/10.1111/gfs.12691>.
- Smart, S.M., Glanville, H.C., Blanes, M. del C., Mercado, L.M., Emmett, B.A., Jones, D.L., Cosby, B.A., Marrs, R.H., Butler, A., Marshall, M.R., Reinsch, S., Herrero-Jáuregui, C., Hodgson, J.G., 2017. Leaf dry matter content is better at predicting above-ground net primary production than specific leaf area. *Funct. Ecol.* 31, 1336–1344. <https://doi.org/10.1111/1365-2435.12832>.
- Suter, D., Frick, R., 2025. *Mélanges standard pour la production fourragère: Révision 2025-2028*. Agric. ADCF Agroscope Zur. (CH) 16.
- Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T., Lehman, C., 2001. Diversity and Productivity in a Long-Term Grassland Experiment. *Science* 294, 843–845. <https://doi.org/10.1126/science.1060391>.
- Trumpp, K.R., Dubeux, J.C.B., García, L., Jaramillo, D.M., Pereira Neto, J.D., Santos, E.R. S., Queiroz, L.M.D., Bretas, L.L., Ruiz-Moreno, M., De Souza, C.H.L., Sollenberger, L. E., DiLorenzo, N., Vendramini, J.M.B., 2025. Integrating forage legumes reduces dependence on N fertilizer and increases the stability of grazing systems. *Eur. J. Agron.* 170, 127708. <https://doi.org/10.1016/j.eja.2025.127708>.
- Verma, S., Herrmann, A., Taube, F., Nyameasem, J.K., Ehrhard, D., Malisch, C.S., Kluf, C., Poyda, A., 2026. Functional diversity enhances grassland productivity, but species identity drives performance. *Agric. Ecosyst. Environ.* 397, 110091. <https://doi.org/10.1016/j.agee.2025.110091>.
- Villellas, J., Ehrlén, J., Crone, E.E., Csörgő, A.M., García, M.B., Laine, A.-L., Roach, D.A., Salguero-Gómez, R., Wardle, G.M., Childs, D.Z., Elderd, B.D., Finn, A., Munné-Bosch, S., Bachelot, B., Bódís, J., Bucharova, A., Caruso, C.M., Catford, J.A., Coghill, M., Compagnoni, A., Duncan, R.P., Dwyer, J.M., Ferguson, A., Fraser, L.H., Griffoul, E., Groenteman, R., Hamre, L.N., Helm, A., Kelly, R., Laanisto, L., Lonati, M., Münzbergová, Z., Nuche, P., Olsen, S.L., Oprea, A., Pärtel, M., Petry, W. K., Ramula, S., Rasmussen, P.U., Enri, S.R., Roeder, A., Roscher, C., Schultz, C., Skarpaas, O., Smith, A.L., Tack, A.J.M., Töpper, J.P., Vesk, P.A., Vose, G.E., Wandrag, E., Wingler, A., Buckley, Y.M., 2021. Phenotypic plasticity masks range-wide genetic differentiation for vegetative but not reproductive traits in a short-lived plant. *Ecol. Lett.* 24, 2378–2393. <https://doi.org/10.1111/ele.13858>.
- Wagg, C., Ebeling, A., Roscher, C., Ravenek, J., Bachmann, D., Eisenhauer, N., Mommer, L., Buchmann, N., Hillebrand, H., Schmid, B., Weisser, W.W., 2017. Functional trait dissimilarity drives both species complementarity and competitive disparity. *Funct. Ecol.* 31, 2320–2329. <https://doi.org/10.1111/1365-2435.12945>.
- Walde, M., Allan, E., Cappelli, S.L., Didion-Gency, M., Gessler, A., Lehmann, M.M., Pichon, N.A., Grossiord, C., 2021. Both diversity and functional composition affect productivity and water use efficiency in experimental temperate grasslands. *J. Ecol.* 109, 3877–3891. <https://doi.org/10.1111/1365-2745.13765>.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. *Nature* 428, 821–827. <https://doi.org/10.1038/nature02403>.
- Wu, S., Lü, X., Liu, Q., Wuda, E., Li, L., Zhao, C., Huang, J., Li, S., Hu, Y., Du, W., Li, H., Chen, C., Luo, L., Raza, A., Yin, C., 2025. The geographical variation in grassland forage quality on the eastern Qinghai-Tibet Plateau is driven mainly by climate. *Ecol. Process.* 14, 12. <https://doi.org/10.1186/s13717-025-00583-3>.
- Zhao, G., 2023. Trends in grassland science: Based on the shift analysis of research themes since the early 1900s. *Fundam. Res.* 3, 201–208. <https://doi.org/10.1016/j.fmre.2022.05.008>.
- Zhao, Y., Liu, Z., Wu, J., 2020. Grassland ecosystem services: a systematic review of research advances and future directions. *Landsc. Ecol.* 35, 793–814. <https://doi.org/10.1007/s10980-020-00980-3>.
- Zhu, X., Zheng, J., An, Y., Xin, X., Xu, D., Yan, R., Xu, L., Shen, B., Hou, L., 2023. Grassland Ecosystem Progress: A Review and Bibliometric Analysis Based on Research Publication over the Last Three Decades. *Agronomy* 13, 614. <https://doi.org/10.3390/agronomy13030614>.