# Species richness: A pivotal factor mediating the effects of land use intensification and climate on grassland multifunctionality

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RESEARCH ARTICLE

# Species richness: A pivotal factor mediating the effects of land use intensification and climate on grassland multifunctionality

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## Abstract

1. Temperate seminatural grasslands harbour unique biodiversity, support livestock farming through forage production, and deliver many essential ecosystem services (ESs) to human society; they are highly multifunctional. However, temperate grassland ecosystems are also among the most threatened ecosystems on earth due to land use and climate changes. Understanding how biodiversity, climate and land use intensification impact grassland multifunctionality through complex direct and indirect pathways is critical to better anticipate the future of these fragile ecosystems.
2. Here, we evaluate how local plant species richness (SR) modulates the effect of land use intensification and climate on grassland multifunctionality (using six key ESs: biomass productivity and stability, forage quality, carbon storage, pollination and local plant rarity) in the French Massif Central, the largest grassland in Western Europe. We sampled 100 grasslands with contrasted fertilization rates and SR, over large elevational and latitudinal gradients related to variation in mean annual temperature (MAT), and drought severity (DS), two key climate change drivers predicted to increase in the future.
3. Using a confirmatory path analysis, we found that SR was the main driver of multifunctionality. We also found significant SR×MAT and SR×fertilization interactions suggesting that warm climate and high fertilization rates alter the biodiversity–ecosystem multifunctionality relationships. Furthermore, increasing temperature and fertilization indirectly influenced multifunctionality by decreasing SR and consequent multifunctionality in warm lowland and highly fertilized grasslands compared to colder montane grasslands or less fertilized ones. DS only impacted some ES individually (e.g. forage quality).
4. *Synthesis and applications*: We identified species richness (SR) as a pivotal factor mediating the effects of land use intensification and climate on multifunctionality through both direct and indirect pathways. Failing to account for changes in SR could thus bias any prediction of, or aggravate, the effects of land use intensification and climate change on ecosystem services delivery in temperate grassland ecosystems. Considering that SR, mean annual temperature and fertilization

are major proxies of three main global change drivers (biodiversity loss, climate change and land use intensification) our study may help to better anticipate the effect of multiple interacting global change drivers on grassland ecosystems.

**KEYWORDS**
biodiversity, climate change, ecosystem services, fertilization, global change, mountain grasslands, structural equation modelling

## 1 | INTRODUCTION

Global change alters biodiversity worldwide and threatens the delivery of essential services that ecosystems provide to people (Millennium Ecosystem Assessment (Program), 2005). Global change is a multifactorial phenomenon that includes different drivers, such as climate change and land use intensification, which determines in complex ways how ecosystems are responding to increasing human pressure. The impacts of different global change drivers (GCDs) have mostly been studied in isolation (Rillig et al., 2019; Turner et al., 2020). However, GCDs may act synergistically or antagonistically on ecosystem services (ESs) delivery (Maestre et al., 2022), which can lead to unpredictable responses of ecosystems to global change. Studying the impact of simultaneous and possibly interacting GCDs on ecosystems is critical to better predict the impact of global change on ecosystems (Maestre et al., 2022).

Temperate seminatural grasslands are biodiversity hotspots that support livestock farming through forage production and provide many other essential ESs (e.g. carbon storage, pollination, water purification, recreation; Bengtsson et al., 2019; Schils et al., 2022). However, grasslands have been largely neglected in global policy discussions (Bardgett et al., 2021), despite representing one of the most endangered ecosystems on Earth due to land use intensification (Newbold et al., 2016) and more recently, climate change (Bardgett et al., 2021). It has been established that land use intensification—for example through excess fertilization—can result in a long-term decrease in biodiversity and decline in the simultaneous delivery of multiple ESs (Allan et al., 2015), referred to as ecosystem multifunctionality (Byrnes et al., 2014). Furthermore, land use intensification has been shown to increase grassland sensitivity to drought and temperature increase (Boch et al., 2021; Cross et al., 2015). Therefore, the negative effect of land use intensification on grassland multifunctionality is expected to increase under climate change. Studying the effect of land use intensification along wide climatic gradients may help anticipate grassland responses to the combined effects of climate and land use changes.

Plant species richness is a key driver of grassland multifunctionality (Maestre et al., 2012) and can modulate the effects of climate and land use intensification through multiple pathways (Figure 1). First, excess fertilization may lead to a drastic decrease in local species richness (Boch et al., 2021; Grime, 1973), which in turn may decrease grassland multifunctionality through an indirect pathway (Hypothesis 1, in Figure 1a; Allan et al., 2015). Second, if fertilization decreases species richness in grasslands, climate may modulate this effect (Hypothesis 2, Figure 1b). In a recent meta-analysis, Humbert et al. (2016) suggested that the fertilization effect on species richness would be weaker under a cold climate, as in upland grasslands. Third, species richness may also modulate the direct effects of climate (Jing et al., 2015) and land use intensification (Wang et al., 2023) on multifunctionality (Hypothesis 3 in Figure 1c). For instance, a higher plant species richness may improve grassland resistance to climate change (García-Palacios et al., 2018; Jing et al., 2015) and buffer the effect of land use intensification on multifunctionality (Maestre et al., 2022). Understanding how climate, land use intensification and plant species richness influence grassland multifunctionality through complex direct and indirect pathways (Figure 1) remains crucial to understand and better predict the effect of multiple interacting GCDs on these fragile ecosystems and the ESs they deliver.

Quantifying ecosystem responses along large climatic (Maestre et al., 2022) and land use gradients (Allan et al., 2015) is a common approach to study the impact of GCDs using space-for time substitution (Blois et al., 2013). Here, we used the French Massif central as a case study to assess the effect of land use intensification, climate and species richness on grassland multifunctionality (Figure S1). The Massif central is the largest grassland area in Western Europe. The dominant agricultural activity is livestock farming. This mountainous region offers a variety of climates ranging from wet temperate in the north to Mediterranean in the south, where grasslands are submitted to intense summer droughts and higher aridity (Figure S1). In addition, large elevational gradient (from 200 m up to 1885 m a.s.l., Figure S1), makes variations in mean annual temperature largely independent from the North-to-South aridity gradient and separates cold mountain from warmer lowland climates. Finally, the topography of the Massif central, characterized by high elevation plateaus that are easily accessible to agricultural machinery, makes land use practices largely independent from elevational gradients as opposed to other mountainous areas (e.g. the Pyrenees see Gibon et al., 2004).

Here, we sampled one hundred grassland fields from 70 commercial farms across the Massif central chosen to maximize the variety of climatic conditions, local management practices and local plant species richness. For management, we focused on the effect of fertilization on grassland species richness and multifunctionality, as fertilization is a major driver of herbage use intensification in permanent grasslands (Boch et al., 2021). We assessed

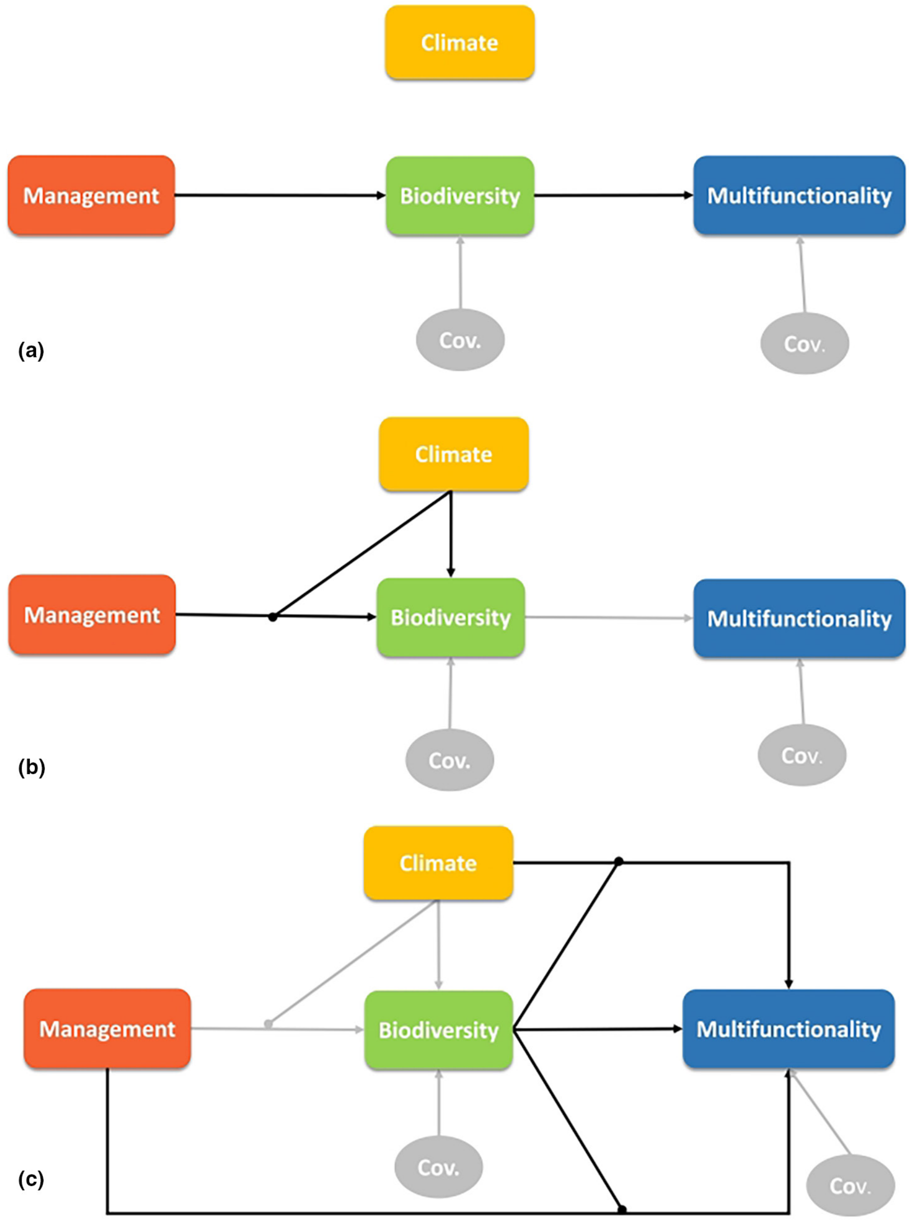


FIGURE 1 Acyclic graph of the three complementary hypothetical relationships among climate, management and biodiversity on multifunctionality. The black arrows represent links expressed by each hypothesis, the grey arrows represent links expressed by complementary hypotheses. (a) Hypothesis 1: Management and climate impact multifunctionality through indirect pathways mediated by changes in grassland biodiversity. (b) Hypothesis 2: The effect of management on biodiversity depends on the local climate. (c) Hypothesis 3: Climate and local management mediate the biodiversity–ecosystem multifunctionality relationship. Cov: model covariables are soil and topographic parameters.

six key ESs related to biomass productivity, fodder quality, carbon stock in the soil, ecosystem stability, quality of habitat for pollinators and plant local rarity, distributed among three CICES categories (*Common International Classification for Ecosystem Services*, Haines-Young & Potschin, 2018). From these ESs we evaluated multifunctionality with two different approaches. We then used confirmatory path analysis (Shipley, 2013) to identify how climate and fertilization modify plant species richness and multifunctionality according to the three complementary hypotheses above-mentioned (Figure 1).

## 2 | MATERIALS AND METHODS

### 2.1 | Site selection

The Massif central is a mountainous region of 85,000 $km^2$ area. The climate is mountainous and semicontinental in the major centre area, with oceanic influences in its northern and western fringes and a Mediterranean climate in the south-eastern part. From 2008 to 2017, we conducted three sampling campaigns of two consecutive years to sample a total 100 grassland fields (50 in 2008–2009, 16 fields in 2014–2015 and 34 fields in 2016–2017) spread along wide latitudinal and elevation gradients. Each grassland field was sampled in only one sampling campaign. All licences and permits to carry out the work were obtained from local authorities and landowners when required.

## 2.2 | Climate, topography, soil and management data

For each grassland field, we gathered information on climate and topographic factors from databases, as well as local management practices and pedological information:

*Climate*—Climate data were collected for each field using the SAFRAN database (Le Moigne, 2002). We extracted four variables of temperature and five of precipitation that were averaged yearly over a period of 20 years, and we computed indexes of drought severity (DS) (Figure S2).

To identify the key climatic variables to consider in our analyses, we conducted a principal component analysis (PCA). The climate variables were well explained by three PCA axes that accounted for 91% of the variance (Figure S2). Based on this analysis, we selected three uncorrelated climatic variables: (i) the mean daily temperature from 2000 to 2019 (hereafter MAT) ranging from 6.7°C to 12.2°C; (ii) the average yearly sum of precipitation from the same period (hereafter MAP) ranging from 665 to 1490 mm; and (iii) the drought severity index calculated 10 years before the sampling date in each field (hereafter DS) ranging from 1000 to 1800 (see Luna et al., 2023; McKee et al., 1993). MAT was highly correlated with elevation ($r = -0.92$) and was related to the length of the growing season separating cold mountain climate from warmer lowland areas.

### 2.2.1 | Topography

Topography indicators (slope and their aspects) were obtained from the Copernicus Land Monitoring Service geographical database (© European Union, 2016, resolution 25 × 25 m). Aspect was converted to an angle from the longitudinal axis, and cosine and sine of the aspects were calculated according to a reference frame where the x-axis corresponded to the longitudinal axis and the *y*-axis corresponded to latitude, allowing us to measure aspect quantitatively according to two variables: coordinate of the aspect angle along the longitudinal axis and along the latitudinal axis (Maestre et al., 2022).

### 2.2.2 | Soils

Soil attributes were assessed from physico-chemical analysis of four soil cores (8 cm in diameter to a depth of 10 cm) collected within each grassland field in spring 2009 for grasslands monitored in 2008 & 2009, and in autumn 2016 for the others. The four soil cores were pooled to make one homogenous sample per grassland field. We focused on soil pH (water pH) and sand content, two major soil variables that well reflect the bedrock (calcareous vs. siliceous bedrock) and soil texture (Le Bagousse-Pinguet et al., 2017), respectively. Sand data were obtained using the LUCAS Topsoil Database (2015). The pH ranged from 4.7 to 7.8. The sand content ranged from 32% to 62% dry soil mass.

### 2.2.3 | Management

We assessed management during both years of sampling campaign using documents filled by farmers, completed by interviews conducted by local farm advisors during winter of both years of the field campaign. When necessary, mandatory administrative documents for fertilization management were consulted. Management information includes:

(i) The total amount of nitrogen fertilization, including both mineral and organic fertilizers, expressed in kg $ha^{-1}$ was assessed. When mineral fertilizers were used, the nitrogen content of the fertilizer was directly used to convert fertilization to kg of nitrogen, by averaging values of both monitoring years. When organic fertilizers were used, we used local reference value of nitrogen content used by local farm advisors that provides the advantage of fitting local studied farming systems, this to make our quantification of fertilization input the most accurate as possible. Mean annual fertilization ranged from 0 to 316 kg N $ha^{-1}$, with a mean total nitrogen fertilization of 62.5 kg N $ha^{-1}$ and a standard deviation of 56.4 kg N $ha^{-1}$. In our sample, total fertilization was driven by organic fertilization, as it accounted for 73% of total fertilization.

(ii) The prominent type of herbage use was calculated according to Luna et al. (2023) as the difference between the total number of grazing periods and of cuts along a 2-year period; positive values indicated the predominance of grazing, negative values indicated the predominance of cutting, while zero indicated equal numbers of grazing periods and cuts.

## 2.3 | Biodiversity data

In each sampled field, the dominant vegetation facies (i.e. a core area of homogenous vegetation, management, topography and soil characteristics) was identified by a botanist of the French National Botany Conservatory, expert to perform the survey. Botanical surveys were conducted in the 3 × 9 m fenced plots (2 per field), avoiding locations near edges of fields and trees as our survey focuses on open grasslands. Surveys were done by the botanists, according to the Braun-Blanquet method at the flowering peak (i.e. 1200 degrees-days, calculated as the sum of mean daily accumulated temperature since February 1st), in spring of two consecutive years of survey. All present plant taxa were identified at the species level.

From the survey, we assessed plant species richness as the average of the total number of plant species observed in a same facies for the 2-year survey, that is in both fenced plots. The species richness value ranged from 12 to 54 species per facies.

## 2.4 | ES data

We assessed six ESs classified according to the three categories of grassland ESs (Haines-Young & Potschin, 2018): 'provisioning', 'regulation and maintenance' and 'cultural' ESs (see Table S1 for detailed methods for each ES). Provisioning ESs were productivity and fodder quality (detailed in Figure S3). Regulation ESs included carbon stock, stability of NDVI and pollination. The cultural ES was local rarity of plant.

## 2.5 | Data preparation

We calculated multifunctionality using the *Z* scores of the six measured ESs in each grassland (Maestre et al., 2012). First, we standardized each ES separately using the *Z* score transformation as follows:

$$Z\ \text{score}_{ij} = \frac{\text{ES}_{ij} - \text{Mean ES}_i}{\text{SD}_i} \qquad (1)$$

where $\text{ES}_{ij}$ is the value of ES *i* in grassland field *j*, $\text{MeanES}_i$ is the mean value of ES *i* calculated for the 100 studied grasslands, and $\text{SD}_i$ is the standard deviation of ES*i,j* calculated for the 100 studied grasslands. We then obtained multifunctionality for each grassland field *j* as the average of the *Z* scores of the six ES assessed.

The average approach may provide biased estimations of multifunctionality if trade-offs among services occur (Byrnes et al., 2014). For instance, the same multifunctionality level can be obtained if all ESs performed at an intermediate level or if some ESs performed at a high value while others performed at a low value. The ESs considered in our study showed weak correlations among them (Figure S4). However, to ensure that our estimation of multifunctionality was not biased by a single ES driving multifunctionality, we also considered a threshold approach of multifunctionality (Byrnes et al., 2014). This approach counts the number of ESs that reach or exceed a given threshold (as the percentage of the maximum value of each of the services observed in the dataset). This maximum was taken as the average of the top 5% values for each ES observed across all study sites to avoid giving too much importance to extreme values. Multifunctionality was calculated for three thresholds (Figure S4).

## 2.6 | Statistical analyses

We conducted all statistical analyses using the statistical software R v.4.3.1. (R Core Team, 2023), the dataset is available on public repository (Allart et al., 2024).

### 2.6.1 | Multifunctionality

We conducted a confirmatory path analysis using the d-sep approach to identify the drivers of grassland multifunctionality. This method is analogue to structural equation modelling analysis (Lefcheck et al., 2015) and allows to consider interactions among variables and non-linear relationships (Shipley, 2009) (Figure 1). The d-sep approach is based on the acyclic graph that describes the hypothetical relationships and independence claims between variables (Figure 1), the latter being tested using the C-statistic (Table S3). Here, we tested for direct and indirect linkages and interactive effects of climate (MAP, MAT, DS), grassland management intensification (fertilization) and local plant diversity (species richness) on multifunctionality.

Prior to confirmatory path analysis, linear models of plant species richness and multifunctionality (Y) were preliminarily fitted separately to test relevant interactions among predictors and quadratic effects. We considered quadratic effects for climatic, soil and management variables to account for potential non-linear effect on species richness and multifunctionality (Maestre et al., 2022). They were then included when significant in the confirmatory path analysis. Following Shipley (2016), we also considered a series of covariables to control for the potential effects of topo-edaphic parameters (slope, aspect, pH, sand content) and the campaign of sampling (2008, 2014 or 2016, considered a categorical factor). Prominent use of herbage was also considered a covariable. The model took the following form (see Supplementary Text 1 for R script):

$$\begin{aligned}
&\text{Y}\tilde{}\,\text{Year} + \text{slope} + \text{Aspect 1} + \text{Aspect 2} + \text{pH} + \text{pH}^2 + \text{Sand} \\
&+ \text{MAT} + \text{MAP} + \text{DS} + \text{MAT}^2 + \text{MAP}^2 + \text{Fertilization} \\
&+ \text{Fertilization}^2 + \text{Prominent herbage use} + \text{MAT: Fertilization} \\
&+ \text{MAP: Fertilization} + \text{DS: Fertilization} + \text{SR} + \text{SR: MAT} \\
&+ \text{SR: Fertilization} + \text{SR: MAP} + \text{SR: DS}
\end{aligned}$$

We used linear models with the function *lm* in the package R *lme4* (Bates et al., 2015), and the most parsimonious linear model was chosen according to AIC with the step AIC function from the MASS package in R (Venables et al., 2002). The variance inflation factor was used to detect and limit excessive multicollinearity possibly induced by interactions with the vif() function from the R package car (Fox & Weisberg, 2019). All quantitative predictors were scaled before building the models and were not correlated (Figure S5, raw data in Figure S6), allowing us to compare predictors contributions to explained variability using standardized regression coefficients.

We calculated the relative importance of fertilization, climate and species richness direct effects on multifunctionality using the scaled estimates multiplied by the adjusted $R^2$ of the models to adjust the estimate to the share of variance in multifunctionality explained by the different predictors. We calculated the relative importance of the direct and indirect effects of each predictor using estimates of climate and fertilization effects on species richness following Le Bagousse-Pinguet et al. (2017).

### 2.6.2 | Individual ESs

Finally, we evaluated the effect of climate, management and species richness on each ES by testing the same linear models as for multifunctionality.

## 3 | RESULTS

The average and threshold indices of multifunctionality were highly correlated, and both approaches provided very similar results (Figure S4). For simplicity, we thus focus hereafter on the average approach for presenting and discussing our results.

### 3.1 | Predictor importance: Species richness drives grassland multifunctionality

We show that plant species richness interacted with Mean Annual Temperature (MAT) and fertilization to determine ecosystem multifunctionality through direct and indirect pathways (adj $R^2$=0.37, Figure 2, see Tables S2 and S3). For direct effects, species richness

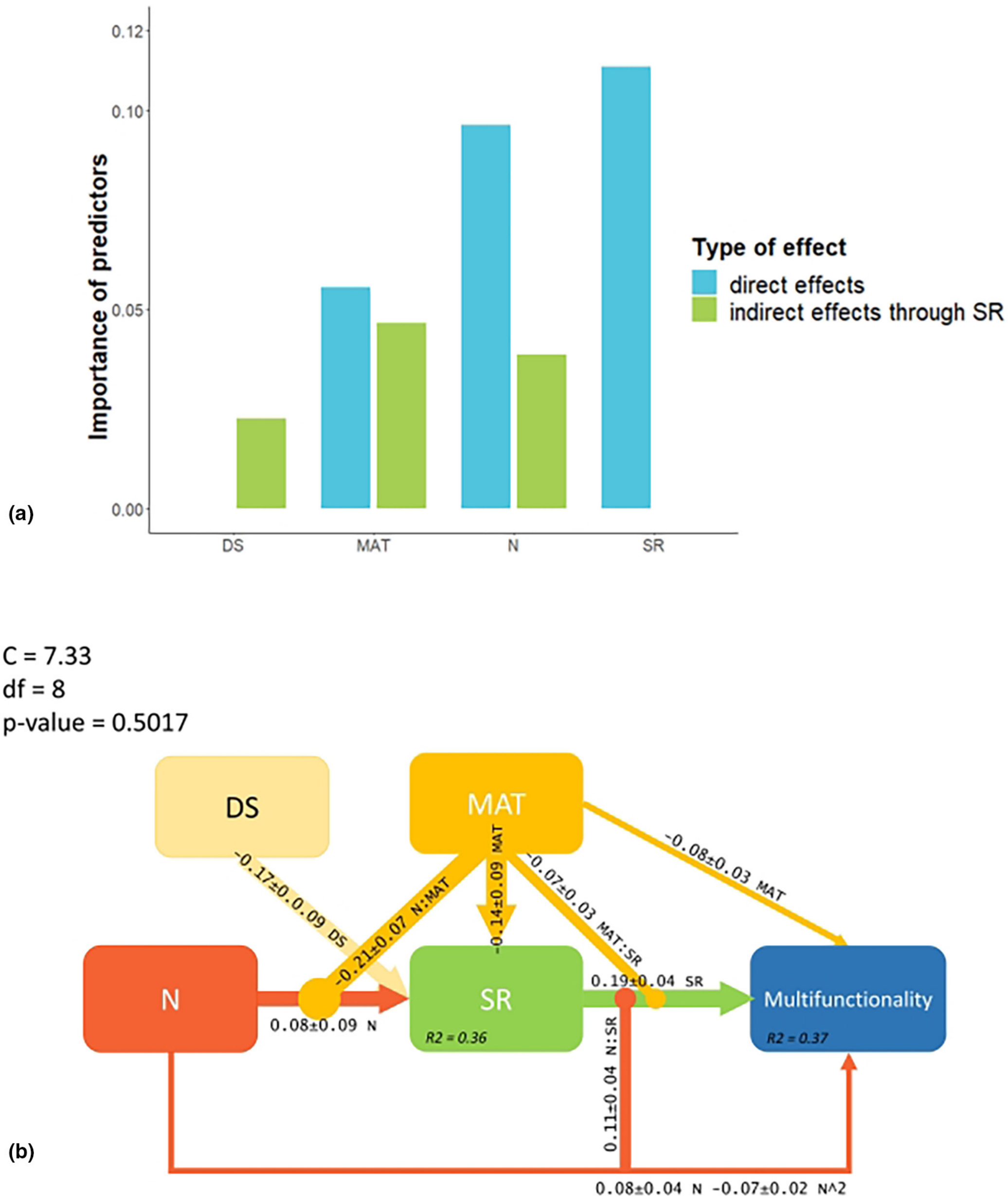


FIGURE 2 Species richness mediated the effect of climate and management on multifunctionality. (a) Relative importance of direct and indirect effects for each predictor for multifunctionality: mean annual temperature (MAT), drought severity (DS), fertilization (N) and plant species richness (SR). (b) Directed acyclic graph depicting the relationships between climate, fertilization, species richness and multifunctionality. Arrows indicate significant relationships between variables. We modelled each link using linear models. We provide a standardized path coefficient along each arrow. Dot-ended arrows indicate interactive effects. We provide the C-statistic of the path analysis (C), degree of freedom (df) and $p$ value. Detailed tests for each independence claim are available in Table S2.

was the main driver of multifunctionality (Figure 2a, see Figure S7 for direct effects with variable number of ESs). The total contribution of species richness and its interactions with fertilization and MAT accounted for 57% of the explained variance in multifunctionality (Figure S8): the main effect of species richness accounted for 29%, and the two interacting effects species richness × fertilization and species richness × MAT accounted for 28% of the explained variance. Drought Severity (DS) did not influence multifunctionality directly but indirectly through a marginally significant effect on species richness ($p = 0.058$, Figure 2). Among the covariables, the prominent type of herbage use was selected in the final best model and accounted for 8% of the explained variance. Importantly, the indirect effects of fertilization and MAT mediated by species richness were as important as their direct effects on multifunctionality (Figure 2a). Mean Annual Precipitation (MAP) alone or in interactions with other drivers was not selected in species richness nor in multifunctionality models (Table S2) and thus was not considered in the path analysis.

### 3.2 | Direct effects of climate, management and species richness on multifunctionality

Species richness correlated positively with higher multifunctionality (Figure 2b). However, its effect was mediated by fertilization and MAT as significant interactions between species richness and fertilization, and species richness and MAT were selected in the final best model (Table S2). The species richness × fertilization interaction indicated that the effect of species richness was stronger in fertilized grasslands than in unfertilized grasslands (Figure 3a). Unfertilized grasslands showed a constant and intermediate multifunctionality level (from 0.5 to 0.6), irrespective of the species richness observed within grassland fields. Fertilized grasslands showed a sharp increase in multifunctionality as species richness increased (from 0 to 1) (Figure 3a). Species-poor and fertilized grasslands showed the lowest level of multifunctionality due to a negative and non-linear effect of fertilization occurring in these grasslands (Figure 3b). In species-rich grasslands,

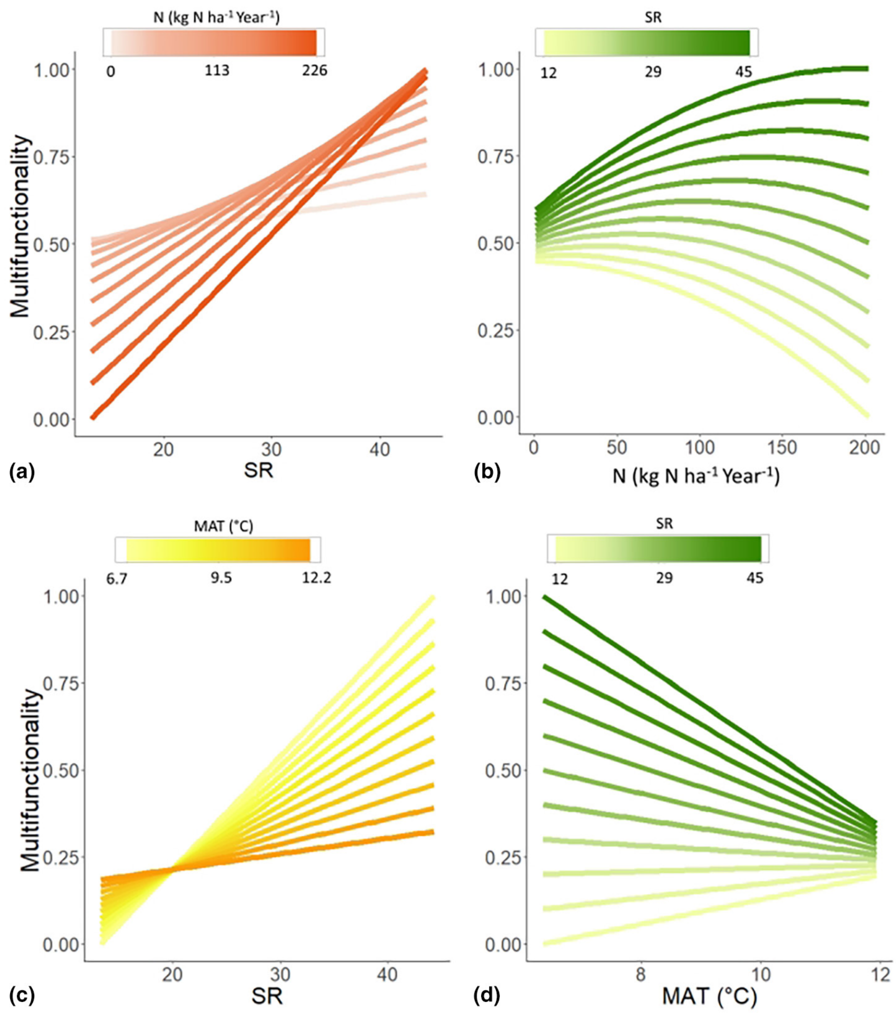


FIGURE 3 Direct effects species richness (SR), fertilization (N, kg N $ha^{-1}$ $year^{-1}$) and MAT on multifunctionality. Panels (a) and (b) show the interactive effect of SR and N on multifunctionality. Panels (c) and (d) show the interactive effect of SR and MAT. We calculated the effects of each interaction using the standardized path coefficient from Figure 2. All other standardized parameter estimates were fixed at their mean value. The colour scale intensity indicated changes in N (red colour scale in panel a), MAT (yellow colour scale in panel c) and SR (green colour scale in panels b and d). In each coloured scale, we indicated the lowest and highest values for N, MAT and SR.

multifunctionality reached a plateau for high levels of fertilization (>100 kg N $ha^{-1}$; Figure 3b).

The effect of species richness on multifunctionality was strong in cold grasslands and weak in warm grasslands due to a significant species richness × MAT interaction (Figure 3c). Accordingly, increasing MAT decreased multifunctionality in species-rich grasslands, while multifunctionality remained constantly low in species-poor grasslands independent of MAT (Figure 3d).

## 3.3 | Species richness mediated indirect effects of climate and fertilization on multifunctionality

MAT and fertilization influenced multifunctionality through indirect effects, as they both modified local species richness (Figure 2b). Variations in local species richness resulted from the MAT × fertilization interaction (Figure 4) and, to a lesser extent, from a negative effect of DS (Figure 2b). Increasing fertilization decreased species richness in warm grasslands (MAT > 9°C), while fertilization benefited species richness in cold grasslands (MAT<9°C) (Figure 4a). Furthermore, species richness sharply declined as MAT increased in fertilized grasslands, while it was not affected by MAT in unfertilized grasslands (Figure 4b).

Species richness response to both MAT and fertilization resulted into variations in grassland multifunctionality. Using the standardized path coefficient from path analysis, we calculated the effect of MAT and fertilization on multifunctionality accounting for their total effects, including direct and indirect effects mediated by species richness (Figure 5). Increasing fertilization had a strong positive effect on multifunctionality in cold upland grasslands (Figure 5a). This positive effect of fertilization can be explained by the positive effect of fertilization increasing local species richness in cold environments (MAT < 9°C) (significant MAT × fertilization interaction conferred an indirect effect, Figure 4a) and the fact that multifunctionality was maximum in species-rich and fertilized grasslands (significant richness × fertilization interaction conferred a direct effect, Figure 5b). In warm grasslands (MAT > 9°C), increasing fertilization decreased multifunctionality non-linearly, with a decline occurring when the fertilization level exceeded 100 Kg N $ha^{-1}$ $year^{-1}$ (Figure 5a). Consequently, increasing MAT had a strong negative effect on multifunctionality in fertilized grasslands, while it had no effect on multifunctionality in unfertilized grasslands (Figure 5b).

## 3.4 | Predictor effects on single ES

The effect of species richness on individual ESs was highly variable, generally weak and strongly ES-dependent (Figure 6). The explanatory power of the ESs models varied from moderate for stability and productivity (e.g. adj $R^2$ = 0.20 and adj $R^2$ = 0.26, respectively, Figure 6) to high for local plant rarity (e.g. adj $R^2$ = 0.74, Figure 6). The contributions of species richness and its interactions with MAT, MAP, DS or fertilization did not exceed 26% of the explained variance in 5 out of 6 ESs models. MAT was the only predictor to explain variability in productivity, apart from soil and topography and contributed to 39% of the explained variance. Prominent herbage use and fertilization contribution as additive effects or in interaction in models ranged from 0% in productivity model to 56% for forage quality (where prominent type of herbage use, fertilization quadratic effect and fertilization × species richness interaction were selected). Model parameters for each ESs are available in Table S2.

# 4 | DISCUSSION

There is an emerging consensus that biodiversity is a key driver of ecosystem multifunctionality (Lefcheck et al., 2015; Maestre et al., 2012) and may determine in large part the response of

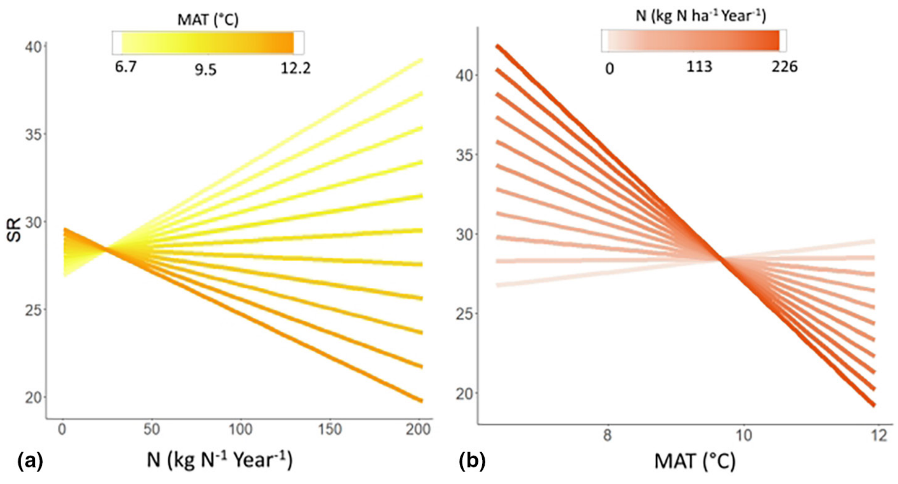


FIGURE 4 Direct effects of fertilization (N) and MAT on species richness (SR). We calculated the predicted effects using the standardized path coefficient from Figure 2. The colour scale intensity indicates the level of MAT (yellow colour scale in panel a) and fertilization (red colour scale in panel b). In each coloured scale, we indicated the lowest and highest values for MAT and fertilization, respectively.

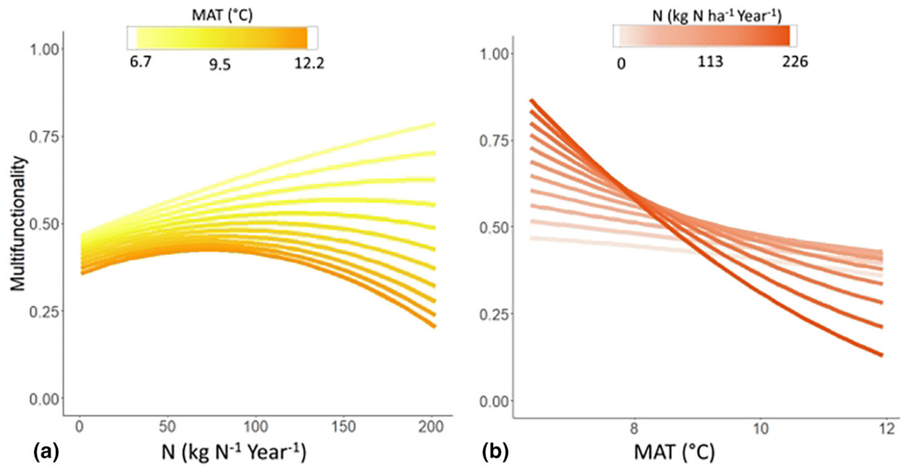


FIGURE 5 Direct and indirect effects of fertilization (N) and MAT on multifunctionality. We calculated the predicted effects using the standardized path coefficient from Figure 2. The colour scale intensity indicates the level of MAT (yellow colour scale in panel a) and fertilization (red colour scale in panel b). In each coloured scale, we indicated the lowest and highest values for MAT and fertilization, respectively.

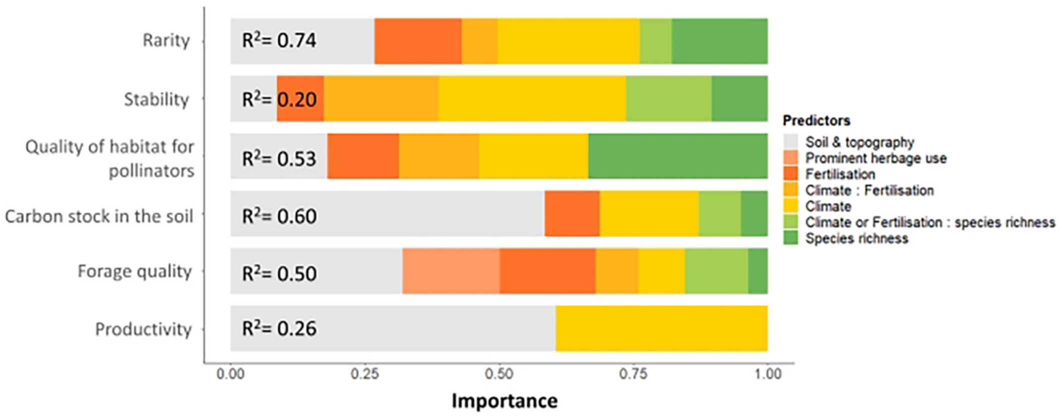


FIGURE 6 Contributions of climate, land use intensification and plant species richness to each individual ecosystem service. The importance of predictors is expressed as the percentage of explained variance (model $R^2$ express total variances), taken as the absolute value of their standardized regression coefficients. Climate included the summed contributions of mean annual temperature and drought severity in best fit models (lowest AIC, see Table S2). Soil and topography included the summed contributions.

ecosystems to ongoing global change (Maestre et al., 2022). However, determining the role of biodiversity in real world conditions remains challenging (Hagan et al., 2021). By considering multiple ecosystem services (ESs) simultaneously—that is multifunctionality—in a regional grassland survey, our study shows that plant species richness was the main driver of multifunctionality (Figure 2), although its importance was more variable and generally weaker when considering each ES separately (Figure 6; Lefcheck et al., 2015). More importantly, our study highlights the pivotal role of species richness in mediating the effect of climate and land use intensification. We identified pervasive interactions between climate and fertilization acting both directly and indirectly through changes in local species richness on multifunctionality, consistent with our hypotheses (Figure 1). The importance of the direct effects of climate and management was as important as their indirect effects mediated by species richness (Figure 2a). Therefore, accounting for the interdependence between biodiversity, management practices and climate may be critical to anticipate the impact of multiple global change drivers on grassland multifunctionality.

## 4.1 | Temperature mediates the effects of biodiversity and fertilization on multifunctionality

By investigating the effect of fertilization across wide elevational and latitudinal gradients, our study reveals the key role of mean annual temperature (MAT) in mediating the effect of management practices and biodiversity on grassland multifunctionality.

In cold upland grasslands, fertilization increased both species richness and multifunctionality. A global meta-analysis by Humbert et al. (2016) showed that the fertilization effect on species richness is highly variable and can sometimes be positive in cold environments such as upland grasslands. Accordingly, fertilization in upland grasslands has been shown to increase the abundance of productive forage plant species at higher elevations (e.g. grass species such as *Arrhenatherum elatius*, *Dactylis glomerata*, *Lolium perenne* and legume species such as *Trifolium pratense* and *Medicago* sp.) (Quétier et al., 2007). Cold mountain environments also limit the extent to which plants can respond to nitrogen supply (Cross et al., 2015), decreasing the competitive ability of these species (Grime, 1973) and promoting their coexistence with slow-growing species originating from higher elevations (Gross et al., 2007). Altogether, our results suggest that current land use intensification acts synergistically with the cold climate of mountain areas to promote highly diverse and multifunctional grasslands (resulting from MAT × fertilization interaction on plant species richness; and MAT × plant species richness interaction on multifunctionality, Figure 2). However, by unravelling the complex interdependency between MAT, species richness and fertilization, our study suggests that such observations may only apply to specific climatic contexts.

In warm lowland grasslands, fertilization had an opposite effect by decreasing both species richness and multifunctionality. More precisely, multifunctionality decreased non-linearly when fertilizer inputs exceeded a certain quantity (above ~100 kg N $ha^{-1}$, see Figure 5a). This non-linear effect of fertilization is consistent with observations from managed grasslands in Germany (Saiz et al., 2022), where a land use intensification threshold above which species richness and grassland multifunctionality dramatically decreased, was identified. Fertilization and associated intensive agricultural practices are known to increase grassland biomass, favouring productive and competitive species in warm lowland areas, threatening plant diversity (Boch et al., 2021) and decreasing grassland multifunctionality (Allan et al., 2015). Overall, our results suggest a strong temperature-dependency of fertilization effects on species richness and highlight its consequences on biodiversity-multifunctionality relationships in grassland ecosystems.

## 4.2 | Fertilization increases the dependency of grassland multifunctionality on climate

A direct consequence of the strong temperature-dependency of the fertilization effect on multifunctionality is that the grassland response to climate is strongly determined by local nitrogen inputs. We observed a sharp decline in multifunctionality as MAT increased in fertilized grasslands, a pattern that was not observed in non-fertilized grasslands (Figure 5b). This result is in line with Van Sundert et al. (2021), who showed a higher sensitivity of vegetation composition and productivity to climate change in intensively managed grasslands. The increased negative effect of fertilization on multifunctionality under a warmer climate allows us to extend this result to multifunctionality.

We identified two complementary pathways explaining the higher sensitivity of intensively managed grasslands to climate (Figure 2). First, increasing temperature may improve nitrogen availability to plants in fertilized grasslands (Cross et al., 2015). Our results are consistent with recent warming experiments conducted in mountainous grasslands in the Alps where warming has been shown to promote lowland competitive species and reduced native plant species form higher elevation (Schuchardt et al., 2023), reducing plant species richness and, as a consequence, multifunctionality. Second, the decline in multifunctionality may be further reinforced by the weakening of the positive biodiversity-multifunctionality relationship observed in warmer conditions (Figure 3c; see Jing et al., 2015 for similar evidence from the Tibetan Plateau). Together, these two complementary processes suggest that the benefit of biodiversity for ecosystem multifunctionality may decrease in a warmer climate if management practices are not adapted accordingly.

The climatic context of the French Massif central allowed us to disentangle the effect of MAT from other important climatic drivers such as mean annual precipitation (MAP) and summer-drought severity (DS; Luna et al., 2023). Although DS and MAP significantly influenced the provisioning of some individual ESs (e.g. forage quality and pollination, see Table S2 for detailed results) (see also Liu et al., 2023), they did not impact grassland multifunctionality directly. Considering the high correlation between DS and latitude (Figure S1), it suggests that Mediterranean grasslands are well adapted to summer droughts and are as multifunctional as temperate grasslands. These results are in accordance with recent findings from arid grasslands (Maestre et al., 2022), where MAT has been identified as the main climatic driver determining the effect of plant diversity and land use intensification on multiple ESs simultaneously. It further supports recent experimental evidences of a strong resistance and recovery of grassland ecosystems to drought manipulation (Van Sundert et al., 2021). However, summer droughts may become more important for grassland multifunctionality in the coming years with climate change, as droughts are predicted to become more frequent in temperate areas of the Massif Central where it used to be absent until the recent anthropogenic climate change (Spinoni et al., 2018).

## 4.3 | Increasing trade-offs among ESs in a warming climate

By further investigating the correlation among ESs (Figure S9), we found that declining multifunctionality with increasing temperature is explained by an increase in the trade-offs among services observed in warm lowland grasslands compared to colder upland grasslands (Figure S9). For instance, weak correlations among ESs were observed in high elevation grasslands (Figure S9), suggesting that these ecosystems can provide high rates of a wide variety of ESs due to synergetic effects between agricultural practices and biodiversity (Quétier et al., 2007). In contrast, in warm lowlands, grassland productivity and forage quality traded off with other ESs, such as stability, carbon storage or rarity (Figure S9). If what we observed through space occurs through time, climate change may increase the conflict between multiple stakeholders with contrasting ESs demands (Bardgett et al., 2021). In this context, preserving grassland biodiversity may be key to preventing multifunctionality decline under climate change and limiting the trade-offs between essential ESs related to food production, ecosystem stability (García-Palacios et al., 2018), climate mitigation (Maestre et al., 2022) and the biodiversity value of grassland ecosystems (Bardgett et al., 2021). Our study calls for an increased awareness of farmers to adapt their agricultural practices to prevent biodiversity loss and grassland multifunctionality degradation in a warmer world. To do so, new approaches building bridges between ecology and human sciences are being developed to improve the management of species-rich grasslands (Molnár et al., 2020) and should be promoted in the context of local adaptation to climate change.

## 5 | CONCLUSIONS

Considering that plant species richness, mean annual temperature and fertilization are major proxies of three main global change drivers—biodiversity loss, climate change and land use intensification—our study may help to better understand the effect of multiple global change drivers on grassland ecosystems. By identifying the complex relationships between management practices, climate and plant species richness in determining grassland multifunctionality, we revealed tight intertwinements between factors involved in multiple global change drivers, consistent with emerging evidence (Maestre et al., 2022; Rillig et al., 2019). Failing to account for changes in local plant species richness could thus bias any prediction of, or aggravate, the effects of land use intensification and climate change on ecosystem services delivery in temperate grassland ecosystems, one of the most threatened ecosystems on earth (Bardgett et al., 2021; Newbold et al., 2016).

## AUTHOR CONTRIBUTIONS

Lucie Allart, Nicolas Gross, Bertrand Dumont, Frederic Joly and Claire Mosnier agreed on overarching research aims; Jean-Noël Galliot contributed to data collection and organized sampling and the original database. Gaël Alvarez analysed soil samples; Donald Luna and Julien Pottier provided data on drought severity index, the prominent herbage use and the stability index; all authors agreed on statistical analyses, the manuscript structure and key messages. Lucie Allart and Nicolas Gross then led the manuscript writing. All authors contributed to the draft revisions and gave final approval for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors whose names are listed above certify that they have no affiliations with or involvement in any organization or entity with any financial interest (such as honoraria; educational grants; participation in speakers' bureaus; membership, employment, consultancies, stock ownership or other equity interest; or expert testimony or patent-licensing arrangements) or nonfinancial interest (such as personal or professional relationships, affiliations, knowledge or beliefs) in the subject matter or materials discussed in this manuscript.

## DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/doi:10.5061/dryad.5qfttdzdg (Allart et al., 2024).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Figure S1.** Map of the studied area (A) with sampled grassland fields presented according to elevation (B), as well as according to mean annual temperature (C) and sum of drought severity (D).

**Figure S2.** PCA of the climatic data from 1994 to 2014 of the grassland fields that was built to select variables necessary to assess the diversity of climatic conditions in our sample.

**Figure S3.** PCA of the chemical composition of grass samples demonstrating important trade-offs among fibre-related components (neutral detergent fibre (NDF), crude cellulosis (CC), acid detergent fibre (ADF), organic matter (OM) and mineral matter (MM)) and more nutritious variables (total fatty acids (TFA), crude protein (CP), digestibility of organic matter (DOM)). This PCA led us to choose crude protein as a proxy for fodder quality.

**Figure S4.** Correlation matrix among ecosystem services and multifunctionality calculated according to the average approach and threshold approach, with thresholds set at 25% (T25), 50% (T50) and 75% (T75).

**Figure S5.** Correlations among predictors used to model multifunctionality: mean annual temperature (MAT), mean annual precipitation (MAP), drought severity (DS), species richness (SR), and prominent herbage use, and fertilization (N).

**Figure S6.** raw data of multifunctionality (a) and species richness (SR) (b) according to the different predictors tested in the analysis: pH, Sand, slope, mean annual temperature (MAT), mean annual precipitation (MAP), drought severity (DS), Prominent herbage use, the two variables of aspects (Aspects 1 and Aspects 2) and nitrogen fertilisation (N).

**Figure S7.** Estimates of the effects of species richness (SR), SR and mean annual temperature (MAT) interaction, and SR and nitrogen fertilisation (N) interaction in the linear models to explain multifunctionality calculated with average approach.

**Figure S8.** Contributions of predictors including climate, land use intensification and plant species richness to multifunctionality.

**Figure S9.** Two PCAs of the single ES calculated with the PCA() function from the FactoMineR package, one with data from grasslands whose scaled MAT value was below 0, i.e. the coldest grasslands of the sample (in blue), and one with grassland data for which the scaled MAT was above 0, that is the warmest grasslands of the sample (in red).

**Table S1.** Presentation of ESs assessments. Productivity and fodder quality belong to the category of provisioning ESs.

**Table S2.** Table of the models obtained from stepAIC for each individual ecosystem service and multifunctionality calculated with the average approach.

**Table S3.** Table of the basis set of d-sep (directional separation) claims we tested to assure the path analysis of Figure 5 (Shipley, 2009).

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