

# Temporal trajectories of plant functional traits in mediterranean grasslands under different grazing regimes

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## Funding information

LIFE-Regenerate – Revitalizing Multifunctional Mediterranean Agrosilvopastoral Systems Using Dynamic and Profitable Operational Practices, Grant/Award Number: LIFE16 ENV/ES/000276

Co-ordinating Editor: Lauchlan Fraser

## Abstract

**Aims:** Mediterranean grasslands are semi-natural ecosystems that have been affected by land-use intensification and abandonment during the past decades. Adaptive multi-paddock grazing regimes, where grazing alternates with long periods of vegetation recovery, have been proposed as a more biodiversity-friendly management compared with continuous grazing. This study aimed to compare the effect of these two different grazing regimes on a set of plant traits in mediterranean grassland vegetation over time.

**Location:** Central part of Sardinia (Italy) at 350 m a.s.l. in a permanent grassland system.

**Methods:** We applied the point quadrat method to quantify the specific contribution of each species along permanent transects in spring and winter from 2018 to 2022. We considered the following plant traits: leaf dry matter content, life forms, flowering start and length of flowering. Overall, we performed 128 surveys and measured traits for 61 species. We ran a linear mixed model to test the effect of season, grazing regimes and years on functional diversity and community-weighted mean for single traits.

**Results:** Adaptive multi-paddock regimes over time increased the leaf dry matter content. However, compared with grazing regimes, seasonality through time had the greatest effect on flowering traits and life forms.

**Conclusion:** The relatively small variation in the plant traits suggests that the mediterranean grassland was rather stable despite wide variation in grazing regimes, probably linked to their long history of human association. Nonetheless, adaptive multi-paddock regimes may have higher beneficial effects compared with continuous grazing, favouring more palatable species and improving soil fertility. By contrast, the high variation in the plant traits over time suggests a high vulnerability of the same grassland to climatic changes.

## KEYWORDS

flowering period, functional diversity, grazing, leaf dry matter content, plant traits, seasonal variability, semi-natural grassland

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## 1 | INTRODUCTION

Mediterranean grasslands are semi-natural ecosystems whose diversity and distribution result from millennia of human land uses related to pastoral activities (Dengler et al., 2014; Malavasi et al., 2023). Driven by environmental constraints, uncertainties and socio-economic factors, rural areas experience a shift in land use, often resulting in abandonment and a loss of biodiversity and ecosystem services at local and landscape scales (Bagella et al., 2016; Bricca, Tardella, Ferrara, Xinfang, et al., 2021). Various management strategies have been developed to optimise resource use and promote vegetation regeneration. Adaptive multi-paddock (AMP) grazing is an intensive grazing strategy in which lightweight, portable fencing systems are used to move animals strategically around the grassland, allowing for dense grazing interspersed by long periods of recovery for vegetation (Clifford et al., 2020; Gosnell et al., 2020). AMP can provide tangible and substantive advantages over intensive and continuous (C) grazing in terms of environmental sustainability and vegetation regeneration (Teague & Barnes, 2017; Apfelbaum et al., 2022). For example, AMP can prevent soil erosion because of overgrazing and improve forage production (Teague et al., 2011; Frongia et al., 2023). Despite this beneficial output, the effects of AMP on Mediterranean grasslands remain poorly investigated.

Understanding and predicting the response of vegetation to management types requires consideration of functional traits besides taxonomic identity (Garnier & Navas, 2012; Fontana et al., 2021; Verdinelli et al., 2022). Functional traits provide information on species' ecological strategies, offering valuable insights into detecting the influence of biotic and abiotic conditions in shaping community diversity and composition (Cadotte, 2017; Bricca et al., 2023). Moreover, functional traits allow for the comparison of vegetation changes across different flora, thus revealing general ecological mechanisms (Díaz et al., 2007; Kahmen & Poschlod, 2008; Carmona et al., 2012; Bricca, Tardella, Ferrara, Panichella, & Catorci, 2021). Among a large number of functional traits (Perez-Harguindeguy et al., 2013), leaf dry matter content (LDMC) captures the "leaf economic-spectrum" with lower values reflecting fast-growing strategies (acquisitive species) and higher values indicating slow-growing strategies (conservative species) (Wright et al., 2004). This ecological information has important implications in grazing management because LDMC expresses the degree of palatability of the plant species: slow-growing species are generally less palatable than fast-growing species (Khaled et al., 2006), and excessive feeding of less-palatable species can harm animal welfare (Catorci et al., 2014). In addition to plant strategies related to resource exploitation, such as LDMC, other functional dimensions play a fundamental role in plant persistence. For instance, the optimal timing of flowering is crucial for plant fitness and has a crucial role in community assembly. The timing of flowering depends on multiple factors like abiotic conditions (temperature and the availability of water, nutrients and light; Kehrberger & Holzschuh, 2019) and biotic conditions (species interaction, community structure, above-ground biomass; Catorci et al., 2017). A prolonged vegetative development period with

late flowering is an ideal growing condition, whereas early flowering is a strategy for a brief or unpredictable growing season (Roux et al., 2006). Furthermore, grazing management practices, such as high stocking rates, can lead to more ruderal vegetation by favouring therophyte species and decreasing other life forms like phanerophytes and geophytes (de Bello et al., 2005; Giarrizzo et al., 2017). The effect of different management practices on semi-natural grassland has mainly been investigated without including a temporal gradient (de Bello et al., 2005; Sebastià et al., 2008; Catorci et al., 2012, 2014; Bonari et al., 2017). Very few studies consider the effect of grazing management over time (Carmona et al., 2012; Giarrizzo et al., 2017). Time is fundamental because assessing the temporal trajectory of changes in vegetation is pivotal for distinguishing between short-term fluctuations in responses to immediate disturbances and gradual shifts in plant composition and diversity over the long term (Kahmen & Poschlod, 2008; Doležal et al., 2011; Bricca, Tardella, Ferrara, Panichella, & Catorci, 2021; Piga et al., 2023).

However, the impact of different livestock management over time on Mediterranean grasslands is less explored compared with temperate grasslands. Mediterranean grasslands are characterised by a longer history of grazing, and higher seasonality in resource availability that favour the growth of annual species, meaning they complete their life cycles before the summer drought (Sternberg et al., 2000; Xu & Baldocchi, 2004; Malavasi et al., 2023; Midolo et al., 2024). Intra-annual fluctuations in weather conditions are expected to promote the coexistence of different species, leading to advantages in some years and boosting temporal biodiversity (Facelli et al., 2005; Elmendorf & Harrison, 2009; Fischer et al., 2020). Therefore, accounting for the impact of management practices across different seasons is crucial for understanding how these practices influence changes in vegetation over time (Sternberg et al., 2000). This knowledge enhances the relevance and applicability of management practices, providing valuable tools for rational management both in terms of conservation and sustainable animal production in the face of climate change.

In this study, our main objective is to investigate the effect of two grazing regimes (AMP and C), seasonality (spring and winter) and their interaction over time on the functional dimension of plant communities. We expect that: (a) AMP enhances functional diversity and composition over time compared to continuous grazing; and (b) plant community over time will depict temporal trajectories depending on the specific season.

## 2 | METHODS

### 2.1 | Study area

The study site was located on a private farm in the central part of Sardinia (Italy) at 350 m a.s.l. (40°8'N – 8°35'E) in a permanent grassland system. The geological substrate belongs to the Plio-Pleistocene volcanic cycle with alkaline, transitional and subalkaline affinity, belonging to the massif of Montiferro (Carmignani

et al., 2016). The climate is mediterranean marked by intense summer drought stress but milder winters. The lowest average minimum temperatures are recorded in January and February (5.2°C), whereas the highest average maximum temperatures occur in July (30.9°C) and August (29.8°C). The rainiest months are November (117.1 mm) and December (110.4 mm), and the driest month is July (6.7 mm) (Arpas, 2019). Average monthly temperatures and monthly precipitation recorded year by year during the study period are reported in Appendix S1. The plant landscape is characterised by the calcifugal, meso-supramediterranean cork oak series, specifically *Violo dehnhardtii-Quercu suberis* Σ (Piga et al., 2023).

The farm is a typical example of a mediterranean agro-silvo-pastoral system. Livestock grazing on the farm comprises two breeds of cow: Charolaise and Sardo-Modicana. The animals' diet combines direct grazing on available forage in permanent grasslands and hay produced on the farm. Hay is mainly provided during the summer season when the seasonal water deficit causes vegetation senescence, during autumn and winter in case of long drought periods that also affect the autumn season, or during winter in case of snow events. In addition, external feed supplements (steam-flaked corn, barley, beet pulp and pellets) are used to meet the nutritional needs of the animals. The farmer employs a vertical transhumance system, which involves the seasonal movement of livestock from mountainous areas to valley regions. Specifically, during the summer and autumn seasons, animals graze the mountain farm units (ca. 900 m a.s.l.). In the winter, animals are moved from the mountain to the hilly farm units (ca. 400 m a.s.l.) to handle births, and they stay there during the spring, during which cattle with suckling calves graze in grasslands that are not mown for hay production.

## 2.2 | Experimental design and vegetation sampling

We set up an experiment to compare the AMP with the conventional C grazing system. AMP involves rotational cattle with high instantaneous stocking rates and resting periods long enough to allow optimal plant regrowth. This management practice has been recommended for decades as a potential tool to manage rangelands to sustain forage productivity and improve livestock management (Clifford et al., 2020). According to the length of the vegetative season in the mediterranean climate, the area of AMP was divided into eight paddocks of 0.3 ha under the same vegetation type and macro-environmental conditions (i.e., elevation and bedrock soil). Considering the whole grazing area, the average stocking rate during the year was ca. 1.5 livestock units (LSU) per hectare. Under AMP, animals grazed with an instantaneous stocking rate of up to 20.6 LSU/ha for 3–8 days in one paddock and then moved to another paddock. This allows each paddock to rest (time from one grazing event to the second grazing event in the same paddock) for 21–35 days. The experiment started in 2018 and vegetation was monitored over the years. Vegetation sampling was carried out during the flowering season in spring and at the second vegetative regrowth between the end of autumn and the start of winter when the plants were well-developed. Indeed, both in summer and at the

TABLE 1 Timeline of seasonal assessments (spring and winter) for 2018–2022.

Assessment	Spring	Winter
Time 0	April 2018	November 2018
Time 1	May–June 2019	December 2019–January 2020
Time 2	May 2020	January 2021
Time 3	April–May 2021	January 2022

beginning of autumn vegetation is in senescence. Because the entire experiment took place on a farm that had been managed with continuous grazing for an extended period, we could only establish baseline data for the AMP grazing system. However, because the site conditions are consistent, we used AMP grazing as the treatment group and continuous grazing as the control group to analyse temporal trends. The assessments conducted during the spring and winter seasons were categorised according to Ciaccia et al. (2022) and are reported in Table 1. We performed vegetation surveys along eight linear permanent transects (replicates) inside the paddocks (AMP) and eight linear transects in the control area (C) (Appendix S2) based on the point quadrat method (Daget & Poissonet, 1969). The surveys were conducted by moving along the transect of 50 m with a stick at a regular interval of 1 m, recording all the species that were touched by the stick during each descent. In total, 128 surveys were performed under the same micro-environmental conditions (i.e., slope 0° and absence of aspect) to avoid a confounding effect of environmental conditions and the management type (Tardella et al., 2020).

The frequency of occurrence of each plant species ( $FS_i$ ) recorded along each transect was converted into cover species percentage (CSP) using the formula:

$$CSP_i = \frac{FS_i}{\sum FS_i} \times 100$$

We used the CSP of each plant species in every transect to construct a matrix representing the species cover across various years and seasons.

## 2.3 | Functional traits collection

As an indicator of species' ecological strategies, we considered the following plant traits: LDMC, life form (LF), start (SF) and length (FL) of flowering time. We measured the LDMC for all those species whose relative contribution accounted for at least 80% of the total species covered in all transects (i.e., the entire database). This choice relies on the assumption that the ecosystem's functioning and services depend strongly on the dominant species (biomass-ratio hypothesis; Grime, 1998). We followed the standardised global protocol of trait measurements. It indicates collecting ten mature leaves from different individuals of each selected species (Perez-Harguindeguy et al., 2013). We avoided leaves with clear signs of disease or herbivory. The leaves were put in plastic bags with water. Collected leaves were weighted to obtain fresh-watered weight (g)

within 48 h in the refrigerator. Further, we put the leaves in an oven at 70°C, and we determined the dry weight (mg).

Regarding the LF, we considered the following groups (Raunkiær, 1934): phanerophytes, nano-phanerophytes, chamaephytes, hemicryptophytes, geophytes and therophytes (Pignatti et al., 2017). Lastly, the information about the start of flowering (ordinal trait from 1 to 12 representing the months) and its length in number of months (end of flowering minus start of flowering) was retrieved from the open-source website Acta Plantarum (<https://www.actaplantarum.org>). However, using the ordinal number of months (e.g., January 1, February 2, ... December 12) can introduce a bias because of the end-of-year transition in the data. Ranking months on such an ordinal scale means that species flowering in January and December have maximum functional distance (1 vs 12) even if the temporal distance is of 1 month. Therefore, to avoid this mismatch between temporal distance between months and functional distance between species, we considered the species flowering trait ranging from 1 (December) to 7 (June).

## 2.4 | Statistical analysis

We calculated the community-weighted mean (CWM) and the functional diversity (FD) to summarise two main facets of the functional plant community combining the CSP and the plant traits (Ricotta & Moretti, 2011). The CWM is widely used to assess the variation of dominant functional strategies along environmental gradients. In the case of a categorical trait (e.g., LF), the index provides the relative frequency of each trait state. As a measure of FD, we considered Rao's quadratic entropy. It expresses the functional dissimilarity between two individuals of a given assemblage selected at random (Botta-Dukat, 2005):

$$FD = \sum_{ij} d_{ij} p_i p_j$$

where  $S$  is the number of species,  $d_{ij}$  is the distance or dissimilarity between the  $i$ -th and  $j$ -th species, and  $p_i$  and  $p_j$  are the specific contributions of  $i$ -th or  $j$ -th species in the transect. As a measure of trait dissimilarity ( $d_{ij}$ ), we selected Gower's distance (Pavoine et al., 2009). We calculated FD and CWM for each trait (LDMC, LF, SF and EF) for each transect with the dbFD function in the FD package (Laliberté et al., 2014). Before calculating the functional indices, LDMC was  $\log_{10}$ -transformed to have a normal distribution (Májeková et al., 2016).

To test for the effect of the interaction between grazing regimes (AMP vs C grazing), season (spring and winter) and time (years) on CWM and FD of every single trait, we fit linear mixed-effect models. In the model, we included grazing, season and time (all categorical variables) as main effects alongside all their pairwise interactions (grazing  $\times$  seasonality; grazing  $\times$  time; seasonality  $\times$  time; grazing  $\times$  seasonality  $\times$  time). In addition, to account for repeated measures over time, we included the transect as a random factor. To test the significance of factors and their interaction included in the

model; we then performed the analysis of variance (ANOVA). We estimated the conditional and marginal explained variance ( $R^2$ ) of each of the mixed models. Marginal  $R^2$  represents the variance explained only by the fixed effects of each mixed model, whereas conditional  $R^2$  accounts for the amount of variance explained by fixed and random effects (Nakagawa & Schielzeth, 2013). Model assumptions, namely normality, homoscedasticity and independence of residuals, were evaluated by visual inspection of residual patterns (Zuur et al., 2010). Models were run with the "lme" function in the *nlme* package (Pinheiro et al., 2023), ANOVA was conducted with "anova" function in the *stat* package (R Core Team 2023, version 4.3.1), and marginal and conditional  $R^2$  were calculated with the "r.squaredG-LMM" function in the *MuMIn* package (Bartoń, 2023).

## 3 | RESULTS

Overall, we found a total of 250 species, of which 61 (Appendix S3) accounted for 80% of the CSP in all transects.

All the results of the ANOVA model on linear mixed models for FD and CWM are reported in Tables 2 and 3. Regarding  $FD_{LDMC}$ , we found a significant effect of season and its interaction with time (Figure 1a).  $FD_{LF}$  shows a significant effect of time and season and their interaction (Figure 1b). The analysis of  $FD_{SF}$  showed significant effects for the season and its interaction with time (Figure 1c), whereas  $FD_{FL}$  was affected by season, time and their interaction (Figure 1d).

Regarding the CWM, the linear mixed-effect model of the  $CWM_{LDMC}$  detected a significant effect of season and its interaction with the grazing regime and time (Figure 2a). Regarding the LF, we found a significant effect on the CWM of chamaephytes for the grazing interacting with the season (Figure 2b). For the CWM of geophytes and therophytes, we found a significant effect of time and the interaction of season with time, but therophytes also exhibited significant variation with seasonality (Figure 2c-e). Further, for CWM of hemicryptophytes, we found the effect of time and season, and the interaction of season with the grazing regime and with time, but also the interaction between the grazing regime, season and time (Figure 2d). CWM of nanophanerophytes showed significant variation only with the interaction between season and time (Figure 2e). Regarding the flowering strategies, we found that, for CWM at the start of flowering there is a significant effect of season and its interaction with time (Figure 2h). Lastly, for CWM of flowering length, we found a significant effect for season, time and their interaction (Figure 2i).

## 4 | DISCUSSION

This study investigated the mid-term effects of grazing regimes and seasons on the functional dimension of mediterranean grassland communities. One of the major findings of this study is that the mediterranean grassland showed different temporal trajectories mostly in response to intra-annual meteorological conditions compared with

**TABLE 2** Results of the linear mixed-effect models of the functional diversity for leaf dry matter content (LDMC), life form (LF), start of flowering (SF) and flowering length (FL).

	LDMC	LF	SF	FL
Grazing	0.03 <sup>n.s.</sup>	0.67 <sup>n.s.</sup>	0.64 <sup>n.s.</sup>	1.75 <sup>n.s.</sup>
Seasonality	<b>59.06***</b>	<b>9.44**</b>	<b>121.34***</b>	<b>30.71***</b>
Time	2.13 <sup>n.s.</sup>	<b>63.32***</b>	1.36 <sup>n.s.</sup>	<b>4.53**</b>
Grazing×Seasonality	2.03 <sup>n.s.</sup>	0.06 <sup>n.s.</sup>	0.01 <sup>n.s.</sup>	1.21 <sup>n.s.</sup>
Grazing×Time	0.79 <sup>n.s.</sup>	1.09 <sup>n.s.</sup>	1.86 <sup>n.s.</sup>	0.15 <sup>n.s.</sup>
Seasonality×Time	<b>7.20***</b>	<b>21.85***</b>	<b>4.30**</b>	<b>7.23***</b>
Grazing×Seasonality×Time	1.66 <sup>n.s.</sup>	0.56 <sup>n.s.</sup>	1.39 <sup>n.s.</sup>	2.04 <sup>n.s.</sup>
Marginal R <sup>2</sup>	0.40	0.63	0.46	0.34
Conditional R <sup>2</sup>	0.48	0.71	0.62	0.49

Note: Grazing regimes (C and AMP), season (spring and winter) and time were categorical predictors included as the main effect plus their interactions. Significant effects ( $p < 0.05$ ) are highlighted in bold. *F*-values of each predictor (single and in interactions) are reported with their levels of significance (n.s.,  $p > 0.5$ ; \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ ). Marginal R<sup>2</sup> is the variance explained by only the fixed effect, whereas conditional R<sup>2</sup> is the variance explained by fixed effect plus the random effect for each model.

**TABLE 3** Results of the linear mixed-effect models of the community-weighted mean for leaf dry matter content (LDMC), life form (Ch, chamaephytes; G, geophytes; H, hemicryptophytes; Np, nanophanerophytes; T, therophytes), the start of flowering (SF) and flowering length (FL).

	LDMC	Ch	G	H	Np	T	SF	FL
Grazing	1.13 <sup>n.s.</sup>	0.79 <sup>n.s.</sup>	2.07 <sup>n.s.</sup>	1.18 <sup>n.s.</sup>	0.25 <sup>n.s.</sup>	0.52 <sup>n.s.</sup>	0.02 <sup>n.s.</sup>	1.13 <sup>n.s.</sup>
Seasonality	<b>68.84***</b>	2.19 <sup>n.s.</sup>	1.36 <sup>n.s.</sup>	<b>7.52*</b>	2.96 <sup>n.s.</sup>	<b>5.95*</b>	<b>26.55***</b>	<b>50.83***</b>
Time	1.55 <sup>n.s.</sup>	0.49 <sup>n.s.</sup>	<b>5.88**</b>	<b>53.86***</b>	1.39 <sup>n.s.</sup>	<b>54.84***</b>	2.62 <sup>n.s.</sup>	<b>30.97***</b>
Grazing×Seasonality	0.06 <sup>n.s.</sup>	<b>4.23*</b>	3.12 <sup>n.s.</sup>	2.12 <sup>n.s.</sup>	0.08 <sup>n.s.</sup>	0.01 <sup>n.s.</sup>	1.27 <sup>n.s.</sup>	1.48 <sup>n.s.</sup>
Grazing×Time	<b>4.11**</b>	0.67 <sup>n.s.</sup>	2.17 <sup>n.s.</sup>	<b>6.04***</b>	0.71 <sup>n.s.</sup>	1.51 <sup>n.s.</sup>	0.12 <sup>n.s.</sup>	2.50 <sup>n.s.</sup>
Seasonality×Time	<b>7.39***</b>	0.67 <sup>n.s.</sup>	<b>22.24***</b>	<b>5.05**</b>	<b>3.12*</b>	<b>25.17***</b>	<b>17.28***</b>	<b>20.30***</b>
Grazing×Seasonality×Time	0.20 <sup>n.s.</sup>	0.63 <sup>n.s.</sup>	1.67 <sup>n.s.</sup>	<b>3.95*</b>	0.12 <sup>n.s.</sup>	0.61 <sup>n.s.</sup>	1.44 <sup>n.s.</sup>	1.97 <sup>n.s.</sup>
Marginal R <sup>2</sup>	0.42	0.09	0.41	0.62	0.09	0.61	0.38	0.62
Conditional R <sup>2</sup>	0.52	0.24	0.51	0.65	0.45	0.70	0.49	0.65

Note: Grazing regimes (C and AMP), season (spring and winter) and time were categorical predictors included as the main effect plus their interactions. Significant effects ( $p < 0.05$ ) are highlighted in bold. *F*-values of each predictor (single and in interactions) are reported alongside their levels of significance (n.s.,  $p > 0.5$ ; \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ ). Marginal R<sup>2</sup> is the variance explained by only the fixed effect, whereas conditional R<sup>2</sup> is the variance explained by fixed effect plus the random effect for each model.

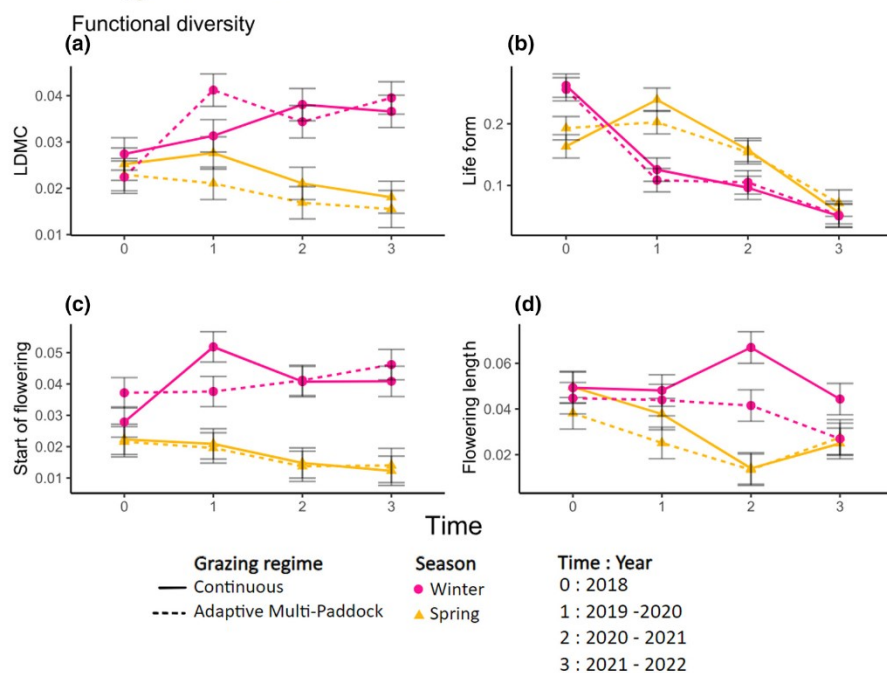
grazing regimes. These findings align with previous research documenting mediterranean grasslands being more sensitive to seasonal variation than to different grazing regimes, probably because of their long history of human association (Sternberg et al., 2000). The plant communities showed a completely different functional portfolio during the winter and spring seasons, whose variation reflects the strong difference in the seasons of the Mediterranean region.

#### 4.1 | Seasonality matters on functional variation over time

Over time, we discovered different magnitudes in the temporal trajectory of  $CWM_{LDMC}$  with a conservation strategy rising over time in the plant community during the spring season. The increase of  $CWM_{LDMC}$  in spring over time can be a result of the change in climatic conditions.

The current projections of climate change in the Mediterranean region forecasted increased temperatures and decreased precipitations (Giorgi & Lionello, 2008). This means an increase in the intensity and frequency of drought stress, with implications for plant species (Reyer et al., 2013). Accordingly, species having conservative strategies are favoured because hard leaves cope better with intense evapotranspiration rates caused by rising temperatures (Poorter et al., 2009). By contrast, winter communities tend to be characterised over time by species having more acquisitive strategies. Also, this variation can probably be linked to global warming with an increase in winter temperatures that favours faster-growing species (Bucher & Rosbakh, 2021).

We found that the flowering schedule of the plant community varied according to the season. Over time winter late-flowering species are replaced by early-flowering species that have a shorter phenology. This can be explained by plants reducing competition and promoting coexistence using shared resources during winter



**FIGURE 1** Predictive trends (mean  $\pm$  SE) of functional diversity for (a) leaf dry matter content (LDMC), (b) life form (LF), (c) start of flowering (SF) and (d) flowering length (FL). For time steps explanation see [Table 1](#).

(Doležal et al., 2019) as temperatures rise. By contrast, we found the replacement of early-flowering species with late-flowering species having the same temporal length for the spring season. In optimal growing conditions, species with late flowering occur in longer vegetative growth periods, whereas early-flowering species are favoured in environments with a short or unpredictable growing season, like the Mediterranean area (Roux et al., 2006). Here, the summer brings drought stress due to long periods of dry weather and extended daylight hours. Accordingly, plants tend to flower earlier to ensure their entire flowering phenology is completed before the onset of summer drought stress (stress-avoidance adaptation or drought escape strategy) (Kooyers et al., 2015). However, we found contrasting patterns, with early phenological spring species replaced over time by later phenological spring species. This counterintuitive effect in the Mediterranean region may have a clear explanation. It has been found that spring species are affected not only by current climatic conditions, but also by past weather. Specifically, a marked increase in autumn temperatures in relation to spring temperatures could lead plants to delay their spring phenology (Gordo & Sanz, 2010). Despite the reason for an anticipated or delayed phenology for winter and spring, this pattern may have profound consequences on the pollinators. For example, early flowering during winter has been associated with a lower number of pollinators in the Mediterranean region (Petanidou et al., 2014). Alternative explanations have been hypothesised, and all of them are plausible given the unpredictability of the mediterranean climate: (a) warmest winters might expose the earliest-flowering species to fewer insect species and/or smaller pollinator populations; and (b) pollinators may have shorter periods of activity in years of earliest flowering, reducing phenological overlap with flowers.

As for flowering and resource acquisition strategies, we found a variation in the life form that can be mostly related to climatic conditions. Specifically, the increase in therophytes is in line with

global warming. Therophytes are annual species well adapted to dry environments because they can exploit the short growing season during late winter and spring when cool temperatures and lower water stress allow plants to grow (Midolo et al., 2024). The decline in hemicryptophyte species during both spring and winter can be attributed to their strategy of vegetative rest, allowing them to avoid adverse environmental conditions. Moreover, geophytes showed higher representation during spring and not in winter. This can be explained by their ability to use the nutrients stored in rhizomes or bulbs to grow through the dense litter in spring (Pykälä, 2005).

## 4.2 | Scarce influence of grazing regimes on functional variation over time

The lack of differentiation in vegetation responses to various grazing regimes can be attributed to the region's long history of human association. Over millennia, in the Mediterranean area, land use may have exerted selective pressures on the local flora, influencing the development and persistence of plant communities. As such, human activities and natural processes in the Mediterranean region have co-evolved, resulting in a socio-ecological system in which grazing is an integral part of land use and biodiversity conservation ("cultural landscape" sensu Antrop, 2005). Thus, the consistent response of vegetation across different grazing regimes may reflect not only their ecological resilience and adaptability, but also their long co-evolutionary history with human activities. Nonetheless, we documented the effect of different grazing regimes on LDMC. Our results are in line with the literature stating that rotational grazing regimes favour the presence of more palatable species (low  $CWM_{LDMC}$ ) (Jacobo et al., 2006). LDMC is a proxy of relative growth rates and expresses the species' ability to

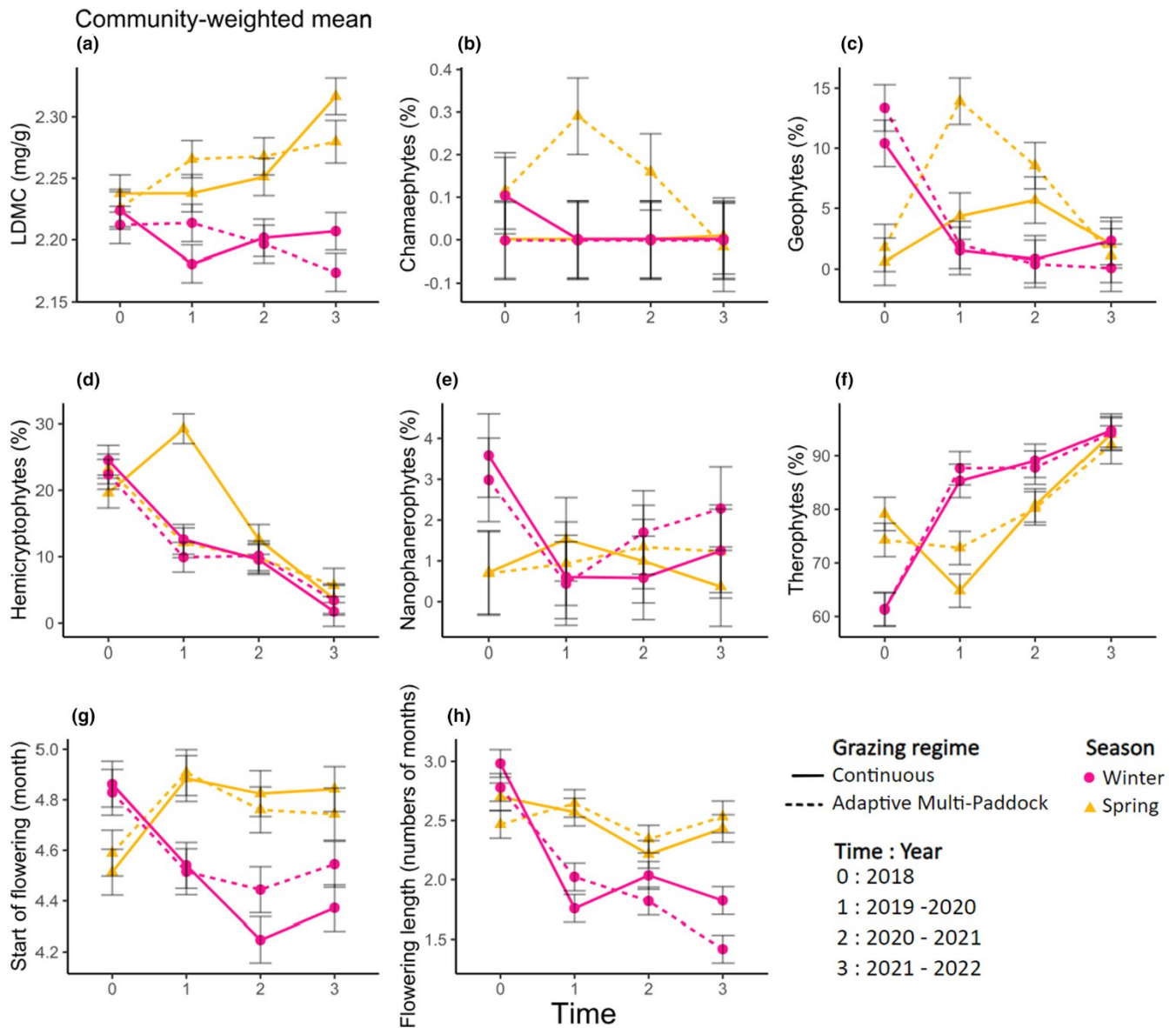


FIGURE 2 Predictive trends (mean  $\pm$  SE) of community-weighted mean for (a) leaf dry matter content (LDMC) (mg/g) and life form (LF, expressed as relative frequency, %) of (b) chamaeaphytes, (c) geophytes, (d) hemicryptophytes, (e) therophytes, (f) nanophanerophytes, (g) start of flowering (months) and (h) flowering length (numbers of months). For time steps explanation see Table 1.

withstand environmental stressors (Wilcox et al., 2021). Species with lower LDMC have faster growing rates and are more appetible to grazers (Khaled et al., 2006; Callis-Duehl et al., 2017). Accordingly, the  $CWM_{LDMC}$  reveals a temporal trajectory ranging from similar values occurring in both grazing regimes at the beginning of the experiment (time0) to different values characterising each grazing regime at the end of the experiment (time3). As a result, AMP needs years to produce a marked response from the plant community after its establishment. This strengthened the importance of evaluating management practices over time, at least in the mid-term. It is hypothesised that the effects of grazing regimes on the ecosystem, including soil health and plant diversity, may not become fully apparent in the short term, being a time-lag in the response to grazing (Zhang et al., 2023). Indeed, in the shorter term, grazing management can influence the structure of

plant communities by removing plant tissues, but a longer term is required to register a remarkable effect on plant community diversity (Briske et al., 2003; Sonnier et al., 2023). Overall, at the end of the experiment (time3) plant community under AMP tends to be characterised by faster-growing species. The shift towards more acquisitive strategies can result from resting periods long enough to allow plant regrowth in conditions of higher levels of nutrients and physical soil indicators of AMP compared with C grazing (Teague et al., 2011; Catalán et al., 2021), which positively affected the species relative growth rates (Laliberte et al., 2012). Notably, the presence of more palatable species over time prevents adverse effects on grazer welfare because of the increase of rumen keratinisation due to excessive feeding on unpalatable species (Catorci et al., 2014). Lastly, because species via their traits can alter the ecosystem services, the presence of more palatable

species with soft leaves is associated with a higher decomposition rate, and, ultimately, soil fertility (de Bello et al., 2010). By contrast, the effect of continuous grazing pressure towards higher  $CWM_{LDMC}$  is more in line with the literature (Díaz et al., 2007). Indeed, under continuous and intense grazing conditions, unpalatable species tend to be avoided by herbivores, increasing their abundance in the plant community, with a dramatic reduction in soil fertility (Seymour et al., 2010).

Regarding the life form, in both grazing practices a transition from “decreasers” to “invaders” seems to favour therophytes over hemicryptophytes. This aligns with Noy-Meir’s hypothesis, highlighting the significance of open space colonisation in response to heightened grazing regimes (Noy-Meir et al., 1989). Hemicryptophytes have their renewal buds at the surface of the ground (Cain, 1950). They are less tolerant to grazing than species with subterranean overwintering buds (Sternberg et al., 2000; Di Biase et al., 2021). Our results reveal that they are the only life form type affected directly by management over time in both grazing regimes. They showed a sharp decrease over the years. Chamaephytes were the only life forms affected by the interaction of grazing regimes and seasons. Specifically, this pattern highlights how AMP only favours this specific life form during springtime. However, the benefits are time-dependent. After an initial increase in chamaephytes, prolonged AMP acts as a filter to reduce them over the years. Both hemicryptophytes and chamaephytes were negatively associated with grazing over a long time. This can generally be attributed to their greater vulnerability to trampling and the fact that their vegetative buds are closer to the soil surface, making them more susceptible to being eaten (McIntyre et al., 1995; Houessou et al., 2012). These findings imply that the impact of the grazing regime can be monitored at the level of life form (McIntyre, 1967). Although grazing affected both the community mean of LDMC and the relative proportion of hemicryptophytes, no effect was detected on flowering traits. This suggests a selective effect of grazing management acting on the vegetative dimension of the plant community but leaving unaffected sexual reproduction.

## 5 | CONCLUSIONS

Worldwide, the response of vegetation to land-use change is a hot topic. The impact of adaptative multi-paddock practices on vegetation and overall ecosystem health has garnered significant attention among various grazing systems. Here, we found that AMP offers a more sustainable alternative that benefits functional plant composition and essential ecosystem services like soil fertility. Implementing adaptative multi-paddock grazing practices can thus be a crucial step towards sustainable land use of mediterranean grasslands. Unlike the season, grazing regimes did not alter the functional dimension of phenology. Over time, changes in plant phenology during winter and spring can lead to a phenological mismatch with pollinators, resulting in negative impacts on both groups of species. Considering the life form, over time, the grazing

regime affected exclusively hemicryptophytes. Therophytes increased their contribution over time regardless of the season and the management practices. However, our results emerge from 3 years after the start of the experiment. Longer-term studies are necessary to have a better understanding of the plant community response. Furthermore, future studies have the potential to provide valuable guidance for implementing management strategies focused on sustainable grassland management as an essential prerequisite for their conservation.

## AUTHOR CONTRIBUTIONS

SB, AB and NAH conceived the idea. AP, MCC and SB contributed to establish the experimental design. NAH, SB, GR, GP and MCC performed the surveys and identified the plants. AB and AP analysed the data. NAH, AB and SB wrote the main draft. All the authors contributed with comments and approved the final version.

## ACKNOWLEDGEMENTS

This manuscript reflects only the authors’ views and opinions, neither the European Union nor the European Commission can be considered responsible for them. The authors are very grateful to the farmers who hosted field experiments: Nanni Caratzu and his family. Stéphanie Gascón acknowledges Fun-METANET project MCIN/AEI/10.13039/501100011033 [Grant Code: PID2020-114440GB-I00]. S. Bagella and M.C. Caria acknowledge the support of NBFC to the University of Sassari, funded by the Italian Ministry of University and Research, PNRR, Missione 4 Componente 2, “Dalla ricerca all’impresa”, Investimento 1.4, Project CN00000033. G. Bonari was funded under the National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4 – Call for Tender no. 3138 of 16 December 2021, rectified by Decree no. 3175 of 18 December 2021 of Italian Ministry of University and Research funded by the European Union – NextGenerationEU; Award Number: Project code CN\_00000033, Concession Decree no. 1034 of 17 June 2022 adopted by the Italian Ministry of University and Research, CUP B63C22000650007, Project title “National Biodiversity Future Center – NBFC.” Open access publishing facilitated by Libera Università di Bolzano, as part of the Wiley - CRUI-CARE agreement.

## FUNDING INFORMATION

The study was supported by the project LIFE-Regenerate – Revitalizing Multifunctional Mediterranean Agrosilvopastoral Systems Using Dynamic and Profitable Operational Practices (grant code: LIFE16 ENV/ES/000276), local responsible Prof. Giovanna Seddaiu.

## CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data are available on the Zenodo repository: <https://doi.org/10.5281/zenodo.13623138>.



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## SUPPORTING INFORMATION

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

**Appendix S1.** Climatic data of study area.

**Appendix S2.** Representation of the study system.

**Appendix S3.** List of measured species.

**Appendix S4.** Temporal trajectories of plant functional traits in mediterranean grasslands under different grazing regimes.

**How to cite this article:** Al Hajj, N., Bricca, A., Caria, M.C., Gascón, S., Piga, G., Pulina, A. et al. (2024) Temporal trajectories of plant functional traits in mediterranean grasslands under different grazing regimes. *Applied Vegetation Science*, 27, e12807. Available from: <https://doi.org/10.1111/avsc.12807>