



Local grazing pressure drives the diversity of flower traits in semi-natural grasslands

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ABSTRACT

Semi-natural grasslands under extensive grazing host a high diversity of plants whose diverse flower traits are crucial for insect pollinators, which are facing a worrying decline. We investigated how grazing regimes in dry calcareous grasslands influence the diversity and composition of flower traits important for pollinators. We measured the taxonomic diversity (TD) of the plant community, as well as the functional diversity (FD) and the community-weighted means (CWM) of seven morphological, phenological, and reflectance flower traits for insect-pollinated species across 116 plots in 22 farms and nearby abandoned areas spanning six regions in Italy and Switzerland. We compared managed and abandoned areas to assess differences in FD and CWM, and fitted two piecewise structural equation models to infer direct and indirect effects of grazing regimes on TD, FD and CWM. Extensive grazing did not alter flower traits' FD compared to abandonment, but favoured flowers' characteristics beneficial to pollinators, e.g., increased CWMs of flower size, flowering period length, and UV reflectance. Across different grazing regimes, local grazing pressure emerged as a key driver of TD and, in turn, of the FD and CWM of several flower traits. Plant communities with a more even distribution of dominant and rare species were positively associated with the FD of flower symmetry, flowering initiation and UV reflectance, as well as the representation of zygomorphic and non-yellow flowers. Maintaining extensive grazing is essential to preserve flower characteristics that are important for pollinators. Managing grazing intensity patterns at local spatial scales is crucial to increase the diversity of flower traits, which, in turn, may support a broad range of insect pollinators.

1. Introduction

Semi-natural grasslands are among the most diverse ecosystems worldwide (Dengler et al., 2014; Habel et al., 2013; Wilson et al., 2012) and maintain important ecosystem functions and services (Bengtsson et al., 2019). These grasslands crucially provide forage and nesting sites to pollinators, driving their spillover across agricultural landscapes (Kennedy et al., 2013; Krimmer et al., 2019; Neumüller et al., 2020; Öckinger and Smith, 2007). Semi-natural grasslands have been shaped by centuries of agricultural practices, like low-intensity grazing and mowing (Hejman et al., 2013), which are still crucial for their maintenance (Halada et al., 2011). In Europe, over the past century, shifts in farming intensity and land use, marked by management intensification

or abandonment, have led to a substantial decline of semi-natural grasslands (Wesche et al., 2012), which are widely threatened (Tsiripidis et al., 2016) and exhibit one of the worst conservation states among terrestrial ecosystems (European Environment Agency, 2010). A severe decline has been documented in semi-natural grassland taxonomic diversity (hereafter 'TD'), affecting both species richness and abundance (Bonari et al., 2017; Dembicz et al., 2021; Gossner et al., 2016; Török et al., 2016), with detrimental effects on functional diversity (hereafter 'FD') (Mouillot et al., 2013), and on multiple ecosystem services, including pollination (Allan et al., 2015; Bengtsson et al., 2019).

The FD is usually defined by the spectrum of functional traits within the community (Tilman, 2001) and is essential for ecosystem

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functioning and services across multiple ecosystems (Cadotte et al., 2011; Cardinale et al., 2012; Díaz and Cabido, 2001), including semi-natural grasslands (Johansen et al., 2019; Prangel et al., 2023). Additionally, the trait values of dominant species within plant communities, as represented by the community-weighted mean (hereafter 'CWM') significantly influence ecosystem functions, in line with the mass-ratio hypothesis (Cadotte, 2017; Grime, 1973). Both FD and CWM largely depend on the taxonomic composition of the community, as TD determines the pool of species and traits within the community assembly.

Over recent decades, trait-based ecology and studies on FD have gained increasing recognition (Green et al., 2022; Zakharova et al., 2019), leading to the collection of a wealth of knowledge and data on plant traits (Kattge et al., 2020), also with special reference to European grasslands (Ladouceur et al., 2019). As a result, FD is increasingly considered a key parameter to inform conservation and restoration strategies aimed at sustaining or recovering ecosystem functioning. Although most efforts have focused on vegetative traits related to leaf-height-seed (LHS) strategy scheme (Westoby, 1998), there is a growing interest in flower traits and their role as determinants of community assembly (E-Vojtkó et al., 2020; Michelot-Antalik et al., 2025).

Flower traits, e.g., flower morphology, color, and phenology, act as *effects traits* (Lavorel and Garnier, 2002), because they influence the attractiveness of plant species to insect pollinators and shape the fundamental niche of flower visitors (Blüthgen and Klein, 2011; Howe and Westley, 1988). Indeed, most pollinators rely on visual cues to find flowers, which also signal potential rewards (Chittka and Raine, 2006; van der Kooi et al., 2023). It is widely acknowledged that plant communities exhibiting diverse flower traits afford pollinators a broad fundamental niche, facilitating niche partitioning (i.e., complementarity) among consumers, thus reducing their interspecific competition. MacArthur's (1955) competition theory established the framework, later expanded by Levine and HilleRisLambers (2009) who showed how niche differences stabilize coexistence. Empirical support comes from Junker et al. (2013), who linked floral trait diversity to pollinator specialization, and Cappellari et al. (2022), who demonstrated that floral diversity expands pollinator dietary niches, particularly reducing competition among generalist bees. Considering that approximately 80 % of flowering plants depend on animals for reproduction (Rodger et al., 2021), floral diversity's role in reducing pollinator competition through niche partitioning become critical, enhancing plant reproductive success and the efficiency of pollination service, also in agricultural systems (Brittain et al., 2013; Campbell et al., 2012; Fontaine et al., 2006; Frund et al., 2013).

Flower traits also act as *response traits* (Lavorel and Garnier, 2002), which are strongly determined by the alterations of biotic and abiotic drivers. Grazing regimes largely shape the composition of plant communities in semi-natural grasslands. It is largely recognised that moderate grazing disturbance promotes species diversity by reducing interspecific competition (Connell, 1978; Grime, 1973; Kleijn et al., 2011; Kleijn and Sutherland, 2003). Conversely, overgrazing generally favours species with traits related to grazing tolerance and avoidance, while undergrazing and abandonment enhance traits that increase the species competitive ability for light, nutrients, and/or space (Blasi et al., 2009; Díaz et al., 2007; Komac et al., 2015; Peco et al., 2012). Different grazing systems influence plant communities by regulating the spatial and temporal distribution of livestock, which can also display different selectivity, grazing behaviour, and body size among different animal species and breeds, influencing plant community assembly (Pauler et al., 2020, 2019; Perotti et al., 2018; Pittarello et al., 2019). Therefore, by altering species composition, grazing shapes the functional space of plant communities with cascading effects on the diversity and patterns of flower traits. Although the effects of grazing on vegetative traits have been largely addressed, few studies have investigated how different grazing regimes impact flower traits (Chen et al., 2022; Pellaton et al., 2023; Rakosy et al., 2022). Indeed, most studies have focused on grazing

as a driver of the abundance of floral resources (e.g., Cutter et al., 2022; Noreika et al., 2019; Tadey, 2015; Woodcock et al., 2014), while the effects on the diversity of flower traits have received far less attention, despite its ecological relevance for pollinator communities and ecosystem functioning. As a result, the influence of different grazing regimes on the FD and CWM of the insect-pollinated communities (hereafter 'flowering species') in semi-natural grasslands remains largely unexplored. Moreover, the potential role of TD as a key mediator in shaping the response of floral traits to grazing pressure has not been adequately addressed, despite its likely importance in linking changes in community composition to functional outcomes. This knowledge gap limits our understanding of how grazing management can be tailored to sustain key ecosystem services such as pollination, as advocated by European biodiversity and agricultural strategies (European Commission, 2012; European Commission 2021a, 2021b).

Here, we aim to fill this gap by providing a novel functional perspective on how grazing shapes the flower trait composition of plant communities. Our specific aims were to assess:

- the difference in the FD and CWM of flower traits between extensively grazed and abandoned semi-natural grasslands;
- the effects of grazing regimes on the TD of the whole plant community;
- the role of TD in mediating the influence of grazing regimes on the flower traits' FD and CWM.

We hypothesized that grazing management largely shapes the flower traits of semi-natural grasslands. Specifically, we expected that: i) extensively grazed grasslands hosted higher FD and distinct CWM values of floral traits compared to abandoned ones, due to the filtering effect of grazing on dominant species and the associated increase in niche partitioning; ii) different grazing regimes influenced the TD of the whole plant community, with moderate grazing pressure and controlled grazing techniques promoting higher species diversity by reducing competitive exclusion; iii) the effects of grazing regimes on the FD and CWM of flower traits was mediated by changes in TD, such that increased diversity would lead to a broader functional space and shifts in dominant floral trait values.

2. Materials and methods

2.1. Study area

This study was conducted within dry calcareous grasslands of the *Festuco-Brometea* (hereafter 'semi-natural grasslands'), recognized as Habitat 6210(*) "Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*) (*important orchid sites)" under the EU Habitats Directive 94/93/ECC (asterisk in parentheses indicates that the habitat may be considered of priority interest if it qualifies as an important orchid site) and the Habitat 4.2.2/4.2.4 in the Swiss habitat inventory. These habitats are among the most widespread grasslands in Europe (Blasi et al., 2012; Preislerová et al., 2022; Squires et al., 2018) occurring on well-drained, low-nutrient calcareous to neutro-alkaline soils. They hold world records for plant species richness at fine spatial grains (Wilson et al., 2012). However, they are facing conservation threats, especially due to the abandonment of traditional management practices in mountain areas (European Environment Agency, 2016), where the vegetational succession to fringe communities and the encroachment of woody species has been increasing in recent decades (De Toma et al., 2024, 2022; Gómez-García et al., 2023; Orlandi et al., 2016).

We selected 11 sites spanning six administrative regions in Italy and Switzerland (Fig. 1), focusing exclusively on grazed pastures to avoid confounding factors like mowing or prescribed burning. A total of 22 farms with stable management practices over the previous decade were chosen (Table 1), representing diverse grazing regimes within the same

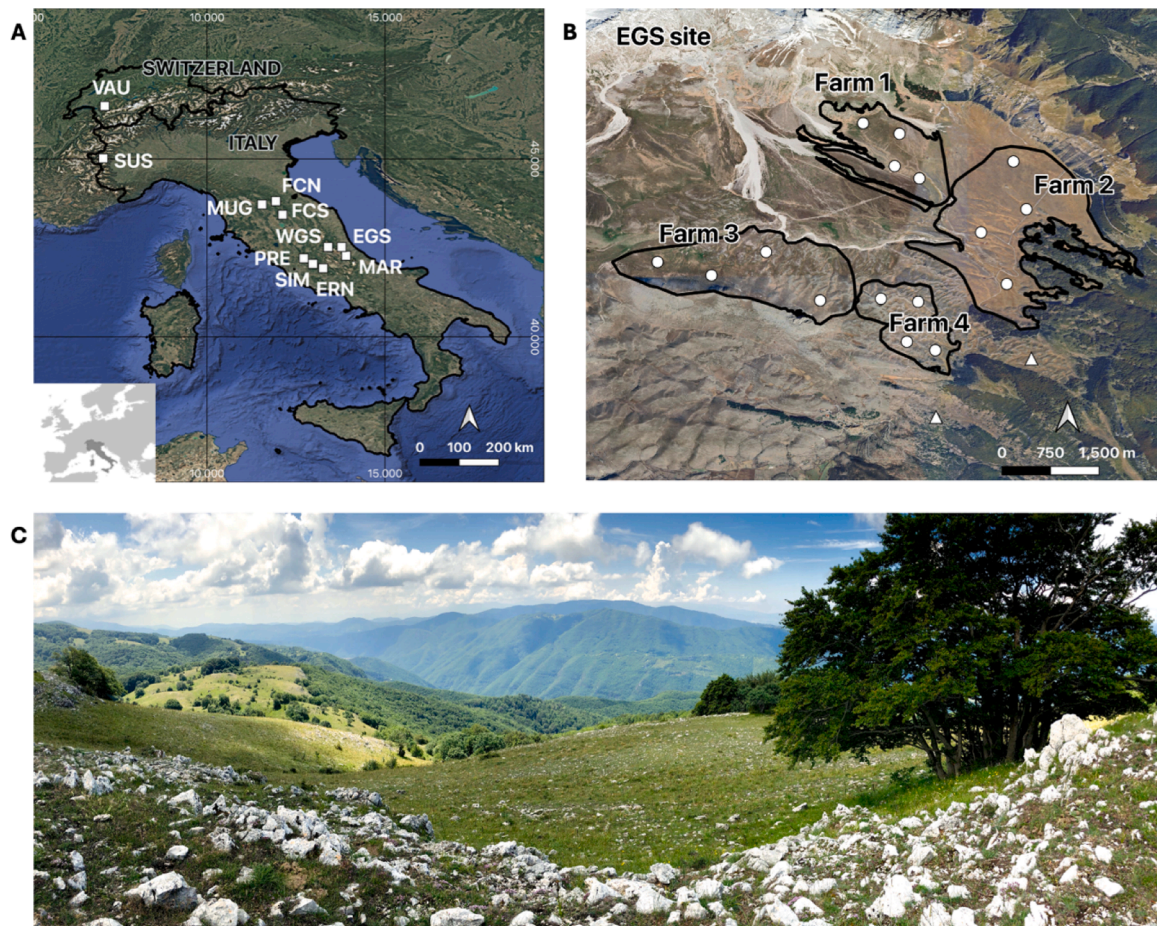


Fig. 1. (A) Location of the study sites distributed in Italy and Switzerland (coordinate system: WGS84 datum). (B) An example of the distribution of farms, grazed plots (circles) and abandoned plots (triangles) within a site. Site acronyms and characteristics are reported in Table 1. (C) Dry calcareous grasslands typical of Central Apennines. Photo credit: F. Napoleone, Mt. Simbruini, Italy.

habitat with relatively homogeneous ecological conditions (Fig. S1). A consistent number of plots per farm (typically 4–6) was maintained, although in some cases logistical constraints, such as limited accessibility imposed a slightly lower number of plots (3). Plots were randomly distributed within each farm, maintaining a minimum 500-meter plot-to-plot distance and checking for topographic and structural homogeneity and representativeness. A total of 96 square plots (16 m², optimal size for grassland sampling following Chytrý and Otýpková, 2003) were sampled for local grazing pressure proxies (2.2), species cover and floral traits (2.3). A KML file with the geographical location of all plots is provided as [supplementary material](#). Data were collected in spring-summer 2018, 2019, and 2022 during the flowering peak of the dominant species, and before the grazing period for seasonally-grazed sites. For seven out of eleven sites, we sampled 20 plots in areas previously grazed and abandoned for approximately thirty years. These areas, designated as control plots, were grasslands originally belonging to the same habitat type, but showed clear signs of secondary succession, with a notable encroachment of shrub species covering more than 30 % of the plot surface. Despite this woody expansion, these plots were still recognizable as grasslands and not fully afforested.

2.2. Grazing regimes and local grazing pressure

Information on grazing regimes was obtained through direct interviews with farmers, local authorities, and agricultural advisors. For each farm, the number of animals of different species (i.e. cattle, sheep, horses) was converted into livestock units (LU: Livestock Units) using species- and age-specific coefficients established by the Commission

Implementing Regulation (EU) No 808/2014. Based on this, the ‘stocking rate’ - a key parameter for quantifying grazing intensity - was calculated as:

$$\text{Stocking rate} = LU / A \times m / 12$$

where *LU* is the number of livestock units, *A* is the grazed area in hectares, and *m* is the duration of the grazing period expressed in months.

We focused on abandoned and extensively grazed grasslands, with very low (0.08 LU·ha⁻¹·year⁻¹) to moderate (0.5 LU·ha⁻¹·year⁻¹) stocking rates. We excluded intensively grazed areas because they were not representative of the target habitat.

The percentage of LU managed through controlled grazing techniques (i.e., rotational grazing and/or shepherding, as opposed to continuous grazing) was used to characterize the grazing system at the farm level (‘Controlled grazing’). The cattle percentage of total LU was used to quantify the relative abundance of cattle compared to other grazing animals (‘Cattle dominance’).

Given that grazing intensity is spatially heterogeneous within farms and the wide extent of the study area precluded the use of GPS collars to track livestock movements in every farm, local grazing pressure was assessed using several well-established, plot-scale proxies commonly adopted in the literature. In particular, we counted the number of not fully decomposed dung from different livestock species deposited since the previous year, an indicator known to be strongly associated with animal presence and activity (Turner, 1998; Stump et al., 2005; Manthey and Peper, 2010). This approach assumes consistent patterns of

Table 1
Environmental and management features of the 22 farms within the nine study sites. The number of heads belonging to different livestock species was converted into livestock units (LU).

Site name	Site ID	Farm ID	N. plots	Elevation (m a.s.l.)		Slope (%)		Area (ha)	Stocking rate (LU·ha ⁻¹ ·year ⁻¹)	Controlled grazing (% LU)	Cattle (LU)	Sheep (LU)	Horses (LU)
				mean	s.d.	mean	s.d.						
Mt. Prenestini	PRE	PRE.1	4	1054	23.20	15.00	9.13	91	0.18	60.18	10.40	20.25	3.00
		PRE.2	4	1105	25.85	12.25	6.13	228	0.57	5.74	221.00	15.00	25.00
Mt. Ernici	ERN	ERN.1	3	1129	48.51	10.67	9.02	349	0.22	55.75	50.00	63.00	0.00
Mt. Simbruini	SIM	SIM.1	6	1412	26.22	15.00	5.48	400	0.31	31.19	105.60	66.00	40.00
Marsica	MAR	MAR.1	3	1057	51.23	30.00	8.66	137	0.59	100.00	0.00	121.50	0.00
		MAR.2	4	1290	70.65	17.50	9.57	259	0.14	67.68	10.00	55.50	16.50
Gran Sasso E	EGS	EGS.1	4	1520	14.14	1.25	2.50	251	0.37	100.00	0.00	225.00	0.00
		EGS.2	4	1585	12.91	3.50	4.43	265	0.08	100.00	0.00	52.50	0.00
Gran Sasso W	WGS	EGS.3	4	1703	80.60	16.25	11.09	430	0.09	100.00	0.00	90.00	0.00
		EGS.4	4	1613	20.62	10.00	5.77	84	0.10	100.00	0.00	19.50	0.00
Mugello	MUG	WGS.1	4	1359	73.94	15.25	11.98	227	0.27	100.00	0.00	105.00	0.00
		MUG.1	5	870	59.16	18.00	5.70	170	0.11	0.00	43.00	0.00	0.00
Casentino N	FCN	MUG.2	6	898	31.27	21.67	11.69	100	0.46	100.00	110.80	0.00	0.00
		CAN.1	12	905	100.31	17.67	6.83	111	0.19	100.00	42.00	0.00	0.00
Casentino S	FCS	CAS.1	2	1013	10.61	10.00	0	32	0.30	0.00	19.6	0.00	0.00
		CAS.2	4	915	26.96	30.75	6.55	120	0.05	0.00	15.00	0.00	0.00
Val di Susa	SUS	SUS.1	4	1685	179.87	9.00	8.12	201	0.36	100.00	174.60	0.00	0.00
		SUS.2	4	1895	21.30	14.00	5.89	323	0.30	100.00	176.80	59.40	0.00
Canton Vaud	VAU	SUS.3	3	1613	58.81	13.00	4.36	47	0.15	100.00	6.00	166.95	0.00
		VAU.1	6	1111	57.73	18.83	6.65	13	0.53	100.00	16.60	0.00	0.00
		VAU.2	3	733	45.97	13.67	9.81	5	0.50	100.00	60.00	0.00	0.00
		VAU.3	3	641	18.15	13.33	2.89	4	0.42	100.00	0.00	3.00	7.00

excretion over time (Schnyder et al., 2010) and comparable dung decomposition rates across sites due to similar habitat conditions - specifically, a dry and temperate climate. We also recorded the percentage of trampled surface, defined as compacted and/or eroded soil caused by livestock movement and resting, which is linked to increased grazing pressure through its effects on vegetation cover and soil integrity (Lai and Kumar, 2020; Teague and Kreuter, 2020). Litter height (average of five random points per plot) and litter cover (visual estimate of surface covered by litter) were also recorded as indicators of biomass removal by grazing (Mapfumo et al., 2002; Elias et al., 2018), since no other disturbance drivers (e.g., mowing or fire) were present in the study system. In areas subjected to year-round grazing, additional indicators of recent livestock activity were measured, including the number of fresh dung pats and the percentage of surface affected by recent trampling or bites. Biting intensity was scored on an ordinal scale from 0 to 3 based on the frequency and extent of visible grazing marks on the vegetation (Orlandi et al., 2016). These variables were subsequently summarized using Principal Component Analysis (PCA), with the first principal component (PC1) representing a synthetic gradient of local grazing pressure for each plot (see ‘2.5 Statistical analyses’).

2.3. Species composition and flower traits

Vascular plant species cover values were estimated through visual assessment of each species vertical ground projection using an ordinal percentage scale. For flowering species with conspicuous flowers, a set of flower traits, i.e., morphological, phenological and reflectance traits, was selected based on their documented importance for plant-pollinator interactions across a wide variety of pollinator guilds (Junker et al., 2013) (Table 2). Although flower reward traits (e.g., nectar amount, sugar and amino acid content) are important for pollinator insects, we did not include them in the study due to their measurement complexity, and to minimize the number of values retrieved from the literature or missing. Floral trait measurements were conducted during the spring and summer, specifically during the species flowering peak. All flowering species were measured, with approximately ten individuals assessed for each species. Flower measures were performed on flower unit, i.e., an aggregation of flowers through which a pollinator can move without flying, which may coincide with individual flowers or aggregation of flowers (e.g., Asteraceae, Apiaceae). Flower height was measured as the vertical distance between the upper part of the flower and the ground (Chapurlat et al., 2015; Sletvold et al., 2016). The flower area was calculated as $A = \frac{1}{4} \pi d^2$ for round flowers and $A = length \times width$ for non-rounded flowers (Chapurlat et al., 2015; Fornoff et al., 2017; Lavi and Sapir, 2015). Flower symmetry was classified into radial or bilateral. According to the protocol of Napoleone et al. (2022b), UV-reflectance was measured using digital photography. Since many flowers exhibit a ‘bull’s-eye’ pattern in UV light to enhance insect recognition (Silberglied, 1979), the outer region of the flower emerged as the most informative area for evaluating variations in UV reflectance among different species, and thus, the maximum reflectance of the periphery of the petals was measured. Color was expressed as the mean value of the light reflectance spectrum (Pellaton et al., 2023; Szitár et al., 2022). Data on color and phenology derived from the BioFlor database (Kühn et al., 2004) and plant species identification manuals (Aeschimann et al., 2004; Pignatti et al., 2017). The same sources were used to retrieve trait values for species for which direct measurement was not possible. For the missing values of the UV reflectance trait, the average percentage reflectance of the species within the 350–380 nm wavelength range was also calculated using the FRd database (Arnold et al., 2010).

Missing trait values (5 % of the total data) were imputed using the ‘mice’ package (v 3.16.0, van Buuren and Groothuis-Oudshoorn, 2011). Imputation was performed based on the mean trait values per genus or, when this information was unavailable, per family. Trait values were

Table 2

Flower traits used to calculate FDs and CWMs.

Trait	Category	Unit	Levels/range	Data structure	Ecological importance	Source
Height	Morphology	cm	2.97 – 1250	continuous	flower recognition	direct measurement; Aeschimann et al., (2004); Pignatti et al., (2017)
Area	Morphology	cm ²	0.02–51.16	continuous	flower recognition	direct measurement; Aeschimann et al., (2004); Pignatti et al., (2017)
Symmetry	Morphology	1/0	radial/bilateral	binary	hosting insects with different foraging adaptations	direct measurement; Aeschimann et al., (2004); Pignatti et al., (2017)
UV reflectance	Reflectance	%	0.24–82.43	continuous	flower recognition	direct measurement; FReD database; BiolFlor database
Color	Reflectance	-	violet (400 nm); blue (450 nm); white (550 nm); yellow (580 nm); pink (650 nm)	categorical	flower recognition	BiolFlor database; Aeschimann et al., (2004); Pignatti et al., (2017)
Flowering initiation	Phenology	Month	1 – 12	integer	onset of resource availability	Aeschimann et al., (2004); Pignatti et al., (2017)
Flowering duration	Phenology	Month	1 – 12	integer	duration of resource availability	Aeschimann et al., (2004); Pignatti et al., (2017)

log- or sqrt-transformed (Májeková et al., 2016).

2.4. Diversity measures

All diversity measures were calculated and statistical analyses were performed using (R Core Team, 2023). The TD was assessed for the entire community of vascular plant species ('vegan' R package, v3.1.163). Species richness was measured as the number of species per plot. Shannon index gives insights on both species richness and on the evenness of species in the community and was calculated as:

$$Shannon = - \sum p_i \ln(p_i)$$

where p_i is the proportional cover of species i .

As compared to the Shannon index, the Simpson's index places greater emphasis on the species with the highest cover and is less sensitive to species with minor cover values. It was measured as:

$$Simpson = 1 - \sum p_i^2$$

In line with findings in the literature (Fornoff et al., 2017), which indicated that the overall FD of plant communities did not influence pollinator species richness, we decided to overlook this component of diversity. Instead, we chose to focus on individual flower traits. The FD for each trait was calculated solely across the insect-pollinated species (i. e., 'flowering species') within the community. It was based on the quadratic entropy (Rao, 1982), calculated as:

$$FD = \sum_{i=1}^{S-1} \sum_{j=i+1}^S d_{ij} p_i p_j$$

where d_{ij} is the difference between the i^{th} and j^{th} species and p_i is the proportion of the species i of the total community.

Furthermore, the average value of each trait calculated considering the cover of species, i.e., the community-weighted means (CWM) (Garnier et al., 2004), was assessed as:

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

where n is the number of species, p_i is the relative cover of species i in the community, and $trait$ is the trait value of the species i .

For binary and categorical traits (i.e., symmetry and color, respectively), CWM was calculated by considering the dominant level (setting $CWM.type = "dom"$) and by transforming traits into dummy variables, subsequently assessing the abundance of each level (setting $CWM.type = "all"$).

Both FD and CWM were assessed using the 'FD' package (v1.0–12.3, Laliberté et al., 2014).

2.5. Statistical analysis

A principal component analysis (PCA; prcomp function, stats package v3.6.2) was performed using the five proxies of local grazing pressure: dung counts, bite marks, trampling intensity, litter height, and litter cover (see '2.2 Grazing regimes'). The first principal component (PC1, 47.99 % of variance) was interpreted as a 'local grazing pressure' gradient and each plot was associated with its score on this axis (Fig. S2, Table S1).

The statistical analysis consisted of two main parts. First, grazed areas were compared with abandoned areas in terms of FD and CWM. For this purpose, we implemented linear mixed-effects models using the 'lme4' package (version 1.1.32). For the CWM of symmetry, we utilized a generalized linear model to account for the binary nature of the response variable, while for CWM of color, we applied mixed-effects multinomial logistic regression to appropriately model the multiple categories of the response variable ('mclgit' package, v0.9.6). Site was included as a random factor in all models to account for unobserved biogeographical and environmental differences across sites. The FD of height, area, and initiation were log-transformed, while FD of symmetry and color underwent quadratic transformation to ensure normality and homoscedasticity of the residuals.

In the second part of the analysis, we focused exclusively on grazed plots to investigate the direct and indirect effects of grazing regimes on the FD and CWM of the flowering communities. To this end, we employed two piecewise structural equation models (SEM, 'piecewiseSEM' package v2.3.0, Lefcheck, 2016), a statistical framework that allows for the simultaneous testing of multiple hypotheses and the quantification of both direct and indirect effects among variables. This approach expands traditional SEM models by allowing the inclusion of random effects and different types of response distributions, making it especially well-suited for ecological data and relatively small sample sizes. Relationships among variables were expressed in a causal network based on prior knowledge and scientific literature (Fig. S3a–b) and then translated into a set of individual equations, one for each relationship, which were evaluated separately and subsequently combined to assess the overall structure of the system. The SEMs included four grazing regime variables - cattle dominance, controlled grazing, stocking rate, and local grazing pressure - as potential drivers of plant diversity. The TD was represented by species richness, Shannon, and Simpson indices of the whole plant community, while FD and CWM were calculated for the flowering species, based on the floral traits reported in Table 2. Each component of the SEM was fitted using linear mixed-effect models ('nlme' package v3.1.160, Pinheiro et al., 2022) with site as random factor, to account for site-specific variability and control for potential biases arising from the unequal number of plots across farms. A generalised linear mixed-effect model ('lme4' package v1.1.32, Bates et al.,

2015) was used for species richness count data, and after exploring overdispersion in model residuals, a Poisson error distribution was used. To ensure that all variables contributed comparably to the models, grazing management variables were standardized. For the CWM of binary and categorical traits, the abundance of each level was used. In order to respect assumptions of normality and homoscedasticity of the model residuals, fine-scale grazing intensity, FD of flower height, flower area, flower UV reflectance, flowering initiation and duration and CWM of white color were log-transformed; the FD of flower color was squared-, and CWM of pink color was sqrt-transformed. Since CWM of blue and purple colors had very low values, indicating their limited presence in the communities, they were aggregated (hereafter 'blue') and log-transformed. Model fit was assessed using Shipley's d-separation test and the Akaike information criterion corrected for small sample size (AICc). The final optimized model was selected because it had the lowest AICc, included the most variables, and showed a statistically non-significant Fisher's C statistic ($p > 0.05$), indicating that the model adequately captured the hypothesized causal structure (Grace et al., 2010).

Before running SEMs, all variables were investigated for collinearity and those with Spearman's rank correlation coefficient > 0.6 were excluded from the models, according to Dormann et al. (2013) (Fig. S4 a-b).

3. Results

3.1. Grazed vs. abandoned

A total of 509 vascular plant species were recorded, including 411 flowering species (tab. S2). The FD for the latter did not significantly differ between grazed and abandoned grasslands, except for the diversity of flower UV reflectance, which was higher in grazed areas (Fig. 2a). The CWM traits exhibited significant differences between grazed and abandoned grasslands (Fig. 2b; Tab. S3–4). Grazing significantly increased flower area, UV reflectance, flowering initiation time, duration, and pink flowers' cover while decreasing plant height (Fig. 3). The CWM for symmetry, instead, did not vary significantly between the two groups (tab. S5).

3.2. Taxonomic diversity response to grazing regimes

Local grazing pressure significantly influenced TD, having a positive effect on the Simpson index, which in turn was positively related to the Shannon index (Fig. 4a-b). In contrast, grazing regimes measured at the farm scale - including stocking rate, controlled grazing, and cattle dominance - did not show any significant effect on TD.

3.3. Taxonomic diversity mediates flower functional response to grazing regimes

Local grazing pressure influenced the FD and CWM of several traits indirectly, through its effect on the Simpson index. Higher Simpson index values were associated with a lower FD of flower symmetry and UV-reflectance and a greater dominance of radially symmetrical and yellow flowers. In contrast, the Shannon index was positively related to the FD of flower symmetry, flowering initiation and UV reflectance, as well as to a greater representation of zygomorphic and non-yellow flowers.

4. Discussion

4.1. Extensive grazing influences community-weighted means more than functional diversity

Biodiversity in semi-natural grasslands largely depends on the maintenance of extensive grazing practices. According to the

'intermediate disturbance hypothesis' (Connell, 1978; Grime, 1973) and the 'land use-moderated conservation effectiveness hypothesis' (Kleijn et al., 2011; Kleijn and Sutherland, 2003), moderate grazing disturbance reduces competitive exclusion, thereby facilitating niche partitioning and promoting species coexistence. However, contrary to our expectations, extensive grazing was not associated with an increase in the flower FD, except for UV reflectance. This could be explained by several mechanisms. On the one hand, many of the species colonizing abandoned grasslands contribute to an increase in flower functional diversity (e.g., *Rosa* spp., *Rubus* spp., *Crataegus monogyna*, *Spartium junceum*). On the other hand, species adapted to grazing may persist for decades after abandonment, thereby contributing to high levels of flower traits' diversity (Johansen et al., 2016). Finally, while wild ungulates alone are not sufficient to preserve the botanical composition of semi-natural grasslands across wide extents, they can contribute to its maintenance (Rupprecht et al., 2022). Overall, our results are consistent with other studies which, although not focused on flower traits, have demonstrated that the abandonment of grazing does not reduce the availability of flower resources for pollinators (Ford et al., 2012; Johansen et al., 2019). Conversely, extensive grazing drove the community-weighted means of the flower traits. A lower flower height in grazed grasslands reflected plants' adaptive strategy to mitigate the effects of livestock disturbance, since growing close to the ground represents a morphological avoidance trait that enhances plant species fitness in grazed areas (Briske, 1996). The higher flower size in grazed areas could be attributed to the fact that many species with large flowers also exhibit mechanical avoidance traits reducing flowers' accessibility to livestock, such as spinescence (e.g., *Carlina acanthifolia* and *Cirsium eriophorum*). Species with longer flowering periods were more abundant under extensive grazing, likely because flowering across long periods may enhance the reproductive success rate, especially during periods of reduced grazing pressure. Our findings suggest that grazing further favors late-flowering species, possibly because traits such as spines (e.g., *Euphorbia spinosa*), chemical defenses (e.g., *Artemisia absinthium*), or a prostrate growth form (e.g., *Seseli montanum*) reduce herbivory, allowing these species to persist and reproduce even during and after the grazing season. Finally, we observed an increase in the UV reflectance of the flower community and an increased prevalence of pink flowers, likely in relation to the abundance of pasture-associated species such as *Centaurea nigrescens* and *Onobrychis viciifolia*, which reflect strongly in these spectral ranges.

Overall, our results demonstrate that, although not determining an increase in flower traits' diversity, extensive grazing favoured several functional traits that are beneficial to insect pollinators. Larger flowers tend to be more attractive because they are more visible (Ohashi and Yahara, 2001) and they signal a greater potential reward (Makino and Sakai, 2007; Ortiz et al., 2021; Tavares et al., 2016) resulting in higher visitation rates and pollinator species richness (Delgado et al., 2023; Junker et al., 2013; Lázaro et al., 2020). The higher UV reflectance observed in grazed areas is crucial for many pollinators for distinguishing flowers (Fornoff et al., 2017; Rae and Vamosi, 2013). Insects detect UV-reflecting flowers with specific patterns that contrast with UV-absorbing backgrounds, such as leaves and soil, including the 'bull's-eyes' of *Asteraceae* which enhance long-distance recognition (Bukovac et al., 2017; Chittka et al., 1994; Koski and Ashman, 2014; Silberglied, 1979). The longer flowering duration observed under extensive grazing also supports pollination to a greater extent than the one observed in abandoned areas by enhancing floral resource availability during months with limited resources, when social bees and many other pollinators remain largely active (Blüthgen and Klein, 2011; Olesen et al., 2008; Scheper et al., 2014; Sutter et al., 2017).

Extensive grazing also increases the abundance of species with pink flowers. This may be advantageous for butterflies, which often prefer pink flowers due to their red-sensitive photoreceptors (Reverté et al., 2016; Simms, 2013; Yurtsever et al., 2010), despite the widely varying color preferences across families and species (e.g., Pohl et al., 2011; Neumayer and Spaethe, 2007; Osorio and Vorobyev, 2008). Notably,

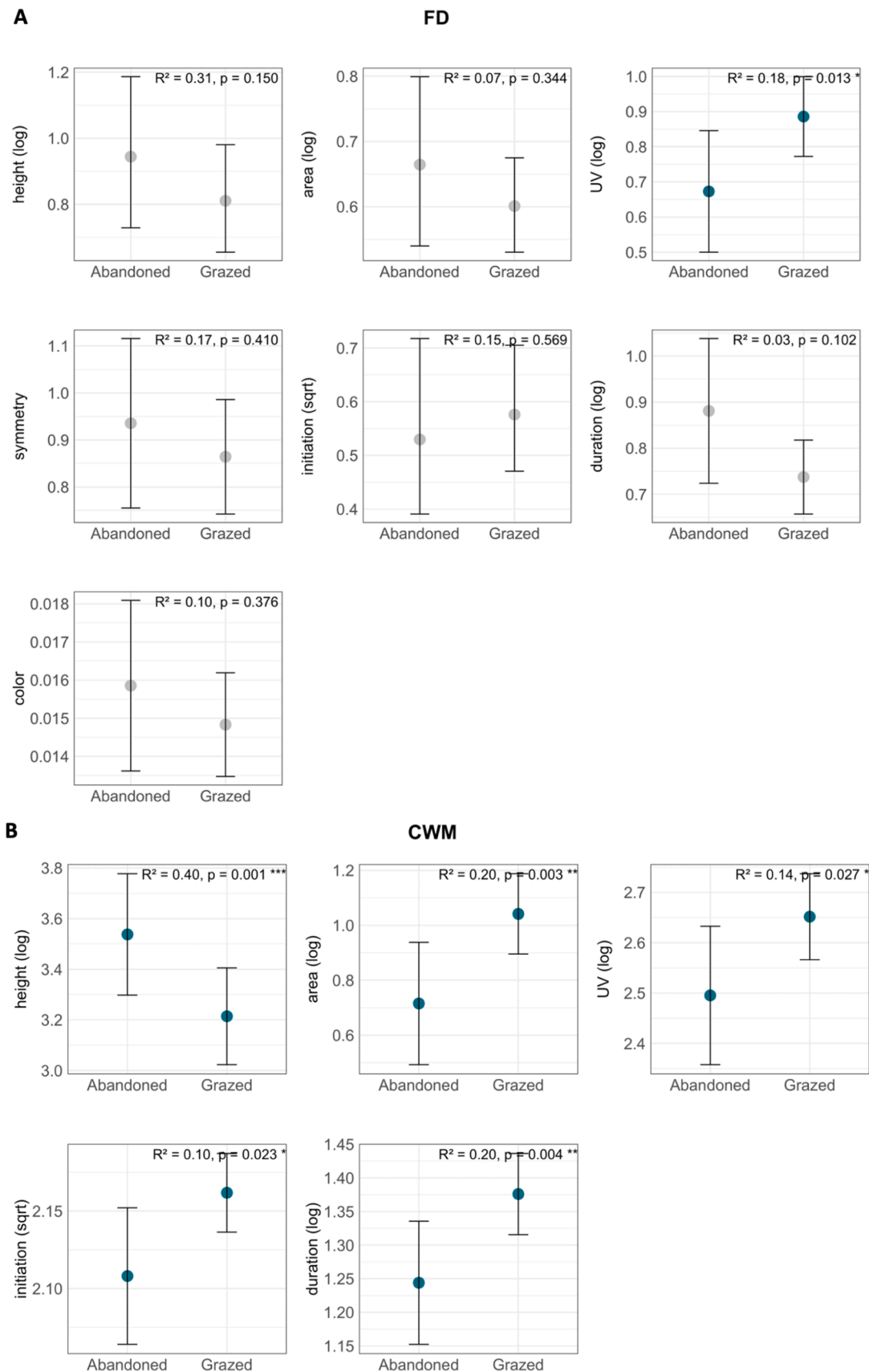


Fig. 2. Flower trait FD (a) and CWM (b) distribution and results of linear mixed models comparing abandoned and grazed areas. The R^2 values indicate the proportion of variance explained by the model. Green dots represent significant relationships, while grey dots indicate non-significant effects. Significance levels are shown as *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$. Trait values used to assess FD and CWM were log- or sqrt-transformed.

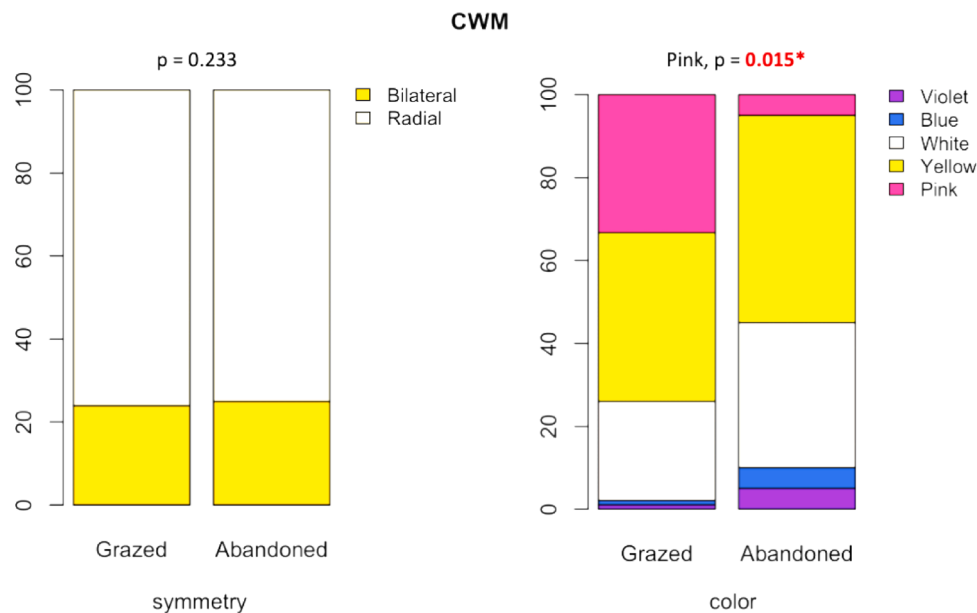


Fig. 3. CWM of symmetry and color in grazed and abandoned plots. Symmetry distribution (left) shows the percentage of bilateral versus radial flower types; color spectrum (right) displays the percentage of dominant reflectance wavelengths.

species like *Onobrychis viciifolia* and *Centaurea nigrescens* are especially significant for *Polyommatus* butterflies, a genus within the Lycaenidae family (Parile et al., 2021; Šlancarová et al., 2012), and for different bee species (Hayot Carbonero et al., 2011; Kells, 2001; Londei and Marzi, 2024). This is particularly significant given the host-plant specificity of butterflies and the close dependence of several butterfly and bee species on extensive agricultural systems, with both groups experiencing severe declines in Europe also due to habitat loss (Ekroos et al., 2020; Guariento et al., 2023; Schwarz and Fartmann, 2021; Warren et al., 2021).

4.2. Local grazing pressure plays a key role in shaping taxonomic diversity

Local grazing pressure emerged as a critical factor influencing the TD of the whole community, with special reference to the diversity of dominant species (Simpson index). Sustaining a sufficiently intense and evenly distributed local grazing pressure within grasslands may help ensure sustainable forage consumption, balanced nutrient provision, and avoid the strong dominance of few species (Napoleone et al., 2022a). Indeed, moderate grazing intensity is widely recognised as a key factor in maintaining species diversity in semi-natural grasslands (Bengtsson et al., 2019; Johansen et al., 2019; Schils et al., 2022). Undergrazing can lead to the spread of competitive species, resulting in reduced diversity (Cislaghi et al., 2019; Zou et al., 2016), while overgrazing may cause dominance by few species with grazing tolerance strategies (Chillo et al., 2017; Díaz et al., 2007; Myrsterud, 2006). Both processes are detrimental to forage quality and species diversity conservation, harming ecosystem conservation and services.

The dry calcareous grasslands here investigated are characterized by low grazing carrying capacity and very low to moderate stocking rates. Within this context, grazing regimes defined at the farm level - such as stocking rate, grazing system, and livestock species - did not significantly influence TD. The stocking rate, recorded at the farm scale, failed to explain TD patterns, likely because its spatial resolution does not reflect the fine-scale heterogeneity in species composition that we observed within farms (Napoleone et al., 2022a). Similarly, grazing regimes often associated with higher biodiversity, such as rotational grazing and/or shepherding (Perotti et al., 2018; Ravetto Enri et al., 2017), exhibited no effect on TD in our case. In contrast with previous studies that found cattle to be associated with higher species richness

and abundance of flowering species as compared to sheep (Carvell, 2002; Cutter et al., 2022; Ravetto Enri et al., 2017; Tóth et al., 2018), we found no significant influence of livestock species on TD.

These findings highlight that, in extensively managed dry calcareous grasslands, the impact of grazing on biodiversity is not adequately captured by farm-level grazing regimes. Instead, it is the actual local grazing pressure that drives the fine-scale patterns of vascular plant diversity. This emphasizes the importance of accounting for within-farm heterogeneity when assessing the ecological outcomes of extensive grazing management.

4.3. Flower traits' patterns strongly rely on species evenness

Local grazing pressure influenced the TD of the whole plant community and, indirectly, the FD and CWM of flowering species. Moderate grazing increased the diversity of dominant species, as indicated by a higher Simpson index, which emphasizes abundant taxa. However, this did not necessarily lead to greater FD of floral traits, as many pasture-related dominant species - such as *Carlina corymbosa*, *Pilosella officinarum*, *Leontodon hispidus* - share similar floral characteristics (e.g. actinomorphic, yellow flowers). In contrast, when high Simpson diversity coincided with a high Shannon index - reflecting a more even distribution of rare species i.e., those with low abundance values in our sampling - FD increased, with greater representation of bilaterally symmetrical and non-yellow flowers. Functionally distinct but less dominant species, such as *Thymus longicaulis*, *Teucrium chamaedrys*, and *Ononis spinosa*, contributed to this pattern. These results suggest that FD of floral traits is enhanced not by dominance-driven diversity, but by a balanced community composition encompassing both dominant and rare species.

The diversity of flower symmetry supports a wide range of pollinators since zygomorphic flowers are often visited by specialized pollinators (Fenster et al., 2004; Keasar, 2020; Poisot et al., 2011; Yoder et al., 2020). Indeed, their evolution from ancestral actinomorphic flowers, around 50 million years after the emergence of angiosperms, coincides with the diversification of specialized pollinators (Citerne et al., 2010; Hileman, 2014; Reyes et al., 2016), as these morphologically complex flowers restrict nectar access and favor specific pollinator groups with appropriate morphologies, such as bees with specialized mouthparts (Jirgal and Ohashi, 2023; Krishna and Keasar, 2018; Lázaro and Totland, 2014; Zhao et al., 2016). Notably, bilateral symmetry frequently

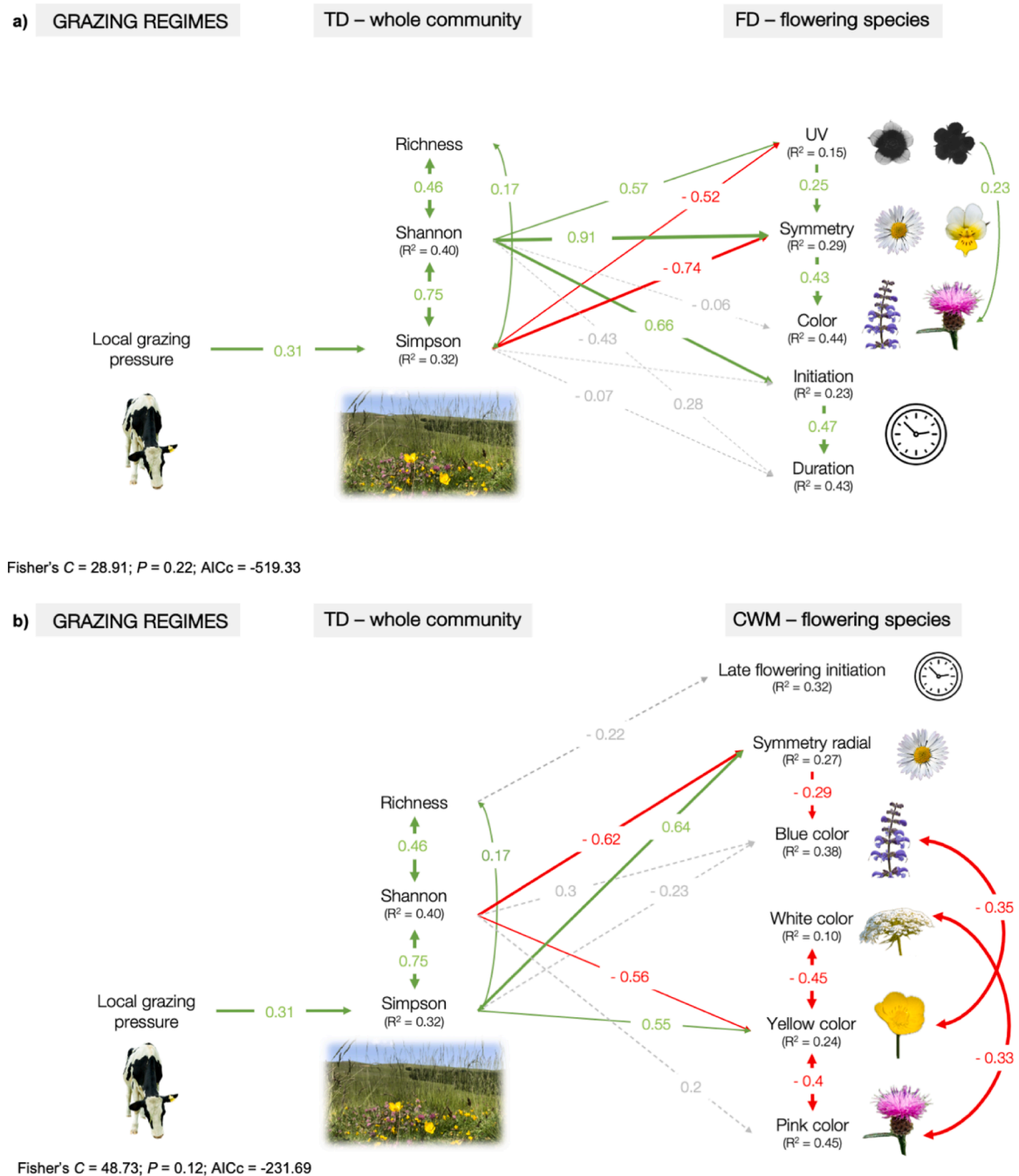


Fig. 4. Structural equation models (SEM) with grazing regimes and taxonomic diversity (TD) as predictors of (a) functional diversity (FD) and (b) community-weighted mean (CWM) of flower traits. Solid and dashed arrows represent, respectively, significant ($p < 0.05$) and non-significant ($p > 0.05$) links; green and red arrows indicate, respectively, positive and negative links. Path coefficients are standardized. Fisher's C statistic, its significance (P), and corrected AIC (AICc) are reported at the bottom.

coincides with tubular corollas, accessible only to long-tongued pollinators (Amorim et al., 2014; Johnson et al., 2017; Nilsson, 1988; Werth, 1997).

Also, the diversity of floral reflectance spectrum, positively correlated with FD of flower symmetry, facilitates the presence of different insect pollinators, owing to the variation in their visual systems and color perception abilities (Harder and Barrett, 2006; van Der Kooi et al., 2021). Many insects are attracted to yellow flowers as this color enhances signals from green receptors and blue and/or UV receptors (Prokopy and Owens, 1983). Nevertheless, abundant blue and violet flowers support a wide range of insects with trichromatic vision and/or blue-sensitive photoreceptors, such as bees and butterflies (Giurfa et al.,

1995; Lunau and Maier, 1995; van der Kooi et al., 2023; van Der Kooi et al., 2021). However, information on the vision of many solitary and wild bees is lacking and other factors such as background vegetation color could also influence insects' ability to identify different flower colors (van Der Kooi et al., 2021).

In conclusion, these insights provide further understanding of how extensive grazing can influence biodiversity patterns in semi-natural grasslands. Our findings suggest that moderate local grazing pressure effectively sustains flower diversity in dry semi-natural grasslands as it ensures an even species abundance, including both dominant and rare species. This potentially supports a broad range of pollinators, including specialist insect groups that are declining due to habitat degradation

(Brodie et al., 2014; Fortuna and Bascompte, 2006).

5. Study limitations and opportunities

We examined the links between extensive grazing and flower functional diversity and traits' composition in semi-natural dry grasslands exploring the role of taxonomic diversity in mediating these links.

Our findings indicate a possible pathway towards conserving the role of dry calcareous grasslands in pollination services through extensive grazing, which favours flower traits beneficial to insect pollinators. It is important to mention that the distribution of grazing pressure within farms significantly affects flower diversity. Therefore, regulating grazing as locally as possible may sustain diverse pollinator communities by maintaining a range of floral traits aligned with their foraging and sensory preferences. This implies that defining grazing regimes at the farm scale is not sufficient: such regimes must be implemented and adjusted at finer spatial scales, taking into account the ecological heterogeneity, e.g., microtopography, typical of semi-natural grasslands, especially in mountainous regions where it substantially influences livestock movements. Local regulation of grazing parameters - including stocking rate, grazing technique, and livestock type - should aim to ensure adequate grazing pressure, also depending on the fine-scale mosaic of vegetation, and avoid, for instance, excessive litter accumulation in some areas and soil erosion in others. This approach is not only relevant to the functional diversity of insect-pollinated species, but also to the conservation status of the habitat and the maintenance of forage yield and quality, as previously demonstrated (Napoleone et al., 2022a).

In this regard, we quantified local grazing pressure as a combined gradient based on several well-established field proxies. While this approach allows for a standardized estimation across sampling units, further studies supported by direct data on livestock movement (e.g., from GPS collars) could contribute to further improving the precision of these estimates. At a broader scale, meta-analyses and reviews will be essential to upscale these relationships across different environmental and management contexts.

Noteworthy, our study did not include empirical data on insect community composition, thus predicting which pollinator insects would occur under different management practices remains beyond the scope of this study. We acknowledge the need for caution when employing flower traits to infer plant-insect interactions, as this approach may oversimplify the complexity of natural dynamics, particularly when observational data on pollinators is missing (Dellinger, 2020; Ollerton et al., 2009; Rosas-Guerrero et al., 2014; but see Ashworth et al., 2015). Flowers attract a broader range of visitors than what is expected solely from flower traits and secondary/less efficient pollinators may also influence flower traits. A future opportunity lies in sampling richness and visitation frequency of insect pollinators to profoundly enhance our understanding of how grazing management influences the precise composition of pollinators via flower traits.

While our study directly addresses the ecological consequences of grazing abandonment - a major driver of land-use changes in mountain grasslands - it does not consider the potential interacting effects of climate change. Future research should therefore investigate how grazing practices and climate-related stressors jointly shape plant-pollinator interactions and grassland functioning over time.

CRedit authorship contribution statement

Francesca Napoleone: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Mas-similiano Probo:** Writing – review & editing, Validation, Investigation. **Raffaella Frondoni:** Writing – review & editing, Investigation. **Michele Lonati:** Writing – review & editing, Investigation. **Simone Ravetto Enri:** Writing – review & editing, Investigation. **Sabina Burrascano:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization. **Giovanni**

Argenti: Writing – review & editing, Investigation.

Author contributions

FN and SB conceived and designed the study; FN, SB, RF, MP, SER, ML, and GA contributed to data acquisition; FN analyzed the data; FN and SB interpreted the data and drafted the manuscript; FN, SB, MP, SER, ML, GA, and RF critically revised the article and gave final approval of the submitted version.

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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.2025.109883](https://doi.org/10.1016/j.agee.2025.109883).

Data Availability

Data will be made available on request.

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