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Managing for conservation: The case study of *Marsilea quadrifolia* L. in wet meadows of Natura 2000 site (N Italy)

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A B S T R A C T

Wet meadows are biodiversity-rich habitats in Europe, central to the Natura 2000 network, hosting threatened species. *Marsilea quadrifolia* L., an aquatic pteridophyte of conservation concern, is a pioneer, disturbance-dependent species relying on open semi-natural wetlands, threatened by changing agricultural practices.

We assessed the effects of traditional management – seasonal grazing and annual mowing – implemented by an organic farm on *M. quadrifolia* and plant community composition in a wet Nature Reserve in Lombardy Region (N Italy), which hosts the extant wet meadow population and the largest known to date. Managed and unmanaged (exclusion) areas were compared using vegetation surveys over four years (2021–2024), assessing species cover, diversity indices, functional Grime' strategies, Ellenberg indicator values, water table fluctuations and *M. quadrifolia* chlorophyll content as a stress indicator.

M. quadrifolia abundance was significantly higher in traditionally managed areas, while plant diversity did not significantly differ among treatments. Unmanaged areas exhibited higher percentage of stress-tolerant and competitive strategies, and a marked reduction in ruderal species, including *M. quadrifolia*, along with lower light demand. Drought limited *M. quadrifolia* in 2022, whereas wetter conditions in 2024 promoted its expansion. Chlorophyll measurements indicated no ecophysiological stress associated with exclusion.

Low-intensity, seasonal grazing combined with mowing maintains open patches, reduces competition, and supports threatened species such as *M. quadrifolia*. Traditional management within Natura 2000 sites remains essential for integrating conservation and agricultural use. Adaptive, context-specific management aligned with hydrological dynamics and plant phenology is essential to sustain wet meadows under changing water availability driven by climate change.

1. Introduction

Wet meadows are biodiversity-rich habitats acting as transitional zones between permanently flooded semi-natural wetlands and mesophilous grasslands. They are among the most species-rich grasslands in Europe, supporting vascular plants, bryophytes, invertebrates, amphibians, and birds adapted to fluctuating water regimes (EEA, 2020; European Commission, 2016). Several wet meadow types are recognized as habitats of Community interest under the EU Habitats Directive (92/43/EEC) and Birds Directive (2009/147/EC), such as habitat 6410 "*Molinia* meadows on calcareous, peaty or clayey-silt soils (*Molinion caeruleae*)" and 6510 "lowland hay meadows (*Alopecurus pratensis, Sanguisorba officinalis*)". These habitats provide key breeding, feeding and resting areas for many migratory birds and other species within the Natura 2000 network in Europe.

Despite their ecological importance, wet meadows have sharply declined across Europe (Wesche et al., 2012). Natural and semi-natural grasslands are among the most deteriorated habitat types, with 75% of all 126 recognized grassland types in Europe in poor or bad conservation status (EEA, 2020). This decline results from abandonment of traditional management, agricultural intensification, mechanization, chemical inputs, and wetland drainage (Corli et al., 2021a; Bonari et al., 2017; Halada et al., 2011). The remaining wet meadows are often highly fragmented and require targeted management or restoration to maintain their ecological functions (European Commission, 2016).

For centuries, wet meadows were integral elements of European

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landscapes, shaped by geographic, climatic, and cultural traditions (Janišová et al., 2023). Their persistence depended on low-intensity agricultural management (Feurdean et al., 2018; Bonari et al., 2017), including hay mowing, grazing or a combination of both practices (Janišová et al., 2023). These extensive practices have been fundamental in maintaining wet meadow biodiversity (Kołos & Banaszuk, 2013). Long-term managed meadows typically support higher vascular plant diversity than recently established or abandoned sites, which tend to be dominated by successional or highly productive species such as *Carex brizoides* L. (Straubinger et al., 2022). Mowing enhances structural heterogeneity by increasing light availability and temperature while reducing soil moisture (Zechmeister et al., 2003), whereas grazing acts mainly through disturbance processes such as defoliation, trampling, and nutrient input via dung and urine (Liu et al., 2015). The ecological effects of these practices depend on their timing, intensity, and the handling of mown vegetation (Humbert et al., 2012).

Mowing and grazing can support rare and threatened species that would otherwise decline under natural succession towards more stable competitive communities (Middleton et al., 2006). Examples include vascular plants such as *Euphorbia palustris* L. (Muller, 2002), *Dactylorhiza majalis* (Rchb.) P.F.Hunt & Summerh. (Wotavová et al., 2004) and *Narcissus poeticus* L. (Fuchs et al., 2024), as well as invertebrates like the bush-cricket *Saga pedo* Pallas (Repetto et al., 2024). Disturbance-dependent bryophytes and annuals, including *Phaeoceros carolinianus* (Michx.) Prosk. and *Arnoseris minima* (L.) Schweigg. & Körte also benefit from traditional management but decline under both intensification and abandonment (Bisang et al., 2021). Although such practices support biodiversity, their application in modern agricultural landscapes must consider economic, social, and regulatory constraints.

Reconciling conservation with agricultural practices requires considering farmers' and stakeholders' perspectives, including potential yield reduction, management costs, and restrictions linked to protected species (Abeli et al., 2022). Nonetheless, agri-environmental schemes (AES) and financial incentives within the EU Rural Development Plan (RDP) can support both biodiversity conservation and farm income (Batáry et al., 2015), particularly when farmers are actively involved and aware of the ecological outcomes (Abeli et al., 2022). Appropriate management – such as mowing and grazing – can sustain threatened meadow species including *Dactylorhiza lapponica* (Laest. ex Hartm.) Soó (Sletvold et al., 2010), and initiatives such as AES (Cordier et al., 2025), INTERREG (e.g., Fuchs et al., 2024) and LIFE projects (e.g., LIFE Ballesteros) have proven effective in preserving high-value meadows. These interventions are especially important where agricultural landscapes deliver key ecosystem services – such as habitat provision, pollination support and water regulation – and where they contribute directly to the conservation of species and habitats of Community interest within the Natura 2000 network. However, inadequate post-intervention monitoring and limited adaptive management can compromise the long-term persistence of both reintroduced and naturally occurring populations (D'Agostino et al., 2024).

The aquatic pteridophyte *Marsilea quadrifolia* L. (Marsileaceae), is a native water clover typical of wet habitats in Eurasia, occurring in shallow lakes, edges of ponds, and anthropogenic wetlands such as ditches, rice fields and wet meadows (Corli et al., 2021a; Tutin et al., 2010). As a pioneer and heliophilous species, it thrives in open, disturbed habitats with limited interspecific competition, but during succession it is rapidly outcompeted by taller species such as Phragmites australis (Cav.) Trin. ex Steud and *Typha angustifolia* L. (Schneider-Binder, 2014), as well as by alien and invasive species including Heteranthera reniformis Ruiz & Pav., Ammannia coccinea Rottb., and Cyperus microiria Steud (Corli et al., 2021b). The species life cycle is tightly linked to water-level fluctuations: under submerged conditions it develops long, flexible petioles with floating leaves, while in emergent conditions petioles are shorter and more rigid. In this terrestrial phase, the plant produces long-lived sporocarps containing micro- and mega-spores that can persist in the sediment for decades, forming a persistent spore bank (Magnes, 2015).

Historically widespread in Europe and once considered a weed in rice fields, *M. quadrifolia* has declined sharply since the 1950 s due to agricultural intensification, mechanization, use of chemicals (Bruni et al., 2013), simplified rotation, and habitat drainage (Corli et al., 2021a). For this reason, the species is now protected under the Bern Convention (Appendix I) and the EU Habitats Directive (Annexes II and IV), and is listed in various Red Lists: globally "Least Concern" (Gupta, 2011), European "Vulnerable" (Christenhusz et al., 2017) and "Critically Endangered" or "Endangered" in several European countries (Corli et al., 2021a), including Italy (Rossi et al., 2016). In Italy, populations occur both in rice fields, where conservation measures combining scientific support, incentives, and farmer participation have shown promising results (Corli et al., 2024; Corli et al., 2025), and in semi-natural wet meadow, which represents the only extant population in this habitat and the largest known in the country, but currently lacks targeted management.

We present a study, supported by the RDP of the Lombardy Region (N Italy), assessing how traditional management – grazing and mowing – affects both the persistence of *Marsilea quadrifolia* and overall wet meadow biodiversity. The research was conducted in the "Pian di Spagna e Lago di Mezzola" Nature Reserve, part of the Natura 2000 network. Within the Reserve, an organic farm received incentives to participate, managing its wet meadows – primarily used for cattle grazing and hay mowing – under the experimental framework. We evaluated the effects of traditional management on *M. quadrifolia* performance and plant diversity, compared to simulated abandonment (i.e., exclusion of seasonal grazing and mowing). Species abundances, community composition, ecological strategies, ecophysiological traits, and key environmental factors were investigated. We hypothesized that traditional management would favour ruderal species including *M. quadrifolia*, enhancing its physiological performance. In contrast, exclusion of management was expected to promote stress-tolerant and competitive strategies, leading to an overall compositional shift. As an aquatic plant, *M. quadrifolia* persistence and performance were also expected to depend on hydrological regime, being negatively affected by lowering of the seasonal water table depth.

2. Material and methods

2.1. Study site

The "Pian di Spagna e Lago di Mezzola" Nature Reserve (Fig. 1) is a Regional Reserve located in the northernmost part of Lombardy, in the province of Como, N Italy (46°10′N 09°25′E, 200 m a.s.L.). The climate is semi-continental, with annual precipitation ranging from 1,100 to 1,300 mm. Mean temperatures vary from 5°C in winter to 23°C in summer, with a mean annual temperature of 12.8°. The Reserve lies at the confluence of the Adda and Mera rivers and encompasses Lake Mezzola and the extensive alluvial plain of Pian di Spagna, at the northern tip of Lake Como. The area is surrounded by three Alpine groups: the Lepontine, Rhaetian and Orobic Alps. The Pian di Spagna alluvial plain, formed by sediment deposits from the Adda river, has relatively recent geological origins, and the substrate is predominantly coarse, silty-sandy materials (Osio & Tartarini, 2010). Covering 1,740 ha, the terrain is mostly flat, shaped by the interaction of natural processes and human interventions. Historically, river flooding promoted marsh development; however, these areas were long considered unproductive and subjected to extensive land reclamation. As a result, the landscape presents a mosaic of habitats, including reed beds, floodplain meadows, and riparian woodlands, supporting high floristic and faunal diversity.

The Reserve is recognized as a wetland of international importance (Ramsar Site no. 117, designated in 1980) and is part of the Natura 2000 Network as both Site of Community Importance and a Special Protection Area (SCI/SPA IT2040042 "Lago di Mezzola Pian di Spagna"). The area

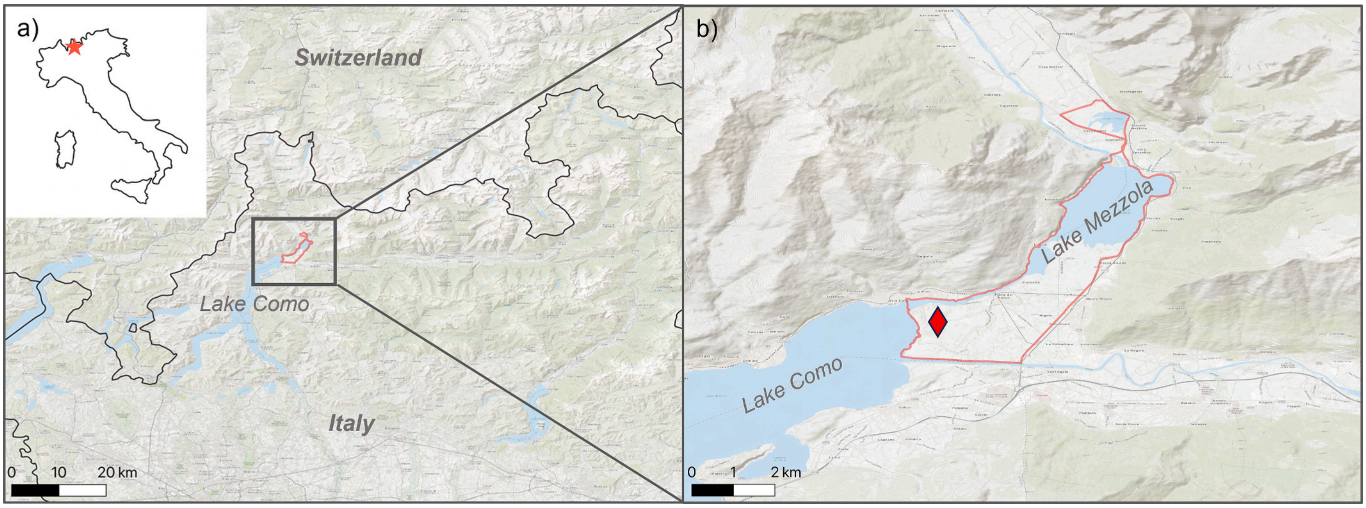

Fig. 1. Study area. a) Location of “Pian di Spagna e Lago di Mezzola” Nature Reserve in northern Italy (red star) and b) detail of the study area within the SCI/SPA boundary (red line). The location of *M. quadrifolia* population is represented with the red diamond. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

is characterized by habitat of Community interest (Directive 92/43/EEC), including: 3150 “Natural eutrophic lakes with *Magnopotamion or Hydrocharition-type* vegetation”, 91E0 “Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior* (Alno-Padion, Alnion incanae, Salicion albae)” as well as 6410 and 6510 habitats. Several species of high conservation value occur within the SCI/SPA, including the biggest Italian population of *Marsilea quadrifolia* L., which has declined elsewhere in the country.

2.2. Experimental context and design

The experimental was conducted in a wet meadow within the “Bio-Angus” organic farm (Sorico municipality, Como province), where *M. quadrifolia* occurs in an area of 2000 m^2. The farm manages 110–120 Black Angus cattle under certified organic conditions, feeding them exclusively with grass and hay. Since 2010, 20–30 animals have grazed the wet meadow (~23’000 m^2) for two to three weeks in spring (April-May), before being moved to alpine pastures for the summer months (June-September). They then return to the wet meadow for grazing in September-October. During the growing season, cattle rely exclusively on pasture vegetation, with no supplementary feeding provided. From late autumn until the following spring, cattle are kept in the cowshed. Mowing is performed once per year during the driest period of summer, with the cut forage sun-dried and baled for use as supplementary feed during the dry period since it has relatively low nutritional value. No other management practice is implemented in the area (e.g., manuring). This management scheme represents the general pattern, although the timing and duration of grazing and mowing may vary slightly among years depending on climate conditions and water levels.

To test the hypothesis that traditional management promotes optimal growth of *M. quadrifolia*, we established a four-year experiment (2021–2024) comparing managed (grazing and mowing) and unmanaged (exclusion of both) treatments. The managed treatment corresponded to a randomly selected area while the unmanaged area was established by installing two electric fences (300 m^2 and 120 m^2) before cattle arrival (21 April 2021). The size and location of the exclusion areas were chosen based on the morphology of the wet meadow and the spatial distribution of *M. quadrifolia* population. Timing and duration of grazing and mowing varied slightly between years depending on climatic conditions and water table depth (Table 1). Due to the rarity and highly restricted distribution of M. quadrifolia in Italy, the study was necessarily limited to a single site, embedding the largest Italian population. While this limits the broader applicability of results, no suitable replicates were available, as the few other Italian populations occur mainly in rice fields, which differ substantially in ecological conditions from the study site (Corli et al., 2021a).

Table 1
Timing of management practices in the wet meadow (spring grazing, mowing, and autumn grazing), vegetation surveys, and water table monitoring (in brackets, the number of monitoring dates) during the 2021–2024 period.

Year	Spring grazing	Mowing	Autumn grazing	Vegetation survey	Water table evaluation (n. survey)
2021	05-may/08-jun	no	No	01-jul	26-apr/05-nov (13)
2022	25-apr/12-may	18-jul	01-oct/15-oct	16-jun	20-apr/20-nov (15)
2023	20-apr/10-may	06-aug	10 oct-18-oct	27-jun	24-apr/01-nov (14)
2024	25-apr/15-may	19-aug	01-oct/14-oct	02-jul	19-apr/14-nov (15)

2.3. Data collection and elaboration

To evaluate the effect of management on *M. quadrifolia* and overall vascular plant diversity, vegetation surveys were conducted annually at the peak of the growing season (late June-early July; Table 1). In 2021, twenty 1 m × 1 m plots (ten replicates per treatment) were randomly distributed within each treatment; due to homogeneous vegetation among plots, ten plots (five per treatment) were resurveyed in subsequent years. For each plot, a vascular plant checklist was compiled to determine species richness, and species abundance was visually estimated as percentage cover. Considering overlapping vegetation layers, total cover could exceed 100%; the percentage cover of each species was then converted into the relative abundance (proportion of each species’ cover to total plot cover). Species nomenclature was harmonized using the *Flora of Italy* database (PFI, 2025). Diversity indices (Magurran, 2013), i.e., Shannon-Wiener (H’), Simpson (1-D) and Pielou’s evenness (J) were calculated for each plot using the *diversity* function in the *vegan* package (Oksanen et al., 2024) with RStudio (R Core Team, 2024). The collected data provide a reliable basis for assessing the performance of *M. quadrifolia* and the overall vascular plant diversity.

To evaluate the influence of management on community functional composition and environmental preferences, ecological strategies for each species and plot were assessed using Grime’s CSR (Competitor, Stress-tolerant, Ruderal) framework (2001) via the *StrateFy* application (Pierce et al., 2017). For each species, the percentage contribution of C, S, and R traits were obtained, and each score (C-, S-, R-) was weighted by the species' relative abundance to compute the Community-weighted mean (CWM) for each plot. Ellenberg Indicator Values (EIVs) for moisture (F), light (L), soil fertility (N), pH (R) and temperature (T) were also obtained (Ellenberg et al., 1991); CWM of each EIV was calculated by weighting species scores by their relative abundance. Life forms and invasiveness status (native or non-native) were recorded for all species (PFI, 2025).

To assess potential ecophysiological stress in *M. quadrifolia*, chlorophyll content was measured using a SPAD chlorophyll meter (SPAD-502, Konica Minolta, Tokyo, Japan) on 15 fully expanded leaves per treatment at two weeks intervals 26 July-18 September 2024; 5 monitoring days).

To evaluate the influence of hydrological regime on *M. quadrifolia* growth and persistence, water table depth was monitored using graduated PVC tubes at six fixed points. Measurements were taken at 15-day intervals from April to November (Table 1). Mean, minimum and maximum water table depth were used as indicators of hydrological regime. Data on monthly air temperature and precipitation were obtained from a weather station located approximately 3 km from the study site (Colico municipality).

2.4. Data analysis

Relative abundances of plant species were used to assess differences among treatment (factorial variable with two levels: managed, unmanaged) and year (factorial variable with four levels: 2021, 2022, 2023, 2024). Community composition was visualized using non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities (*metaMDS* function, *vegan* package, $k = 2$, 100 random starts), with stress values < 0.2 considered acceptable.

Differences in community composition based on relative abundance of species among management practices, years, and their interaction were tested using permutational multivariate analysis of variance (PERMANOVA; *adonis2* function, *vegan* package). Homogeneity of multivariate dispersion was verified prior to analysis using the *betadisper* function with permutation tests. Due to the unbalanced design, separate models were fitted for treatment, year, and their interaction. Species contributing most to differences among treatment and year were identified using *SIMPER* analysis.

Differences in abundance of indicator species, species richness, diversity indices, and CWM of each EIV (i.e., F, L, N, R, T) were analysed using two-way ANOVA with treatment and year as factors. For EIVs, a correlation matrix was computed to assess the relationships among the ecological indicator values. Post-hoc comparisons were performed using Tukey's HSD, and assumptions of normality and homogeneity of variance were checked, with data transformations applied when necessary.

The influence of functional strategies at community composition was assessed using factorial ANOVA on the CWM, with dominant functional strategy component (C, S, or R), treatment, and year as factors, including all main effects and interactions. Chlorophyll content was used as a proxy for ecophysiological stress and analysed using a generalized additive model (GAM) with treatment as a fixed factor and monitoring date as a smoothed term to account for temporal trends. Effects of treatment on invasiveness and life-forms composition were not analysed since all species were native and life-form composition was homogeneous. All analyses were performed in R (R Core Team. (2024), 2024.

3. Results

3.1. Community composition and biodiversity metrics

The complete floristic surveys recorded 37 vascular plant taxa belonging to 20 families (Table S1). Cyperaceae was the most represented family (8 species, 22%), followed by Poaceae (4 species, 11%), Asteraceae and Fabaceae (3 species each, 8%). Plot-level species richness ranged from 4 to 18 species, with all species being native; only *M. quadrifolia* is considered a threatened species.

NMDS ordination indicated no clear clustering by treatment or year (stress $= 0.22$), suggesting a relatively homogeneous community composition (Fig. S1). PERMANOVA detected a small but significant effect of treatment ($R^2 = 0.049$, $F = 2.458$, $p = 0.023$), while year ($R^2 = 0.180$, $F = 3.365$, $p = 0.001$), and the interaction year × treatment ($R^2 = 0.294$, $F = 2.498$, $p = 0.001$), showed a stronger effect, highlighting temporal variation and minor differences in management influence over time.

Species richness varied significantly across years (Table 2) but was not affected by management practices. Mean richness increased over time, reaching 12.4 ± 1.6 species in managed plots and 13.6 ± 1.1 in unmanaged plots in 2024 (Table 3). Diversity indices (Shannon-Wiener, Simpson, and Pielou) did not differ significantly among years (Table 2), although unmanaged plots tended to show slightly higher diversity and evenness over time compared to managed plots (Table 3).

3.2. Indicator species abundance

Marsilea quadrifolia was the main driver of compositional dissimilarities between treatments, accounting for 16.7% of the total Bray-Curtis dissimilarity (Fig. 2a; Table S2). Its relative abundance was significantly higher in managed (52%) than unmanaged plots (34%; Fig. 3; Table 2; Table S1). *Carex vesicaria* (6.7%) and *C. elata* (5.3%) also contributed to treatment differences, although their relative abundance did not differ significantly between managed and unmanaged plots (Table 2; Fig. 3; Table S1). Conversely, *Equisetum palustre* and *Phragmites australis* contributed significantly to dissimilarities between treatments (Table S2), showing higher relative abundance under unmanaged conditions (Table 2; Fig. 3). Interannual variations were observed for several species (Table S2). *M. quadrifolia* remained the top contributor to dissimilarity across all years (16.8%; Fig. 2b), with relative abundance generally stable over time (Table S2), although it increased in the managed treatment and decreased in the unmanaged one (Fig. 3). Over

Table 2
Results of the ANOVAs testing the effects of Year, Treatment (Managed vs Unmanaged), and their interaction (Year × Treatment) on biodiversity metrics (species richness, Shannon-Wiener Index, Simpson Diversity Index, and Pielou's Evenness Index), the relative abundance of indicator species (i.e., *Marsilea quadrifolia, Phragmites australis, Carex vesicaria, Carex elata, Equisetum palustre*), and Ellenberg indicator values, namely soil fertility (N), temperature (T), moisture (F), light (L), and soil pH (R). Reported are F-values and significance levels. Significance codes: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; + $p < 0.1$; n.s. = not significant.

	Year (F; sign.)	Treatment (F; sign.)	Year x Treatment (F; sign.)
Biodiversity metrics			
Species richness	6.601; ***	0.938; n.s.	0.934; n.s.
Shannon-Wiener Index	0.697; n.s.	3.179; +	0.447; n.s.
Simpson Index	0.412; n.s.	3.698; +	0.546; n.s.
Pielou Index	0.125; n.s.	3.260; +	0.495; n.s.
Indicator species abundance			
M. quadrifolia	0.19; n.s.	3.65; ***	0.87; n.s.
P. australis	3.79; *	14.72; ***	3.46; *
C. vesicaria	6.92; ***	0.04; n.s.	1.23; n.s.
C. elata	8.02; ***	0.02; n.s.	1.81; n.s.
E. palustre	1.22; n.s.	7.28; *	1.42; n.s.
Ellenberg indicator values			
N	0.750; n.s.	2.780; n.s.	0.630; n.s.
T	1.053; n.s.	2.278; n.s.	2.070; n.s.
F	1.403; n.s.	0.730; n.s.	0.575; n.s.
L	1.040; n.s.	7.844; ***	1.782; n.s.
R	1.211; n.s.	2.133; n.s.	0.214; n.s.

Table 3
Diversity metrics in managed and unmanaged plots from 2021 to 2024. Values are presented as mean (and standard error). Annual values and overall means are reported for each management type in bold.

	Year	Species richness (N)	Shannon-Wiener Index	Simpson diversity Index	Pielou's evenness
Managed	2021	10 (0.7)	1.492 (0.163)	0.637 (0.067)	0.640 (0.064)
	2022	7.4 (1.1)	1.276 (0.177)	0.574 (0.077)	0.641 (0.056)
	2023	12.8 (1.0)	1.509 (0.097)	0.668 (0.028)	0.594 (0.024)
	2024	12.4 (1.6)	1.488 (0.265)	0.620 (0.084)	0.587 (0.075)
	Mean	**10.9 (0.9)**	**1.442 (0.176)**	**0.624 (0.064)**	**0.615 (0.053)**
Unmanaged	2021	10.7 (0.9)	1.580 (0.160)	0.665 (0.060)	0.667 (0.047)
	2022	9.6 (0.5)	1.602 (0.150)	0.724 (0.045)	0.709 (0.061)
	2023	11.4 (0.7)	1.673 (0.196)	0.737 (0.049)	0.683 (0.065)
	2024	13.6 (1.1)	1.947 (0.110)	0.786 (0.034)	0.750 (0.041)
	Mean	**11.3 (0.8)**	**1.700 (0.154)**	**0.728 (0.047)**	**0.702 (0.053)**

this period, C. vesicaria and C. elata increased significantly in their contribution to dissimilarity (9.5 and 5.9%, respectively), and their relative abundance significantly increase over time (Table 3), peaking in 2022 for the former and in 2024 for the latter (Fig. 3). Equisetum palustre and Phragmites australis contributed less to community dissimilarities across years (Fig. 2b), although *P. australis* increased significantly toward the end of the monitoring period, while *E. palustre* remained relatively stable (Fig. 3; Table S2).

3.3. Functional strategies and ecological preferences

CSR strategies varied in the wet meadow, with ruderal species being the most frequent (13 species), followed by stress-tolerant species (10 species; Table S1). Competitor species were the least represented (3 species). Community-weighted means (CWM) of CSR components revealed consistent patterns (Fig. 4; F $F_{2,126} = 92.21$; $p < 0.001$), with the C component lower than S and R. The significant interaction between Strategies × Treatment ($F_{2,126} = 5.09$; $p = 0.007$) indicated that the R component was higher in managed plots, whereas both S and C components were higher in unmanaged plots.

Ellenberg indicator values (N, T, F, L, R) showed strong positive pairwise correlations among nutrient, temperature, moisture, and light values, while soil pH (R) was negatively correlated with the other indicators (Table S3), suggesting contrasting environmental gradients. All ecological requirements (EIV) tended to be higher in managed plots except for soil pH. However, significant differences were detected only for CWM of light L (Table 2). Life-form composition was consistent across treatments: hemicryptophytes dominated the community (36%), followed by geophytes (22%) and therophytes (16%; Table S1).

3.4. Ecophysiological traits and environmental conditions

Water table depth fluctuated strongly both temporally and inter-annually (−100 to + 35 cm), reflecting variable groundwater availability driven by climate and lake-level dynamics (Fig. S2a). 2021 was the coldest year (mean 13.2°C), with a mild and unexpectedly rainy summer. 2022 was the driest year (1165 mm), with the water table remaining below the soil surface during the entire monitoring period. Alternating drawdowns and floods marked 2023, whereas 2024 was persistently wet (1811 mm), with the water table consistently above the soil surface. Mean annual temperature rose by 1.4°C over the study period, peaking at 14.6°C in 2024, with August maxima of 33.3°C (Fig. S2b).

Chlorophyll content in *M. quadrifolia* was slightly higher in managed plots (31.1 vs 30.4 SPAD units), although management alone was not significant (t value = -1.641, $p = 0.103$). Chlorophyll content exhibited significant temporal fluctuations only in the managed treatment (edf = 3.826, $p < 0.001$), with peaks at the beginning and towards the end of the study (Fig. 5) while the unmanaged treatment showed a more linear trend over time (edf = 1.00, $p = 0.178$).

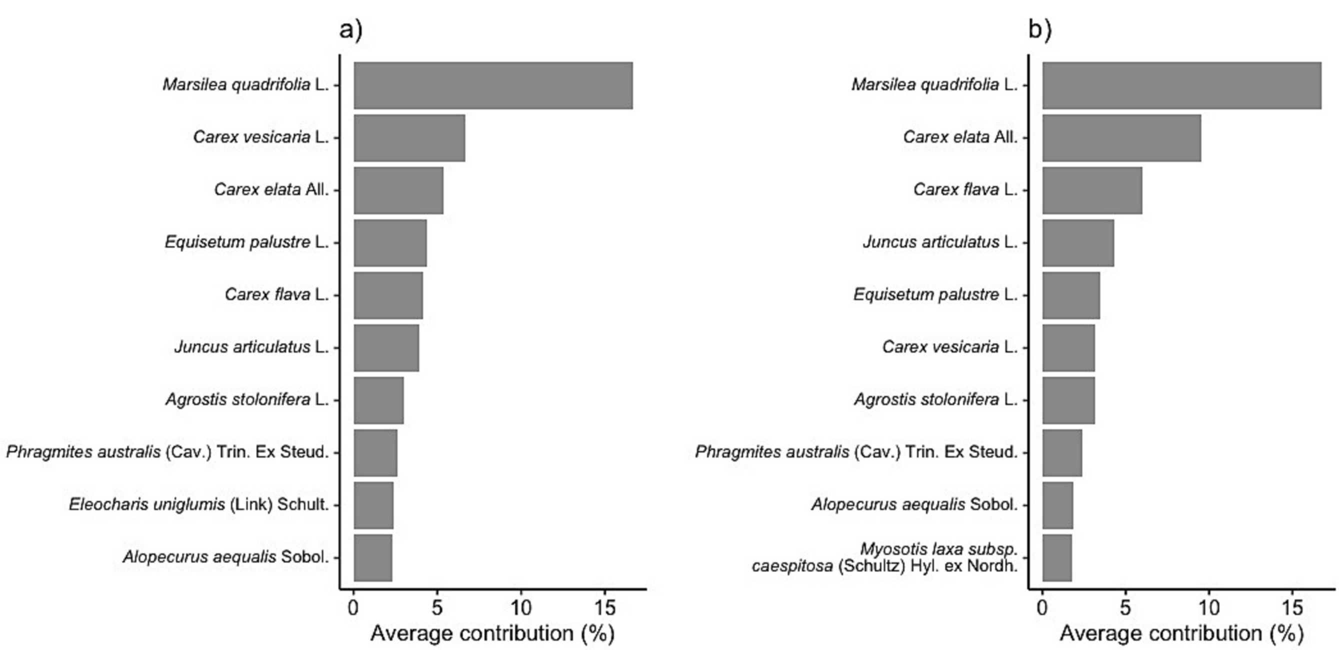

Fig. 2. Top discriminant species identified through SIMPER analysis. The bar plots show the average contribution (%) of the most influential species to dissimilarity between a) management and unmanaged treatment and b) 2024 and 2021.

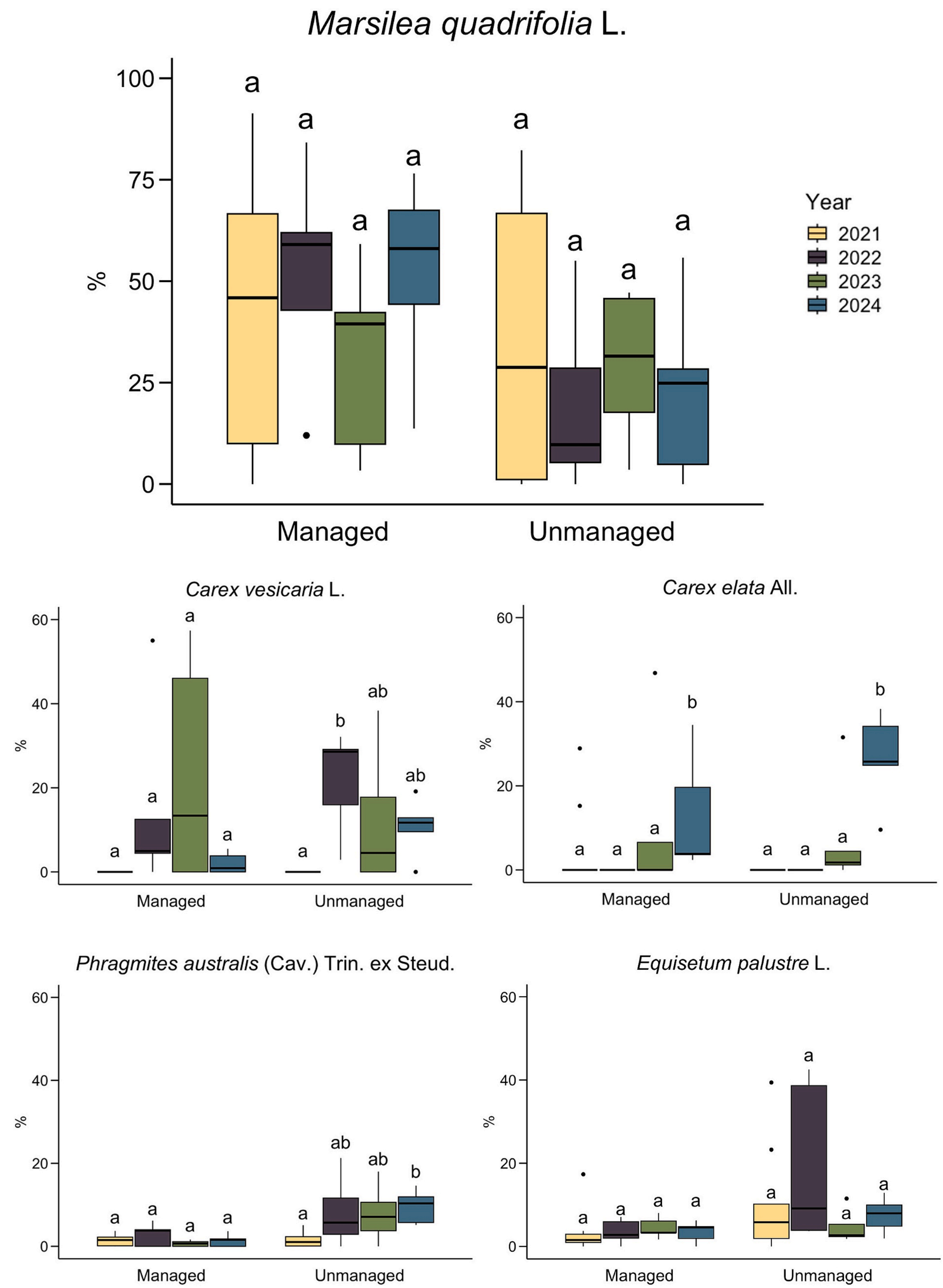

Fig. 3. Abundance of the most representative species in managed and unmanaged plots in the years of monitoring. Box plots show the median per group (solid line), boxes represent the 25th and 75th quartiles, whiskers represent the normal data range, and dots represent outliers. Letters indicate significant differences ($p < 0.05$) between years in managed and unmanaged treatments according to Tukey's post hoc test.

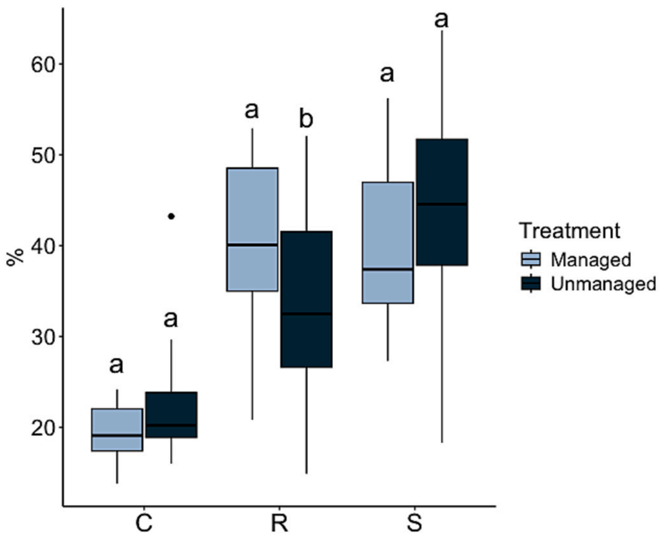

Fig. 4. Community-weighted mean (CMW) of Grime's CSR components (C = Competitor, S = Stress-tolerant, R = Ruderal) in managed and unmanaged treatment. Boxplots represent the relative contribution of each functional strategy within the plant community, weighted by species' relative abundance. Letters indicate significant differences ($p < 0.05$) between treatments according to Tukey's post hoc test.

4. Discussion

This study aimed to assess how traditional management practices (i.e., grazing and mowing) influence both wet meadow communities and the persistence of species with high conservation value, such as Marsilea quadrifolia. Overall, the plant community was relatively homogeneous under both managed and unmanaged plots, as highlighted by the NMDS results. It was dominated by hemicryptophytes and consisted exclusively of native species. This pattern likely reflects the combined effect of low-to-moderate management intensity and water levels which can limit the establishment of invasive species and dense vegetation cover (Yu et al., 2018). Biodiversity metrics provided only limited evidence of differences among treatments, with slight variation in Shannon, Simpson and Pielou indices. Simulated abandoned areas showed marginally higher diversity and evenness – values consistent with wet meadows conditions (e.g., Kulik et al., 2023) – suggesting a gradual post-management recovery towards richer communities typical of well-developed wet meadows (Hille et al., 2018). Temporal trends indicated a non-significant species accumulation under abandonment likely due to reduced disturbance. Nevertheless, the moderate diversity observed in managed plots, particularly species richness, aligns with patterns reported for semi-natural grasslands under grazing and mowing (Bonari et al., 2017; Janišová et al., 2023).

Grazing reduces dense vegetation, promotes defoliation, trampling and nutrient input (Liu et al., 2015), creating open micro-habitats, which in turn affect seed production, temperature and light availability, ultimately influencing plant establishment (Hessle & Danielsson, 2024). When combined with mowing, these disturbances intensify (e.g., increased sunlight exposure and reduced standing vegetation; Zechmeister et al., 2003), creating ideal conditions for pioneer, light-demanding species like *M. quadrifolia* (Corli et al., 2021a). The findings of this study demonstrate that traditional practices play a key role in sustaining *Marsilea quadrifolia* and shaping wet meadow communities. Managed plots consistently supported higher relative abundance of the species, whereas unmanaged plots showed declines, alongside increases in other species such as *Phragmites australis* and *Equisetum palustre*, in line with previous observation on long-term succession in wet meadows (Joyce, 2014, Schneider-Binder, 2014) and in artificial carp ponds (Käsermann & Moser, 1999). This dynamic aligns with the ecology of *M. quadrifolia*, a pioneer, ruderal (*sensu* Grime, 2001) heliophilous species thriving in open, disturbed habitats with limited interspecific competition, as also supported by disturbance indicator values (Chytrý et al., 2024). Interesting results have been observed in other contexts where habitats supporting the species have been actively managed, such as semi-natural grasslands (Janišová et al., 2023; Bonari et al., 2017) paddy fields (Corli et al., 2021b) and ponds (Magnes, 2015). In the latter case, *M. quadrifolia* benefits from management practices such as periodic pond drawdown and vegetation removal, which also provide a reproductive advantage by promoting sporocarps formation and long-term population stability. Similar responses have also been reported for other threatened species, such as for *E*leocharis carniolica W.D.J.Koch, which is sensitive to hydrological changes and relies on periodic

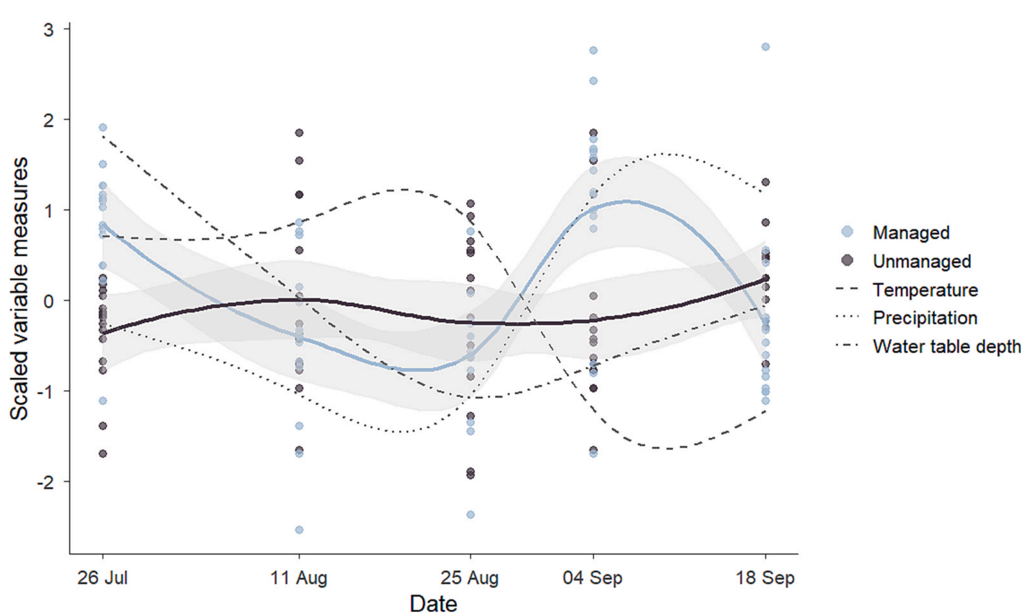

Fig. 5. Seasonal trends of scaled environmental variables and chlorophyll content recorded in 2024 from late July to mid-September in managed and unmanaged plots. Lines represent smoothed trajectories (loess) for chlorophyll (Managed and Unmanaged), temperature, precipitation and water table depth. Points show raw measurements. Shaded areas around smoothed lines indicate the 95% confidence intervals.

disturbance to persist and successfully establish (Niemczyk et al., 2023).

Interestingly, *Marsilea quadrifolia* was the main driver of compositional dissimilarities between treatments. Other species such as *Carex vesicaria, C. elata, Phragmites australis* and *Equisetum palustre* strongly influenced the community, with the latter increasing in the absence of grazing and mowing. Managed plots experience reduced standing vegetation and small-scale disturbances, which reduce competition, increase resource availability, and create recruitment gaps, thereby favouring ruderal (Moog et al., 2005), fast-growing species and maintaining open and more disturbed conditions (Reutimann et al., 2023). In contrast, abandoned areas had dense vegetation, leading to low-light conditions, which impose chronic environmental stress and select for stress-tolerant species. This pattern reflects ecological succession from ruderal to stress-tolerant strategies (Zhang et al., 2024). Consistent with expectations, Ellenberg indicator values indicated elevated light, temperature, soil nutrients, and pH in managed plots, highlighting how grazing and mowing create resource-rich microsites favouring pioneer and ruderal species.

The positive effect of grazing and mowing depends on frequency, intensity, and timing. Moderate grazing promotes biodiversity, as predicted by the grazing optimisation theory (Wan et al., 2015), by altering interspecific competition or inducing compensatory growth (Collins et al., 1998). In contrast, overgrazing damages plants and favors species with grazing avoidance or tolerance strategies (Guo et al., 2020), reducing diversity and increasing biotic homogenization (Liang et al., 2021). At moderate stocking densities, cattle preferentially selectively grazed vegetation (Oñatibia et al., 2020), potentially affecting diversity more than non-selective defoliation. Although precise stocking rates would help quantify effects, the meadow hosts a low-density with only 20–30 animals, a seasonal grazing regime typical of Natura 2000 management, which supports biodiversity without causing structural degradation.

Importantly, the study site is located within a Natura 2000 site, where traditional agricultural activities are permitted and have historically shaped the landscape, while conservation objectives are still ensured. The wet meadow primarily provides organic fodder for cattle, but also hosts a species of European conservation concern, illustrating how productive grasslands can simultaneously support biodiversity within Natura 2000 Network. This dual role aligns with Bonari et al. (2017) and Janišová et al. (2023), who emphasize integrating traditional practices, such as haymaking and grazing, to balance conservation and agricultural use. In the system adopted by BioAngus farm, cattle graze the wet meadow from late spring to early summer and again in early to mid-September, with hay mowing in late summer. Seasonal grazing and late-summer mowing support early, low-competitive species (Janišová et al., 2023), orchids (Mládek et al., 2006), seed production (Janišová et al., 2023), and benefit fauna such as whinchat and amphibians (Mester et al., 2020). These outcomes exemplify the multifunctional role of traditional agro-pastoral systems within protected European landscapes.

Hydrology strongly influenced community composition and the performance of *M. quadrifolia*, which is particularly sensitive to water availability (Corli et al., 2021a). Water table fluctuations during the study period affected growth: the 2022 drought limited expansion, while wetter conditions in 2024 promoted it. At the plot scale, vegetation further mediated plant responses: unmanaged areas exhibited a clear buffering effect on chlorophyll trend over time, whereas managed plots were more sensitive to environmental fluctuations. Despite this, the species showed remarkable resilience, with chlorophyll values indicating no ecophysiological stress and reporting comparable trends to those recorded in paddy fields (e.g., 28.80 ± 0.17 SPAD Unit; Corli et al., 2025). Moderate nutrient inputs from cattle likely supported *M. quadrifolia* populations, in line with Ellenberg indicator values and previous findings (Corli et al., 2021a). Management and hydrology likely interact: grazing and mowing reduced competition during wet years and mitigate stress during dry periods by maintaining open patches. This combination of seasonal grazing, hay mowing, moderate disturbance, and suitable hydrology may explain why this site hosts the largest known population of *M. quadrifolia* in Italy.

Co-designed management plans have proven effective in enhancing long-term conservation outcomes (Reed et al., 2018). Protected areas such as Natura 2000 sites can leverage agri-environmental policies to promote traditional practices that maintain biodiversity and sustainable land use. The BioAngus farm illustrates successful implementation, potentially scalable to other European wet meadows. Long-term success, however, requires farmer engagement, economic viability, continuous monitoring, and dedicated financial incentives (Abeli et al., 2022; Batáry et al., 2015). This is especially relevant given the widespread decline of grassland species in Europe (Wesche et al., 2012) and the need to meet EU Biodiversity Strategy targets. Strengthening farmer participation within Natura 2000 governance remains essential to secure long-term commitment to traditional practices. While this study focuses on a single site, it demonstrates how Natura 2000 wet meadows rely on traditional management to sustain high-value species and maintain semi-natural grassland identity.

CRediT authorship contribution statement

Anna Corli: Writing – review & editing, Writing – original draft, Formal analysis, Data curation. **Aurora Panizza:** Writing – review & editing, Writing – original draft, Data curation. **Simone Orsenigo:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Silvano Lodetti:** Writing – review & editing, Formal analysis. **Graziano Rossi:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Margherita Tognela:** Writing – review & editing, Writing – original draft, Data curation.

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Simone Orsenigo reports financial support was provided by Lombardy Region. Anna Corli (Corresponding author) and Simone Orsenigo (Co-author) reports financial support was provided by National Recovery and Resilience Plan. If there are other authors, they 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. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jnc.2026.127251.

Data availability

Data will be made available on request.

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