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The impact of environmental factors and management on the fitness of *Carlina acaulis* subsp. *caulescens* (Lam.) Schübl. et G. Martens in mountain mesic meadows

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Abstract: The stemless carline thistle (*Carlina acaulis* subsp. *caulescens*) is a plant species commonly found at lower altitudes in the Central European mountains. Although it is still relatively frequent in the area, there has been a decrease in its numbers in the last decades. This research aims to determine the impact of the management of mountain mesic meadows and habitat factors on the morphometric variability of *C. acaulis* and species composition patterns of accompanying vegetation. The study was carried out in the central part of the Sudetes Mountains (SW Poland) on a network of 42 plots randomly established within mesic grasslands. Topographic factors and soil granulometry, physical properties, and nutrient concentrations were studied. The set of morphometric parameters was measured in situ. Canonical correspondence analysis (CCA) was used to analyse the vegetation species composition. The analyses indicated that exchangeable magnesium concentrations and maximal soil water capacity had the strongest effect on the grassland plant species composition among the studied environmental variables. These levels were also significantly influenced by grazing management. After biometric analyses, the leaf rosette diameter was selected as the best morphometric measure of the *C. acaulis* individual's fitness. These plants showed the most vigorous growth on mowed meadows and abandoned ones significantly inhabited by grazing animals.

Key words: Grassland communities, habitat factors, stemless carline thistle

1. Introduction

Some grassland plant communities belong to phytocoenoses, characterised by their high conservation value in Central Europe (Kahmen and Poschlod, 2008; Wilson et al., 2012). In addition to their high natural value, meadows are a major part of the agricultural production systems supporting farmers' livelihoods (Isselstein et al., 2005; Randall et al., 2023). However, due to socioeconomic changes, many seminatural grasslands in Europe have been degraded by fallowing or the introduction of intense farming methods (Havlová et al., 2004; Nardi and Marini, 2021; Pornaro et al., 2021). These changes are the main factors responsible for the degradation and loss of seminatural meadows (Dengler et al., 2020). This problem seems particularly pronounced in mountain meadows (Pruchniewicz, 2017). For example, Prévosto et al. (2011) observed a sharp decrease in protected species after successional changes in the vegetation of previously seminatural habitats. This is also the case, among others, in Sudetian mesic meadow communities inhabited by numerous rare species (Pruchniewicz and Żołnierz, 2014; Pruchniewicz, 2017).

One species sensitive to the degradation of plant communities is the stemless carline thistle (*Carlina acaulis* L.). The stemless carline thistle (Asteraceae) is a hemicryptophyte plant species found in low-yield pastures, moderately dry meadows composed of clay soil (Oberdorfer, 2001), and sites up to 2000 m above sea level (Tutin et al., 1976), which are all widespread in central and southern Europe (Meusel et al., 1965). In Poland, most of these sites are located in the mountainous areas in the south of the country (Meusel et al., 1965; Piękoś-Mirkowa and Mirek, 2006).

There are two subspecies of *Carlina acaulis*. The first is *Carlina acaulis* subsp. *caulescens* (Lam.) Schübl. et G. Martens, which produces a (1) 3–30 (50)-cm tall stalk (Oberdorfer, 2001); the second is *C. acaulis* subsp. *acaulis*, a true stalkless plant reaching a height of only 1–3 cm (Oberdorfer, 2001). Mass extraction of *Carlina acaulis* for decorative purposes has reduced its population, forcing the intro-

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duction of partial legal protection of the species (Trejgell and Tretyn, 2007). Populations of this species have decreased where they typically grow, and this decrease can be explained by adverse effects related to the degradation of plant communities where they reside, which, in turn, may be related to changes in the management of mountain meadows in recent decades. Classic protection methods are insufficient because natural succession limits this species' flowering (Trejgell et al., 2009b). In addition, anthropogenic disturbances and the height of accompanying vegetation may affect the recruitment of seedlings and the size and durability of the population, as described in cases concerning the closely related *Carlina vulgaris* (Löfgren et al., 2000). *C.acaulis* is a law protected in Poland; however, passive methods are not very effective, and, according to Trejgell et al. (2009a), this species needs active methods of protection employing ex situ propagation to maintain its population in highly transformed sites.

Various authors have studied ways to use morphological and functional traits to evaluate plant species responses to environmental factors and human impact on grasslands and other ecosystems (Díaz et al., 2001; Louault et al., 2005; Kahmen and Poschlod, 2008).

We measured the morphometric variability of the populations and related it to diverse habitat factors and management methods. Our survey aimed to find a morphological parameter that is easy to measure in the field and can be used as a fitness indicator in monitoring *C. acaulis* populations in mountain grasslands with various ecological and management characteristics.

The goal of this study was to verify the following research hypotheses (H):

H1: The habitat factors and management methods used in mesic meadows impact the species composition patterns of vegetation accompanying *Carlina acaulis*.

H2: The morphometric features of *Carlina acaulis* individuals are affected by environmental factors and management methods.

2. Materials and methods

2.1. Data collection

The field research was conducted in the central part of the Sudetes, encompassing the ranges of the Sowie, Suche, and Bardzkie Mountains. The areas inhabited by *Carlina acaulis* were selected based on previous studies (Pruchniewicz and Żołnierz, 2014). These areas represent the vegetation of mountain mesic meadows (of the *Arrhenatheretalia* order) subject to mowing (7 plots) and grazing (16 plots); some areas were abandoned (19 plots). The imbalance in the number of sample plots reflects the different land management methods in the area. *C. acaulis* subsp. *caulescens* is the study's focus. Plots of 1 m^2 of quadrate shape were randomly placed within patches occupied by *C. acaulis* within the studied meadows. From each plot, the following were sampled: relevé, topographic parameters, morphometric measures of *C. acaulis*, standing crop of accompanying vegetation, and soil samples for physicochemical analyses. Aspect and slope values measured with a compass and clinometer were then used to calculate the potential annual heat load according to formulas developed by McCune (2007).

As the targeted species is legally protected in Poland, the collection of biometric data was carried out only in situ without causing any damage to the plants. Based on preliminary measurements, 5 individuals were selected from each plot. The rosette diameter of the selected specimens was close to the median of the local population. A relevé was then sampled on the same plot, and topographic parameters were recorded (exposure, slope inclination, and hypsometric height). The above-ground biomass of the accompanying vegetation in the immediate vicinity of each measured individual (<30 cm) was sampled using a frame with an inner size of 5 × 5 cm. Five replicates of the soil samples were taken from each plot using a cylinder (10 cm in diameter; 15 cm in height) to test physicochemical properties. Soil depth was measured with a steel rod at 5 randomly chosen points within each plot.

2.2. Soil analysis

In the laboratory, biomass samples were dried at 85 °C to maintain constant weight. The soil samples were divided into 2 parts in the laboratory. The first was used in the texture analysis, and the second in the analyses of physicochemical properties. The soil samples were air-dried and sieved through a 2-mm mesh sieve. The samples were then used to perform physicochemical analyses using the methods described by Allen (1989) and Radojević and Bashkin (2006). Maximum soil water capacity (MSWC) was determined with the gravimetric method. Loss-on-ignition (as a rough measure of the organic matter content) was determined by igniting the soil samples in a muffle oven at 600 °C for 6 h. The soil texture was determined areometrically, and the pH in the water electrometrically. Total nitrogen was determined using the Kjeldahl method. Soluble phosphorus was determined colometrically using the Olsen method. Exchangeable potassium, magnesium, and calcium were extracted with the 1M ammonium acetate pH 7.0 and determined using a SpectraAA 200 spectrometer in emission measurement mode (K; Ca) or atomic absorption mode (Mg).

2.3. Statistical analysis

Species richness (S) was expressed by the number of species on the research plot. The Shannon–Wiener diversity index was calculated according to the formula $H' = -\sum_{i=1}^{s}(pi \times \ln pi)$, the evenness index (J') according to the formula $J' = \frac{H'}{\ln S}$, where $pi = \frac{ni}{N}$, ni - is the abundance of the ith species (%), N - the sum of the abundance of all species, and S - the total number of species. The calculations were conducted using MVSP v. 3.131 software (Kovach, 2007). The analyses used mean Ellenberg ecological indicator values (Ellenberg et al., 1992) weighted by species coverage for light (L), humidity (F), acidity (R), and trophy (N). Statistical analyses were performed in Statistica v. 13 (Tibico Software Inc., 2017). The agreement of the data with the normal distribution was analysed with the Shapiro–Wilk W test. Homogeneity of variances was checked using the Levene's test. Variables deviating from normality were investigated using the following nonparametric methods: Spearman correlation or Kruskal–Wallis analysis of variance. Normally distributed variables were tested with the following parametric tests: Pearson's correlation and one-way analysis of variance with posthoc testing of significance of differences using Tukey's test for different n. In the case of multiple regression and canonical consistency analysis, collinear variables were eliminated. For this, the following method was used: removal of correlated variables at the level >0.7 and coefficient VIF >5. The calculations were conducted in RStudio software v. 1.4.1717 (RStudio Team, 2022) with the Faraway package (Faraway, 2016). Based on these calculations, the variables concerning the fraction of the soil particle size composition were eliminated from further ordination analyses. To determine the variability of the studied communities and reveal the main gradients of the environment through the analysis of species composition, a detrended correspondence analysis (DCA) was performed in CANOCO v.5 (ter Braak and Šmilauer, 2012). Based on the detrended correspondence analysis results, the generalised additive model (GAM) was used to fit species response curves along the first DCA axis. A Loess smoothing model was also used. Based on the length (5.1 SD) of the gradient represented by the first canonical axis of the DCA, the method of direct ordination, canonical correspondence analysis (CCA), was selected (Jongman et al., 1987; ter Braak and Šmilauer, 2012). The aim of CCA was to determine the impact of habitat variables on the species diversity of the studied phytocoenoses. The significance of the variables was tested with the Monte Carlo permutation test with a stepwise selection of variables. The leaf rosette diameter was selected as the best measure of *Carlina acaulis* fitness after it appeared as the strongest factor in the PCA analysis.

3. Results

3.1. Impact of mountain mesic meadows management on their habitat properties

To determine the impact of the management of mountain mesic meadows on the properties of their habitats, variance analysis was applied. The results (Table 1) demon-

Table 1. Means with standard errors of topographic parameters, physicochemical properties of soils, and Ellenberg index numbers across meadows with contrasting management practices. The values marked with letters (a–c) indicate significant differences obtained after Tukey's test for different n and the Kruskal–Wallis test at $p < 0.05$.

	Meadows	**Pastures**	**Abandoned**
Altitude [m a.s.l.]	536.71 ± 4.32a	739.75 ± 23.23b	560.05 ± 24.76a
Slope [grade]	4.29 ± 0.46	5.16 ± 0.36	5.00 ± 0.00
Soil depth [cm]	18.39 ± 3.22	24.97 ± 2.70	30.58 ± 2.71
Heat load [MJ cm^{-2} year^{-1}]	0.88 ± 0.00	0.87 ± 0.00	0.87 ± 0.00
Stone [%]	10.52 ± 2.12	13.85 ± 1.18	12.70 ± 1.08
Sand [%]	53.98 ± 1.91ab	66.03 ± 1.52b	49.87 ± 3.95a
Dust [%]	31.72 ± 2.38ab	18.67 ± 1.35a	32.75 ± 3.92b
Silt [%]	3.78 ± 0.50b	1.46 ± 0.22a	4.68 ± 0.63b
pH	5.52 ± 0.05	5.45 ± 0.09	5.24 ± 0.10
Organic matter [%]	6.78 ± 0.63	9.32 ± 0.77	7.81 ± 0.75
Maximum soil water capacity [%]	56.54 ± 2.67a	77.34 ± 3.73b	74.15 ± 7.68ab
N [%]	0.26 ± 0.02	0.35 ± 0.03	0.31 ± 0.02
P [mg kg^{-1}]	12.09 ± 1.28a	18.34 ± 2.12ab	27.38 ± 3.28b
K [mg kg^{-1}]	109.02 ± 7.32	130.63 ± 11.28	152.27 ± 21.79
Mg [mg kg^{-1}]	118.23 ± 11.66	109.49 ± 10.85	131.49 ± 13.67
Ca [mg kg^{-1}]	823.10 ± 74.45	892.73 ± 87.64	745.30 ± 83.03
L_Ellenberg	7.32 ± 0.09	7.25 ± 0.04	7.29 ± 0.10
F_Ellenberg	4.68 ± 0.09	4.82 ± 0.11	4.82 ± 0.17
R_Ellenberg	4.67 ± 0.79	5.06 ± 0.13	5.56 ± 0.19
N_Ellenberg	4.54 ± 0.25	3.86 ± 0.21	4.06 ± 0.26

strate the significant influence of land management on the concentration of phosphorus in the soil. The meadows being mowed are located mainly in the lower parts of the mountain and pastures in higher mountain areas. The relationship between the hypsometric altitude, maximum soil water capacity, and the granulometric composition of soils turned was significant (Table 1). In the case of the remaining variables, no significant differences were found between the different ways of using the meadows.

3.2. Patterns of species composition of *Carlina acaulis* accompanying vegetation

In the DCA analysis, the total variance in the vegetation data was 28.7%. The gradient length represented by the first canonical axis was 5.1 standard deviations. Correlations between Ellenberg values, *Carlina acaulis* density, and the calculated DCA values for samples ("sample scores") reveal that vegetation diversity was significantly determined by the Ellenberg humidity index (DCA second axis Rs = 0.440; p = 0.004).

The species response curves along the first DCA axis fitted with the GAM were used to determine the relationship between the coverage of the stemless carline thistle and the accompanying vegetation. The results are presented in Figure 1. The highest coverage of *Carlina acaulis* was noted in the grassland patches, with a high proportion of the grasses *Deschampsia caespitosa*, *Calamagrostis epigejos*, and *Holcus lanatus*. The lowest *C. acaulis* coverage was noted in grasslands inhabited by *Agrostis capillaris*, *Hieracium pilosella*, *Festuca rubra*, and *Leontodon autumnalis* species.

In the CCA, the first axis explained an 11.6 % cumulative variation, and the second axis 20.8 %. All axes explained 32.7% of the total variation for vegetation. In the Monte Carlo permutation test with stepwise selection of variables, soil concentrations of exchangeable magnesium and maximal soil water capacity appeared to be the environmental variables with the strongest effect on plant species composition (Table 2, Figure 2). Animal grazing was the only management method that significantly influenced the community structure.

3.3. Morphometric variability of *Carlina acaulis* against management, habitat, species composition and productivity of accompanying vegetation

The differentiation of the stemless carline thistle plants was observed on the research plots for coverage, density, and biometric parameters. The results are summarised in

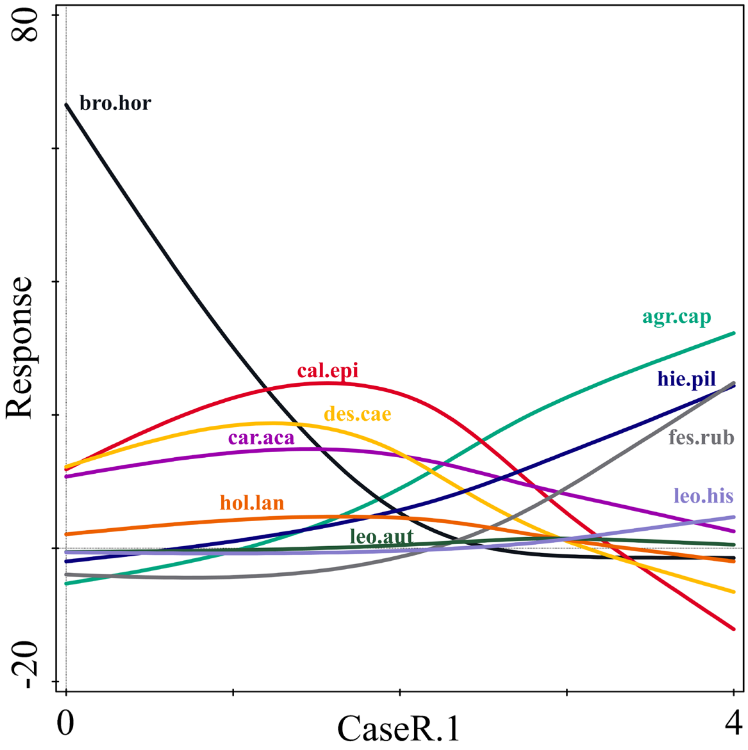

Figure 1. Species response curves along the first DCA axis fitted with a generalised additive model (GAM). Only *Carlina acaulis* and species with coverage higher than 10% are included. See the supplementary material for the list of abbreviations of the species names.

Table 2. Results of the selection of variables during canonical correspondence analysis (CCA) and the influence of the variables acting together (conditional term effects). The table lists only the variables significant at $p < 0.05$.

Name	**F**	**p**
Mg	3.74	0.002
MSWC	2.82	0.004
Pastures	2.55	0.004
Ca	2.07	0.012
Altitude	1.73	0.044
Heat load	1.73	0.03
Soil depth	1.61	0.042

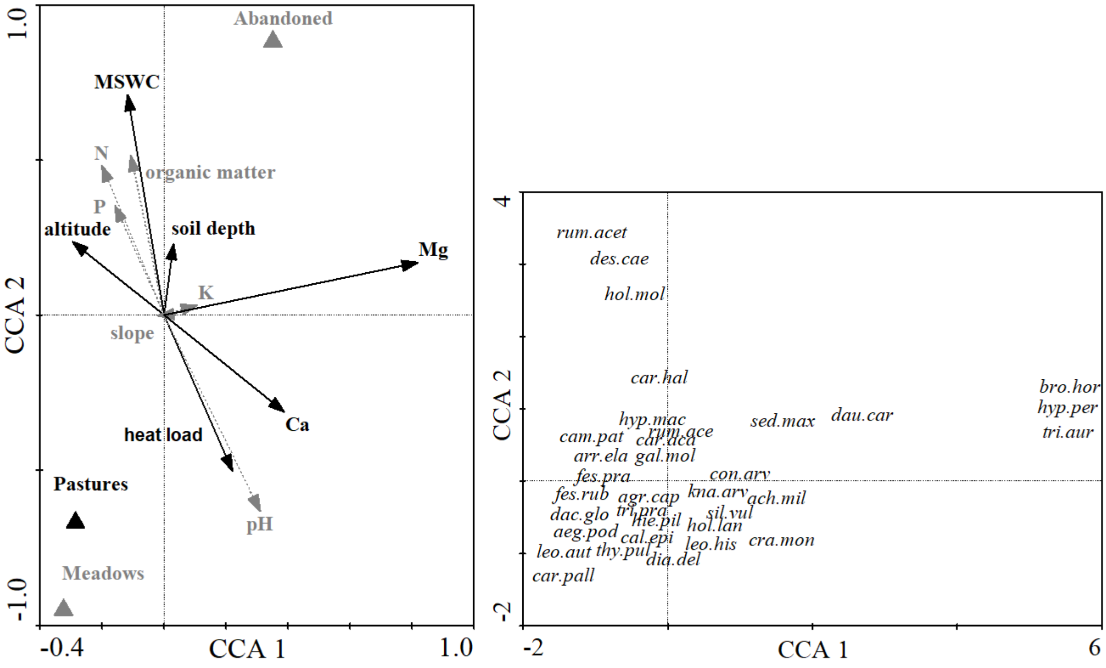

Figure 2. CCA ordination diagram for environmental variables and plant species. Vectors of significant variables are marked in black. See the supplementary material for the list of abbreviations of the species names.

Table 3. In the correlation coefficient calculated between the leaf rosette diameter and the parameters characterising the accompanying vegetation (total biomass on an area of 1 m^2, coverage of all species, diversity value, equality parameters, percentage of shared trees, herbs, and grasses in the vegetation) showed a significant relationship with total biomass of the accompanying vegetation (Rs = –0.462; p = 0.002), Shannon–Wiener diversity index (Rs = –0.330; p = 0.033), and the number of species (Rs = –0.333; p = 0.031). Correlation analyses between the diameter of the *C. acaulis* rosette and habitat factors revealed significant correlations with hypsometric height (Rs = –0.634; p = 0.000), maximum water capacity (Rs = –0.542; p = 0.000), and organic matter (Rs = –0.445; p = 0.003).

An analysis of variance was performed to determine the influence of management on the diameter of the rosette (Figure 3). The results showed a significant effect of management on the tested species (F = 17.84; p = 0.000003).

4. Discussion

We focused on the morphometric variability of the studied populations of *Carlina acaulis* and related it to the diverse habitat factors and management methods in this study. The survey aimed to find an easy way to measure mor-

Table 3. Means with standard errors and min–max values of the parameters describing the condition of *Carlina acaulis* individuals.

	Mean	SE	Min	Max
Carlina acaulis coverage [%]	9.75	1.93	2.00	75.00
Number of individuals on 1 m^2	3.38	0.37	1.00	11.00
Inflorescence diameter [cm]	4.44	0.15	2.10	6.50
Stalk length w/o rosette [cm]	9.79	0.73	5.00	28.00
Leaf rosette diameter [cm]	43.77	2.10	20.00	74.00
The length of 3 leaf blades closest to the median of the measurement [cm]	18.75	1.17	4.40	31.30
The mean width of 3 leaf blades closest to the median of the measurement [cm]	5.71	0.38	1.80	9.82

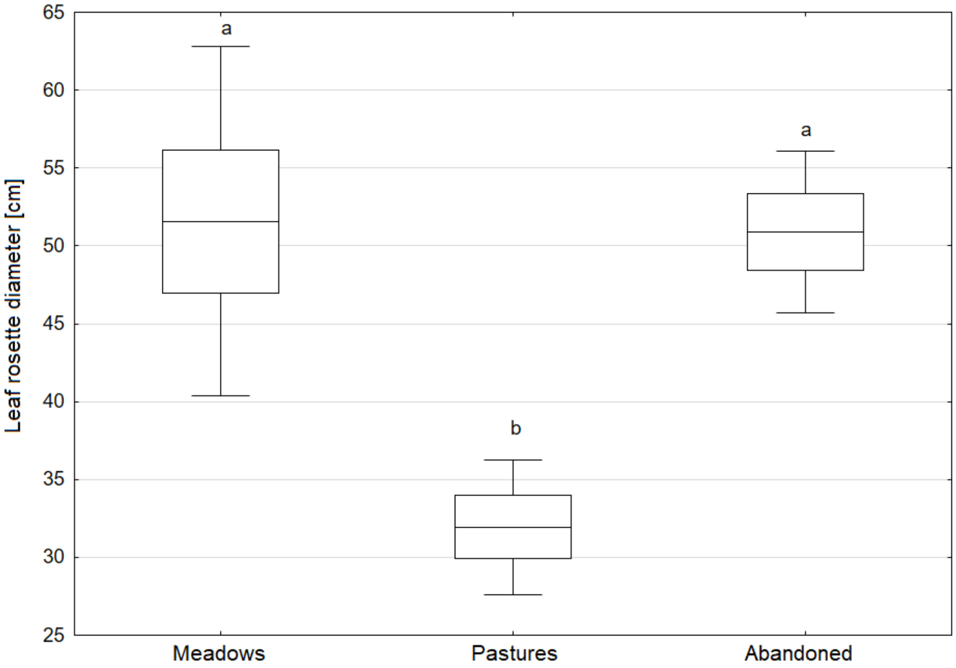

Figure 3. Influence of management on the leaf rosette diameter of *Carlina acaulis*.

phological parameters, which could be used to monitor *C. acaulis* populations. The study showed a significant relationship between the land management methods and several environmental features of the studied habitats. Such a relationship appeared significant for concentrations of exchangeable phosphorus forms. The highest concentrations were recorded in the soils of the abandoned meadows and the lowest ones in the mowed meadows. We also found a positive relationship between hypsometric attitude, maximum soil water capacity, and granulometric composition, which is connected with the historical management in the study area and in line with the results of our previous study (Pruchniewicz and Żołnierz, 2014). We later tried to find a relationship between habitat features and the species composition of *Carlina acaulis*'s accompanying vegetation. Soil parameters (exchangeable forms of Mg and Ca in the soil, maximum water capacity, soil depth), altitude, and heat load were the habitat variables significantly affecting the species composition of the vegetation. Animal grazing was the only management method that significantly influenced species composition. A number of studies concerning the relationships between the species composition of mountain meadows, habitat properties, and management methods exist (Marini et al., 2007; Wellstein et al., 2007; Gusmeroli et al., 2012; Cachovanová et al., 2012; Pruchniewicz and Żołnierz, 2014; Pruchniewicz, 2017). These studies indicate different environmental factors affecting the species composition of meadows. Therefore, it can be assumed that local specificity plays a crucial role as a background for the influence of the management methods on the meadow species composition.

Our study observed a relatively large variability of individuals in the *Carlina acaulis* population. The noted differences concerned the parameters describing the coverage or density of individuals on the study plots and morphometric features discussed here. Among the examined habitat factors, a negative relationship was found between the leaf rosette's diameter and altitude, maximum water capacity, and organic matter. Regarding management practices, mowing and abandonment resulted in positive effects, whereas grazing resulted in negative consequences. The literature on the ecology of *C. acaulis* is relatively sparse. In their research on another *Carlina* species, *C. onopordifolia* Besser, Denisiuk et al. (2009) drew attention to the positive impact of climate conditions on species growth. Dragoljub et al. (2004) emphasised the positive relationship between the amount of light and the stem growth of *Carlina acaulis*. Those results were also indirectly confirmed in our study, in which a negative correlation was found between the leaf rosette diameter and the total biomass of accompanying species shading the *Carlina acaulis* individuals. Trejgell et al. (2009b) pointed out that shading by trees reduces the flowering of *C. acaulis*.

According to Eriksson et al. (1995), no relationship exists between the occurrence of *Carlina vulgaris* populations and the abundance of nutrients in the soil, which is also reflected in our study results for *Carlina acaulis*. Löfgren et al. (2000), in their work on *C. vulgaris*, pointed out a positive relationship between the degree of community disturbance and the population growth rate. Moreover, another study found a relationship between the distribution of *C. vulgaris* and soil moisture influencing seed germination (Klinkhamer et al., 1996). Trejgell et al. (2009b) emphasised that ecological succession associated with introducing trees may reduce the species' flowering. *Carlina acaulis* L. and other species in the mesoacidophilous grasslands respond best to medium or low grazing intensity, according to Barbaro et al. (2004). This result was also confirmed in our research. Species response analysis shows a decrease in *C. acaulis* cover following an increase in the abundance of species degrading the mesic meadows, such as *Deschampsia caespitosa*, *Calamagrostis epigejos*, and *Holcus lanatus*. Interestingly, the lowest cover of *C. acaulis* was noted on plots with a high abundance of species typical to the mesic meadows, such as *Agrostis capillaris*, *Hieracium pilosella*, *Festuca rubra*, and *Leontodon autumnalis*. Melnyk et al. (2021) noted that the populations of *Carlina acaulis* in Vohlynia-Podillia (Western Ukraine) mainly refer to the dry grassland occuring in Central Europe: *Brachypodieta pinnati, Bromopsideta inermis, Cariceta humilis,* and *Festuceta valesiacae.*

Our results might be seen as equivocal to a certain degree. *Carlina acaulis* tolerates competition pressure from cooccurring vegetation, even when it produces high biomass. Such a situation is typical in abandoned grasslands, with vegetation often dominated by one expansive species, as Louault et al. (2005) described. On the other hand, in our study, *C. acaulis* can be classified as grazing-avoiding, as grazing-avoiding, *sensu* Louault et al. (2005). Louault et al. (2005). We believe that the fitness of individual species populations should receive attention in the long term monitoring no less so than studying the composition of vegetation.

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References

Allen SE (1989). Chemical Analysis of Ecological Materials. Second Edition, Blackwell Scientific Publications, Hoboken, NJ, USA.

Barbaro L, Dutoit T, Anthelme F, Corcket E (2004). Respective influence of habitat conditions and management regimes on prealpine calcareous grasslands. Journal of Environmental Management 72 (4): 261-275. https://doi.org/10.1016/j.jenvman.2004.05.006

Cachovanová L, Hájek M, Fajmonová Z, Marrs R (2012). Species richness, community specialization and soil-vegetation relationships of managed grasslands in a geologically heterogeneous landscape. Folia Geobotanica 47: 349-371. https://doi.org/10.1007/s12224-012-9131-3

Dengler J, Biurrun I, Boch S, Dembicz I, Török P (2020). Grasslands of the palaearctic biogeographic realm: Introduction and synthesis. In: Goldstein MI, Della Sala DA, DiPaolo DA (Eds.), Encyclopedia of the World's Biomes. Volume 3: Forests – Trees of Life. Grasslands and Shrublands – Sea of Plants. Elsevier, Amsterdam, the Netherlands. pp. 617-637. https://doi.org/10.1016/B978-0-12-409548-9.12432-7

Denisiuk Z, Chmura D, Adamski P (2009). Flowering and generative reproduction in isolated populations of endangered species *Carlina onopordifolia* Besser (Asteraceae) in Poland. Polish Journal of Ecology 57 (1): 89-97.

Díaz S, Noy-Meir I, Cabido M (2001). Can grazing response of herbaceous plants be predicted from simple vegetative traits? Journal of Applied Ecology 38 (3): 497-508. https://doi.org/10.1046/j.1365-2664.2001.00635.x

Dragoljub G, Šavikin-Fodulović K, Mišić D, Giba Z, Konjević R (2004). *In vitro* stem elongation of stemless carline thistle. Plant Growth Regulation 44: 65-69. https://doi.org/10.1007/s10725-004-2602-7

Ellenberg H, Düll R, Wirth V, Werner, Paulißen D (1992). Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica 18, 2 Auflage, Verlag Erich Goltze KG, Göttingen (in German).

Eriksson Å, Eriksson O, Berglund H (1995). Species abundance patterns of plants in Swedish semi-natural pastures. Ecography 18: 310-317. https://doi.org/10.1111/j.1600-0587.1995.tb00133.x

Faraway J (2016). Practical Regression and ANOVA in R on CRAN, Linear Models with R. 1st Edition, August 2004; 2nd Edition, July 2014: CRC Press. “Extending the Linear Model with R”: CRC Press. 1st Edition, December 2005. 2nd Edition, March 2016.

Gusmeroli F, Della Marianna G, Fava F, Monteiro A, Bocchi S, Parolo G (2012). Effects of ecological, landscape and management factors on plant species composition, biodiversity and forage value in Alpine meadows. Grass and Forage Science 68: 437-447. https://doi.org/10.1111/gfs.12007

Havlová M, Chytrý M, Tichý L (2004). Diversity of hay meadows in the Czech Republic: major types and environmental gradients. Phytocoenologia 34 (4): 551-567. https://doi.org/10.1127/0340-269X/2004/0034-0551

Isselstein J, Jeangros B, Pavlu V (2005). Agronomic aspects of biodiversity targeted management of temperate grasslands in Europe – A review. Agronomy Research 3 (2): 139-151.

Jongman RHG, ter Braak CJF, van Tongeren DFR (eds) (1987). Data Analysis in Community and Landscape Ecology. Pudoc, Wageningen, the Netherlands.

Kahmen S, Poschlod P (2008). Effects of grassland management on plant functional trait composition. Agriculture, Ecosystems & Environment 128: 137-145. https://doi.org/10.1016/j.agee.2008.05.016

Klinkhamer PGL, de Jong TJ, de Heiden JLH (1996). An eight-year study of population dynamics and life-history variation of the “biennial” *Carlina vulgaris*. Oikos 75 (2): 259-268. https://doi.org/10.2307/3546249

Kovach Computing Services (2007). MVSP v3.13p.

Löfgren P, Eriksson O, Lehtilä K (2000). Population dynamics and the effect of disturbance in the monocarpic herb *Carlina vulgaris* (Asteraceae). Annales Botanici Fennici 37: 183-192.

Louault F, Pillar VD, Aufrère J, Garnier E, Soussana JF (2005). Plant traits and functional types in response to reduced disturbance in a semi-natural grassland. Journal of Vegetation Science 16: 151-160. https://doi.org/10.1111/j.1654-1103.2005.tb02350.x

Marini L, Scotton M, Klimek S, Isselstein J, Pecile A (2007). Effects of local factors on plant species richness and composition of Alpine meadows. Agriculture, Ecosystems & Environment 119 (3-4): 281-288. https://doi.org/10.1016/j.agee.2006.07.015

McCune B (2007). Improved estimates of incident radiation and heat load using non-parametric regression against topographic variables. Journal of Vegetation Science 18: 751-754. https://doi.org/10.1111/j.1654-1103.2007.tb02590.x

Melnyk VI, Kovalchuk IO, Dovhopola LI, Shapran YP (2021). Geographical distribution, habitats and modern state of *Carlina cirsioides* (Asteraceae) populations. Biosystems Diversity 29 (1): 17-27. https://doi.org/10.15421/012103

Meusel H, Jager E, Weinert E (red)(1965). Vergleichende Chorologie der Zentraleuropaischen Flora 1. Text. 2 Karten. VEB Gustav Fischer Verlag. Jena (in German).

Nardi D, Marini L (2021). Role of abandoned grasslands in the conservation of spider communities across heterogeneous mountain landscapes. Agriculture, Ecosystems & Environment 319: 107526. https://doi.org/10.1016/j.agee.2021.107526

Oberdorfer E (2001). Pflanzensoziologische Exkursionsflora: Für Deutschland und angrenzende Gebiete (in German).

Piękoś-Mirkowa H, Mirek Z (2006). Rośliny Chronione. Warszawa: Multico Oficyna Wydawnicza (in Polish).

Pornaro C, Spigarelli C, Pasut D, Ramanzin M, Bovolenta S et al. (2021). Plant biodiversity of mountain grasslands as influenced by dairy farm management in the Eastern Alps. Agriculture, Ecosystems & Environment 320: 107583. https://doi.org/10.1016/j.agee.2021.107583

Prévosto B, Kuiters L, Bernhardt-Römermann M, Dölle M, Schmidt W et al. (2011). Impacts of land abandonment on vegetation: successional pathways in European habitats. Folia Geobotanica 46: 303-325. https://doi.org/10.1007/s12224-010-9096-z

Pruchniewicz D (2017). Abandonment of traditionally managed mesic mountain meadows affects plant species composition and diversity. Basic and Applied Ecology, 20: 10-18. https://doi.org/10.1016/j.baae.2017.01.006

Pruchniewicz D, Żołnierz L (2014). The influence of environmental factors and management methods on the vegetation of mesic grasslands in a central European mountain range. Flora 209: 687-692. https://doi.org/10.1016/j.flora.2014.09.001

Radojević M, Bashkin V (2006). Plant analysis. In: Practical Environmental Analysis. Royal Society of Chemistry Publishing, Cambridge, UK.

Randall KJ, Ellison MJ, Yelich JV, Price WJ, Johnson TN (2023). Changes in forage quality and cattle performance with short-duration grazing of mesic meadows in the intermountain west. Rangeland Ecology & Management 87: 13-21. https://doi.org/10.1016/j.rama.2022.10.005

RStudio Team. RStudio (2022). Integrated Development Environment for R; RStudio, PBC, Boston, MA, USA. Available online at: http://www.rstudio.com/

ter Braak CJF, Šmilauer P (2012). Canoco Reference Manual and User’s Guide: Software for Ordination, Version 5.0. Microcomputer Power, Ithaca, NY, USA.

Tibico Software Inc. (2017). Statistica (data analysis software system), version 13. http://statistica.io.

Trejgell A, Tretyn A (2007). Analysis of flowering ability of regenerated *Carlina acaulis* subs. *simplex* plants. Acta Agrobotanica vol. 60 (2): 39-44.

Trejgell A, Bednarek M, Tretyn A (2009a). Micropropagation of *Carlina acaulis* L. Acta Biologica Cracoviensia Series Botanica 51/1: 97-103.

Trejgell A, Dąbrowska G, Tretyn A (2009b). In vitro regeneration of *Carlina acaulis* subsp. *simplex* from seedling explants. Acta Physiologiae Plantarum 31: 445-453. https://doi.org/10.1007/s11738-008-0252-5

Tutin TG, Heywood VH, Burges NA, Moore DM, Valentine DH et al. (1976). Flora Europaea. Plantaginaceae to Compositae, vol. 4. Cambridge University Press, Cambridge, UK.

Wellstein C, Otte A, Waldhardt R (2007). Impact of site and management on the diversity of central European mesic grassland. Agriculture, Ecosystems & Environment 122 (2): 203-210. https://doi.org/10.1016/j.agee.2006.12.033

Wilson JB, Peet RK, Dengler J, Pärtel M (2012). Plant species richness: the world records. Journal of Vegetation Science 23: 796-802. https://doi.org/10.1111/j.1654-1103.2012.01400.x

Supplementary material
The list of the species names and their respective abbreviations.

Species name	**Abbreviation**
Achillea millefolium	*ach.mil*
Aegopodium podagraria	*aeg.pod*
Agrostis capillaris	*agr.cap*
Alchemilla sp.	*alch*
Anthoxanthum odoratum	*ant.odo*
Arrhenatherum elatius	*arr.ela*
Betula pendula	*bet.pen*
Briza media	*bri.med*
Bromus hordeaceus	*bro.hor*
Calamagrostis epigejos	*cal.epi*
Campanula patula	*cam.pat*
Campanula rapunculoides	*cam.rap*
Campanula rotundifolia	*cam.rot*
Carlina acaulis	*car.aca*
Cardaminopsis halleri	*car.hal*
Carex pallescens	*car.pall*
Cirsium arvense	*cir.arv*
Convolvulus arvensis	*con.arv*
Crataegus monogyna	*cra.mon*
Cynosurus cristatus	*cyn.cri*
Dactylis glomerata	*dac.glo*
Danthonia decumbens	*dan.dec*
Daucus carota	*dau.car*
Deschampsia cespitosa	*des.cae*
Dianthus deltoides	*dia.del*
Euphrasia rostkoviana	*eup.ros*
Festuca pratensis	*fes.pra*
Festuca rubra	*fes.rub*
Fragaria vesca	*fra.ves*
Galium mollugo	*gal.mol*
Hieracium pilosella	*hie.pil*
Holcus lanatus	*hol.lan*
Holcus mollis	*hol.mol*
Hypericum maculatum	*hyp.mac*
Hypericum perforatum	*hyp.per*
Knautia arvensis	*kna.arv*
Lathyrus pratensis	*lat.pra*
Lathyrus sylvestris	*lat.syl*
Leontodon autumnalis	*leo.aut*
Leontodon hispidus	*leo.his*
Lotus corniculatus	*lot.cor*

Luzula campestris	*luz.cam*
Luzula multiflora	*luz.mul*
Phleum pratense	*phl.pra*
Picea abies	*pic.abi*
Pimpinella saxifraga	*pim.sax*
Plantago lanceolata	*pla.lan*
Poa pratensis	*poa.pra*
Polygala vulgaris	*pol.vul*
Potentilla erecta	*pot.ere*
Ranunculus repens	*ran.rep*
Rosa canina	*ros.can*
Rubus sp.	*rub*
Rumex acetosa	*rum.ace*
Rumex acetosella	*rum.aceto*
Sedum maximum	*sed.max*
Silene vulgaris	*sil.vul*
Sorbus aucuparia	*sor.acu*
Stellaria graminea	*ste.gra*
Thymus pulegioides	*thy.pul*
Tragopogon pratensis	*tra.pra*
Trifolium aureum	*tri.aur*
Trisetum flavescens	*tri.fla*
Trifolium hybridum	*tri.hyb*
Trifolium pratense	*tri.pra*
Trifolium repens	*tri.rep*
Veronica chamaedrys	*ver.cha*
Veronica officinalis	*ver.off*
Vicia cracca	*vic.cra*
Vicia sepium	*vic.sep*
Vicia tetrasperma	*vic.tetr*