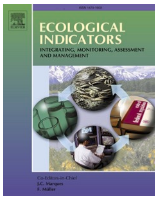
Ecological Indicators 146 (2023) 109740

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



Drivers of species-specific contributions to the total live aboveground plant biomass in Central European semi-natural hay grasslands

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ARTICLE INFO

Keywords:
Abandonment
Climate
Functional diversity
Biomass inequality
Niche differentiation
Soil

ABSTRACT

Semi-natural grasslands are known to provide numerous ecosystem services, of which one of the most important is production of biomass. However, the contribution of individual plant species to the total biomass is much less well understood. This study addressed questions concerning community structure and responses of species-specific biomass (s-AGB) to gradients in soil acidity and fertility, topographical and climatic features, and disturbance regimes in mown and abandoned grasslands in the Sudetes Mountains (Central Europe). It identified pH as the most significant environmental gradient affecting turnover in s-AGB, and mowing cessation, temperature, and precipitation also had significant effects. Further, it showed high inequality in biomass among co-occurring plant species. It also showed that biomass inequality (measured by the Gini coefficient) among interacting species decreases with increasing functional diversity (Rao's index). This study highlights that common plant species (in terms of frequency) play a major role in contributing to the total aboveground biomass (*t*-AGB). However, less frequent species are also significant contributors to the *t*-AGB. Thus, the combined contribution of infrequent species to the *t*-AGB should not be neglected. Our findings support the mass ratio hypothesis stating that ecosystem functions such as biomass production depend on dominant species. On the other hand, high niche differentiation ensures the coexistence of less competitive species with the dominants by the variety and complementarity of functional traits. Infrequent and non-dominant species were the core of the diversity seen in the studied grasslands. The maintenance of species diversity in grasslands should be prioritized in nature conservation policies to ensure the sustainability of ecosystem services.

1. Introduction

Grasslands are one of the most widespread ecosystems in the world, covering up to approximately 40 % of the land surface (Gibson, 2009). These ecosystems are mostly dominated by graminoids (grass and grass-like species). However, they host a high diversity of other life-forms (Biurrun et al., 2021; Dengler et al., 2014; Gibson, 2009; Raduła et al., 2020; Veen et al., 2009). They are a habitat for wildlife (Bonari et al., 2017; Zulka et al., 2014), and provide numerous ecosystem services, such as soil and water protection (Habel et al., 2013; Zhao et al., 2020). There are many different types of grasslands, but their common feature is the production of biomass, and they therefore play a crucial role in the world's carbon cycle, in addition to being essential for the animal production industry and for global food security (O'Mara, 2012).

Grassland productivity has been the subject of numerous studies in both basic and applied ecology (Scurlock et al., 2002). Aboveground biomass production is the most frequently studied component of plant productivity, and measurements of peak aboveground biomass are often used as a surrogate for net aboveground primary productivity (Bhandari and Zhang, 2019; Kahmen et al., 2005; Xia et al., 2018), with it most often measured as the total clipped standing biomass (Hejcman et al., 2010; Kahmen et al., 2005; Pavlů et al., 2013). Overall biomass sample

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https://doi.org/10.1016/j.ecolind.2022.109740
Received 14 October 2022; Received in revised form 25 November 2022; Accepted 27 November 2022

figures are also sometimes divided into living and dead matter components (Bedia and Busqué, 2013; Gross et al., 2009; Lanta et al., 2009), or partitioned into functional groups (Kassahun et al., 2021; Pokorny et al., 2004; Semmartin et al., 2007; Zeeman et al., 2019). A number of local experiments have focused on the variation of aboveground biomass production in temperate grasslands in different European regions (Bernhardt-Römermann et al., 2011; Dodd et al., 1994; Galvánek and Lepš, 2012; Hector et al., 1999; Hejcman et al., 2010; Lepš, 2004; Maire et al., 2012). However, no study has yet examined the fine-scale biomass distribution of coexisting species and the causes of variation in species-specific aboveground biomass (s-AGB) across a broad range of gradients in soil acidity and fertility, topographical and climatic features, and disturbance regimes. The assessment of aboveground biomass distribution among species in grassland ecosystems has been extremely rare in both observational (Andueza et al., 2016; Qi et al., 2021) and experimental studies (Lepš, 2004). This approach has also been rare even in experimental manipulations of species-poor artificial plant assemblages (Maire et al., 2012), or has been limited to dominants only (Hejcman et al., 2007).

In an ecological context, the amount of s-AGB serves as a measure of species' success in the plant community (Colgan & Asner, 2014). Species abundance is influenced by species interactions and is therefore subject to the effects of competition for available resources (Herben et al., 2007). European semi-natural grasslands are mostly dominated by grasses (Padullés Cubino et al., 2022; Večeřa et al., 2021). The ecological success of grasses can be linked to wind-pollination, effective long-distance dispersal, establishment and short germination rates, and resilience to continuous disturbance (Linder et al., 2018). However, semi-natural grasslands can have a rich diversity of species, including various sedges, rushes and forbs, including legumes. Many species of these groups are poor competitors and have scarce distribution in semi-natural grassland communities; despite this, they are strongly associated with grassland habitats (Lennon et al., 2011; Markham, 2015). It has long been recognized that plant communities typically consist of a few common species (often dominant) and many rare ones (Preston, 1948). The mass ratio hypothesis (Grime, 1998) states that ecosystem properties are primarily determined by the traits of the dominant species. However, several recent studies have shed light on the importance of rare species for ecosystem functioning (Lyons et al., 2005; Soliveres et al., 2016). Thus, even if a single, infrequently occurring species is meaningless relative to overall biomass production, the combined contribution of such infrequent species to total biomass production should not be neglected. This assumption was based on the high species diversity seen in semi-natural grasslands, resulting from the co-occurrence of species with contrasting frequencies (Pärtel et al., 2001). Semi-natural grasslands are an example of ecosystems with few broadly distributed species and many species with low frequency distribution (the core-satellite hypothesis; Hanski, 1982).

There is limited understanding of the factors that cause inequality of biomass (size inequality) distribution among coexisting species at the plant community level in grassland ecosystems. An inequality of species abundance is a universal phenomenon in both animal and plant communities (Ulrich et al., 2010), which can be measured by using an index intended to study the income inequality, known as the Gini coefficient (Weiner & Solbrig, 1984). Identifying the mechanisms driving species relative abundance is a primary concern in ecology (McGill, 2010). The recent study by Qi et al. (2021) showed that species-dimension biomass inequality in stressful alpine grassland ecosystems is dependent on environmental and productivity gradients. In this study we employed the trait-based approach, which is particularly useful in elucidating plant coexistence patterns in competitive communities (Maire et al., 2012; Padullés Cubino et al., 2022). Among various plant functional traits, the leaf-height-seed (LHS) strategy scheme represents fundamental plant functions and major dimensions of plant adaptation strategies (Westoby, 1998). An important leaf trait is specific leaf area (SLA), which is related to resource acquisition and relative growth rate; plant height at maturity reflects the competitive ability for light; and seed mass describes the reproduction strategy (Díaz et al., 2016; Westoby, 1998; Westoby et al., 2002).

It is noteworthy that recent studies have shown that species abundance and their distributions in grasslands depend on deterministic processes, and more specifically on habitat filtering, which promotes the dominance of phylogenetically related species (mostly grasses), whereas niche differentiation has a positive effect on the species diversity of less competitive plants (Maire et al., 2012; Padullés Cubino et al., 2022). Based on this hypothesis, we predict high biomass inequality among coexisting plant species, in particular between dominant grasses and infrequent forbs. We also predict that high variation in functional traits at the plant community level (high functional diversity) has a stabilizing effect on biomass inequality among species. Building on the hypothesis that most of the plant diversity in the community is maintained by niche differentiation, we predict species turnover and associated variation in s-AGB along environmental gradients which presumably influence the availability of particular plant species niches.

In this study, we specifically asked: How uneven is the distribution of biomass among co-occurring plant species in grasslands? What is the role of widely distributed and rare (in terms of frequency) species in biomass production in grasslands? How do different functional groups (grasses, sedges and rushes, legumes and other non-legume short and tall forbs) contribute to these frequency distribution classes? Does functional diversity explain biomass inequality among different species? What are the key factors affecting s-AGB? To answer these questions, mown and abandoned species-rich mesic grasslands in the Sudetes Mountains of Central Europe were studied.

2. Methods

2.1. Study area and field sampling

The study was carried out in the Sudetes Mountains in Poland and the Czech Republic (49°54′–51°02′N, 14°30′–17°37′E), an area encompassing approximately 5500 km^2, in an area with elevations ranging from 350 to 950 m above sea level (Fig. 1). The mean annual temperature varies from 6.3 °C to 9.3 °C (mean 8.3 °C) and the annual precipitation ranges from 721 to 1600 mm (mean 982 mm) (Karger et al., 2020). The bedrock consists mostly of acidic and poorly weathered igneous and metamorphic rocks.

Two types of Natura 2000 habitats listed on the EU Habitats Directive Annex I (Council Directive 92/43/EEC) were sampled: lowland hay meadows (habitat code 6510) and mountain hay meadows (habitat code 6520) These corresponded in phytosociological terms to *Arrhenatherion* and *Triseto-Polygonion* alliances, respectively (Chytrý et al., 2007; Kącki et al., 2021; Rodríguez-Rojo et al., 2017). According to the pan-European system for habitat identification, these vegetation types are recognized as low altitude mountain hay meadows and medium altitude mountain hay meadows (Chytrý et al., 2020). The vegetation in question is the type of traditionally managed (mown once or twice per year) and species-rich semi-natural hay meadow typically found on mesic soils.

Sampling was conducted in the years 2018–2019 during the peak of the growing season before the first cut at the end of June and into July. This is the traditional time for the first cut in Central Europe (Mašková et al., 2009). Unlike in other studies, this study utilized a measured weight of individual vascular plant species rather than their cover percentage, as the latter is a subjective estimate of the actual abundance (Chiarucci et al., 1999).

We sampled 28 regularly mown grasslands and 30 abandoned (5–15 years) grasslands. All abandoned sites were in the initial stages of secondary succession, with low and infrequent occurrences of late succession (woody) species (Fig. S-1, Table S-1, Supplementary material). At each grassland site, a 10 × 10 m focal plot was established. Live aboveground biomass (AGB) was measured by clipping individual plant species' shoots at ground level from four quadrat frames measuring 0.4

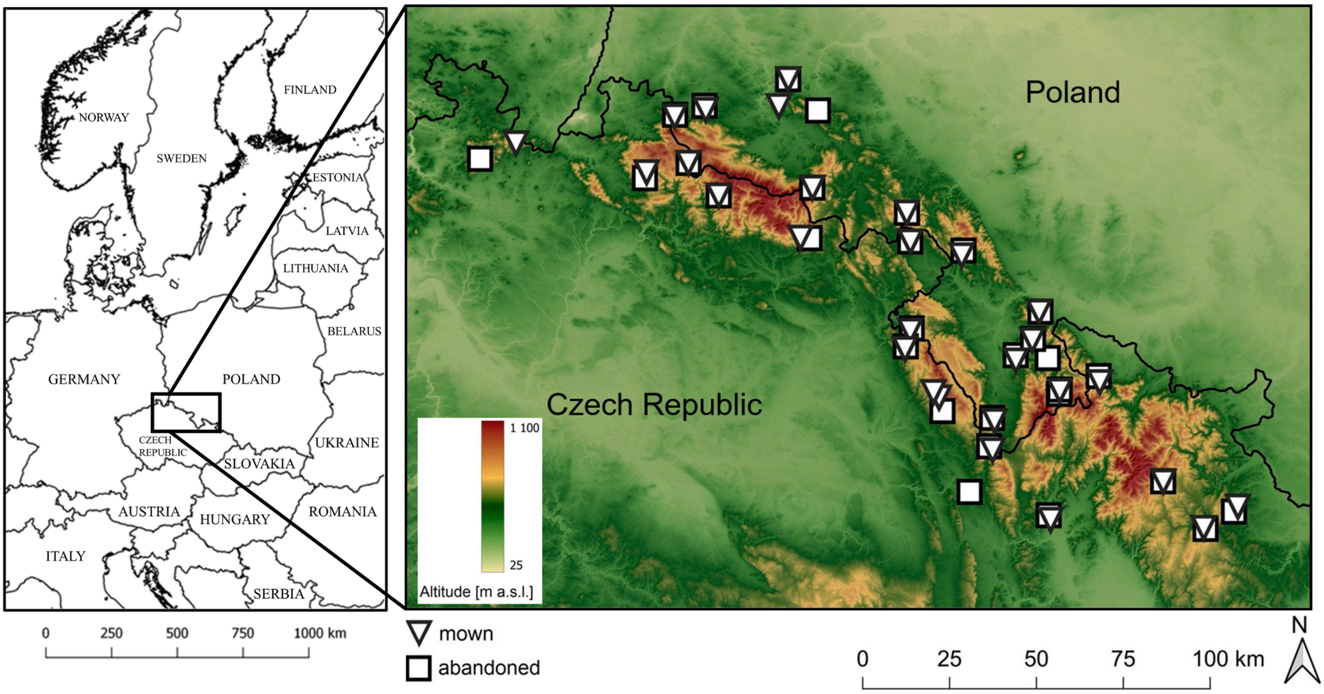

Fig. 1. Distribution of sampling sites in the study area.

× 0.4 m (0.64 m^2), which were placed evenly in the four corners of the focal plot (1 m from focal plot borders). Fresh biomass was hand sorted into individual plant species at the site. The four plots combined were considered a sample. Sorted plant material was pre-dried indoors at room temperature for approximately 10 days and then dried in a forced-air circulation drying oven at 60 °C for 24 h to a constant weight that facilitated the determination of the dry matter content of individual species per 0.64 m^2. Dead standing biomass and ground litter were excluded from sampling and weight measurements due to the inability to differentiate individual plant species.

This study focused on s-AGB, but it also reported the *t*-AGB. The *t*-AGB was expressed as the sum of the s-AGB recorded in each sample (sum of the s-AGB measured from four 0.4 × 0.4 m plots). The s-AGB and *t*-AGB were reported on a g/m^{-2} basis (Table S-1, Supplementary material). Semi-natural grasslands in the Sudetes Mountains were found to have high variation in s-AGB and *t*-AGB data (Table S-1, Supplementary material). The *t*-AGB ranged from 208.4 to 700.0 g m^{-2} (mean 365.6 ± 108.2 SD).

2.2. Soil chemical analysis

To determine soil properties, five soil samples were collected from each focal plot using a 10-cm-deep soil core. These samples were then combined into a bulk sample. Soil samples were air-dried, biomass residues and roots were removed, and then the samples were ground in a mortar until the material could pass through a 2 mm sieve. All chemical analyses were performed in an accredited laboratory of the Crop Research Institute in Chomutov, Czech Republic. Plant-available calcium, potassium, magnesium, and phosphorus were extracted by the Mehlich III method (Mehlich, 1984), and concentrations were determined by inductively coupled plasma optical emission spectrometry (GBC Scientific Equipment Pty ltd., Melbourne, Australia). Determination of pH ($CaCl_2$) was done using a pH meter (Sentron Wellinq, Leek, The Netherlands). Total nitrogen soil concentrations were determined using the Kjeldahl method, and organic carbon concentrations by the conventional oxidation procedure incorporating chromosulfuric acid and colorimetry (AOAC, 1984).

2.3. Statistical analyses

Two groups of species were distinguished based on their frequency distribution in the dataset. The group of frequent species included species with a relative frequency higher than 30 %, whereas the group of rare species included species with a relative frequency lower than that threshold. Within these groups, the proportion of different growth forms was analyzed: grasses (Poaceae), legumes (Fabaceae) and other non-legume short and tall forbs (herbaceous, dicotyledonous flowering plants), sedges and rushes (Cyperaceae and Juncaceae).

The proportional abundance of s-AGB was expressed as the proportional (0–1) ratio of s-AGB to the *t*-AGB in each sample. The relative proportion of s-AGB was used to determine the cumulative contribution of individual species relative to the *t*-AGB. The s-AGB data were sorted from highest to lowest values, which were then used to generate the cumulative proportion curve.

Plant biomass inequality was quantified for each sample using the Gini coefficient. The Gini coefficient was used as a measure of mean biomass difference among species at the plant community level. The values of Gini range from 0 to 1. The value zero corresponds to plant communities with perfect biomass equality, whereas a theoretical maximum of one corresponds to plant communities dominated by a single species. Linear regression was used to examine the relationship between the Gini coefficient and Rao's functional diversity index (Lepš et al., 2006; Rao, 1982). Determination of Rao's functional diversity index was based on traits including leaf specific area (SLA), plant height at maturity, and the seed mass. Functional trait data were retrieved from the LEDA database (a database on the life-history traits of the Northwest European flora) (Kleyer et al., 2008), and are a subset of a previously used data set by Lengyel et al. (2020). The Rao diversity index was used as an independent variable to explain variation in Gini using the linear regression model. Normality of data was checked with the Shapiro-Wilk test. The Breusch-Pagan test was used to test for heteroskedasticity. In addition, Spearman's rank correlation coefficient was used to express the coexistence patterns of species at the plant community level based on the raw s-AGB data.

Determinants of s-AGB were analyzed using redundancy analysis (RDA), with the ordination axes of RDA corresponding to the dominant gradients in species composition constrained by environmental factors. The raw s-AGB data were transformed using Hellinger transformation (Legendre and Gallagher, 2001). This type of transformation reduces the double-zero problem, which is common with vegetation-plot data, and gives low weights to species with low counts and many zeros. Hellinger-transformed s-AGB data were used as response variables in multivariate analyses. The ordination analyses utilized the set of explanatory variables acquired from direct field measurements and freely accessible databases. It then categorized them into five groups representing climate, topography, land management, soil properties, and vegetation parameters (Table 1). The annual sum of precipitation and the annual mean temperature representing the explanatory group climate were derived from CHELSEA (Climatologies at high resolution for the earth's land surface areas) at a resolution of approximately 1 km × 1 km (Karger et al., 2020). The group topography included three topography-related indices calculated based on the Digital Elevation Model (EU-DEM) at 25 m resolution (https://www.eea.europa.eu; accessed on 15 January 2022). The analyses utilized the Topographic Wetness Index (TWI), Diurnal Anisotropic Heat Load (DAH), and Topographic Ruggedness Index (TRI), which all measure factors known to impact vegetation variability in mountainous areas (Moeslund et al., 2013). TWI quantifies terrain driven factors impacting soil water distribution. It was calculated with the MFD-md algorithm (Qin et al., 2011) according to the guidelines of Kopecký et al. (2021). DAH reflects the amount of solar energy potentially reaching the surface of the ground (Hengl and Reuter, 2009). TRI reflects local differentiation of altitude (Hengl and Reuter, 2009). The explanatory group soil included pH, total nitrogen (%), total organic carbon (%) and plant-available potassium, phosphorus, calcium and magnesium (mg kg^{-1}). The explanatory group vegetation parameters were comprised of vegetation cover (%) and ground litter cover (%), which were both estimated visually from the focal plot. For several sites information about time since abandonment was limited or uncertain, and therefore two strikingly different land management types (mown and abandoned) were used as explanatory variables. Only significant and nonlinearly related explanatory variables were selected by applying the forward selection procedure with false discovery rate (FDR) correction of the *p*-values. The forward selection procedure resulted in a parsimonious model that avoided collinearity among significant explanatory variables. The adjusted coefficient of determination (R^2 adj) was used as the measure of the ratio of the explained variation to the total variation in the global model. Permutation tests (with 999 permutations) were used to assess the significance of the relationships found in multivariate analyses.

Table 1
Summary of explanatory variables employed in RDA.

Explanatory variables	min–max	Mean ± SD
Climate		
Temperature (°C)	6.3–9.3	8.3 ± 0.8
Precipitation (mm)	721–1600	982 ± 216
Topography		
DAH	−0.25–0.26	0.02 ± 0.12
TWI	9.0–15.0	11.3 ± 1.4
TRI	0.6–8.5	2.9 ± 1.6
Soil properties		
pH	3.4–6.9	4.7 ± 0.7
C (%)	3.0–17.4	5.3 ± 2.5
N (%)	0.3–1.4	0.5 ± 0.2
P mg kg^{-1}	8.6–238.9	60.8 ± 40.6
K mg kg^{-1}	113.9–705.9	233.8 ± 114.6
Ca mg kg^{-1}	311.3–7427.8	1729.3 ± 1370.5
Mg mg kg^{-1}	49.7–778.4	217.9 ± 131.7
Vegetation parameters		
Herb layer (%)	40.0–100.0	86.7 ± 13.1
Ground litter layer (%)	0.0–95.0	47.5 ± 37

Explanation: DAH – Diurnal Anisotropic Heat Load; TWI – Topographic Wetness Index; TRI – Topographic Ruggedness Index.

In addition to the direct ordination analysis, we constructed the *t*-value biplots for s-AGB in order to test and visualize pairwise relationships between s-AGB and its controlling factor (Ter Braak and Looman, 1994; Šmilauer & Lepš, 2014). The *t*-value biplot is a statistical technique which is used to approximate the *t*-value of the regression coefficients of a multiple regression model, where we used species as the response variable and environmental variable as the predictor. In the *t*-value biplot diagram, the plant species were individually shown by arrows. For each significant explanatory variable, a circle was drawn (known as Van Dobben circles) with its diameter equal to the length of that variable's arrow (here plotted as symbols). The *t*-value biplots show a positive or negative relationship at < 0.05 between s-AGB and the explanatory variable, if the *t*-values of respective regression coefficients were>2 in the absolute value. Response variables with arrows that end in Van Dobben circles had significant relationships (red circle: positive; blue: negative) with particular explanatory variables. The shorter the arrow is for species within the circle in the *t*-value biplot diagram, the stronger the relationship with the explanatory variable.

Data were analyzed using R statistical software (https://www.r-project.org) with the "car", "DescTools", "dplyr", "ggpubr", and "vegan" packages. Ordination analyses were performed in CANOCO 5 (Šmilauer & Lepš, 2014). The nomenclature of taxa follows Euro + Med PlantBase (https://ww2.bgbm.org/EuroPlusMed/; accessed on 10 January 2022).

3. Results

3.1. Contributions of species and species groups to the aboveground biomass

A total of 165 plant species were identified in biomass samples. This included 27 species of grasses, 85 species of short and 27 species of tall forbs, 16 species of legumes, and 10 species of sedges and rushes. A total of 28 species were frequent (species with a relative frequency > 30 %), and combined formed 79 % of the *t*-AGB, on average (Table 2, Fig. 2). Almost a half of these species (46 %) were grasses, 29 % were short forbs, 14 % were legumes, 7 % were tall forbs, and 4 % were sedges and rushes. A total of 137 species were rare (species with a relative frequency < 30 %), and combined formed 21 % of the *t*-AGB, on average. More than half of these species were short forbs (56 %), whereas grasses were only 10 % of the species pool, 18 % were tall forbs, 9 % were legumes, and 7 % were sedges and rushes.

Species with the highest relative proportion to the *t*-AGB (≥5%) were *Festuca rubra* (17.1 %), followed by *Agrostis capillaris* (10.8 %), *Arrhenatherum elatius* (8.7 %), *Alopecurus pratensis* (6.6 %) and *Dactylis glomerata* (6.0 %). These grass species dominated in biomass in both land management categories (Table S-1, Supplementary material). They formed approximately half (49.2 %) of the *t*-AGB. The remaining 50.8 % of the *t*-AGB was dependent on 160 species. A total of 15 species with the relative proportion to the *t*-AGB < 5 % and ≥ 1 % formed 29.6 % of the *t*-AGB. The majority of species (145 out of 165) each accounted for < 1 % of the *t*-AGB, on average. The summed s-AGB of these species formed on average 21.2 % of the *t*-AGB (Fig. 3). The distribution of s-AGB proportions was strikingly similar for both land management categories (Table S-2, Supplementary material).

The Gini values ranged from moderately high (0.53) to very high (0.87), with the mean equal to 0.71 (±0.08 SD). Linear regression showed a negative significant correlation between biomass inequality among coexisting species (Gini) and functional diversity (Rao) (Fig. 4). The inequality in biomass distribution among species decreased with increasing functional diversity of the community ($R^2 = 0.2$; $p < 0.001$). Also, a number of pairwise correlations were found between some s-AGB (Table 2, Table S-3, Supplementary material).

Table 2
Summary of the most frequent species (>30 %) and their correlations with other species. The five most productive species are underlined.

Species	Relative frequency (%)	Relative proportion ± SD	Strongest positive correlation (Spearman at p < 0.05)	Strongest negative correlation (Spearman at p < 0.05)
grass species				
<u>*Agrostis capillaris*</u>	84	10.8 ± 0.1	*Festuca rubra* (0.55)	*Arrhenatherum elatius* (−0.41)
<u>*Alopecurus pratensis*</u>	52	6.6 ± 0.2	*Trisetum flavescens* (0.35)	*Campanula patula* (–32)
Anthoxanthum odoratum	45	0.4 ± 0.0	*Plantago lanceolata* (0.47)	*Arrhenatherum elatius* (−0.29)
<u>*Arrhenatherum elatius*</u>	72	8.7 ± 0.1	*Galium mollugo* (0.45)	*Plantago lanceolata* (−0.48)
<u>*Dactylis glomerata*</u>	76	6.0 ± 0.1	*Schedonorus pratensis* (0.50)	*Potentilla erecta* (−0.40)
Elytrigia repens	43	1.7 ± 0.0	*Phleum pratense* (0.48)	*Geranium sylvaticum* (−0.35)
<u>*Festuca rubra*</u>	95	17.1 ± 0.2	*Agrostis capillaris* (0.55)	*Arrhenatherum elatius* (−0.42)
Holcus lanatus	40	0.5 ± 0.0	*Achillea millefolium* (0.50)	*Geranium sylvaticum* (−0.33)
Holcus mollis	53	3.3 ± 0.1	*Hypericum maculatum* (0.57)	*Schedonorus pratensis* (−0.40)
Phleum pratense	47	1.4 ± 0.0	*Elytrigia repens* (0.48)	–
Poa pratensis	88	1.8 ± 0.0	*Equisetum arvense* (0.29)	*Leucanthemum vulgare* (−0.44)
Schedonorus pratensis	47	1.9 ± 0.0	*Trisetum flavescens* (0.62)	*Hypericum maculatum* (−0.45)
Trisetum flavescens	62	1.9 ± 0.0	*Schedonorus pratensis* (0.62)	*Holcus mollis* (−0.40)
short-forbs				
Achillea millefolium	69	1.3 ± 0.0	*Holcus lanatus* (0.50)	*Cirsium helenioides* (−0.27)
Alchemilla monticola	47	0.6 ± 0.0	*Ranunculus acris* (0.61)	*Arrhenatherum elatius* (−0.30)
Galium mollugo	62	3.5 ± 0.1	*Arrhenatherum elatius* (0.45)	*Scorzoneroides autumnalis* (−0.36)
Plantago lanceolata	41	2.2 ± 0.1	*Trifolium repens* (0.66)	*Arrhenatherum elatius* (−0.48)
Ranunculus acris	41	0.5 ± 0.0	*Plantago lanceolata* (0.63)	*Galium mollugo* (0.33)
Rumex acetosa	74	0.2 ± 0.0	*Plantago lanceolata* (0.50)	*Knautia arvensis* (−0.42)
Stellaria graminea	45	0.3 ± 0.0	*Leucanthemum vulgare* (0.40)	*Tragopogon pratensis* (−0.29)
Veronica chamaedrys	88	1.8 ± 0.0	*Ranunculus acris* (0.48)	–
tall-forbs				
Heracleum sphondylium	31	0.3 ± 0.0	*Angelica sylvestris* (0.42)	*Leontodon hispidus* (−0.28)
Hypericum maculatum	59	3.3 ± 0.1	*Holcus mollis* (0.57)	*Schedonorus pratensis* (−0.45)
legumes				
Lathyrus pratensis	50	1.4 ± 0.0	*Galium mollugo* (0.40)	–
Trifolium repens	40	0.6 ± 0.0	*Trifolium pratense* (0.72)	*Arrhenatherum elatius* (−0.38)
Vicia cracca	53	0.4 ± 0.0	*Vicia sepium* (0.38)	*Avenella flexuosa* (−0.27)
Vicia sepium	36	0.2 ± 0.0	*Festuca rubra* (0.45)	*Festuca rubra* (−0.32)
sedges and rushes				
Luzula multiflora	31	0.3 ± 0.0	*Anthoxanthum odoratum* (0.46)	*Dactylis glomerata* (−0.31)

Species with low frequency including 14 species of grasses, 25 species of tall-forbs, 74 species of short-forbs, 12 species of legumes, 9 species of sedges and rushes, and 3 other species are not shown.

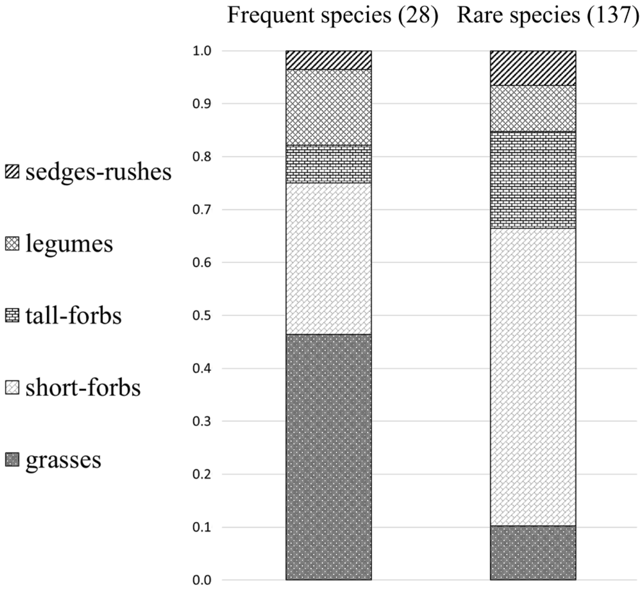

Fig. 2. Proportion of growth forms within the groups of frequent and rare species.

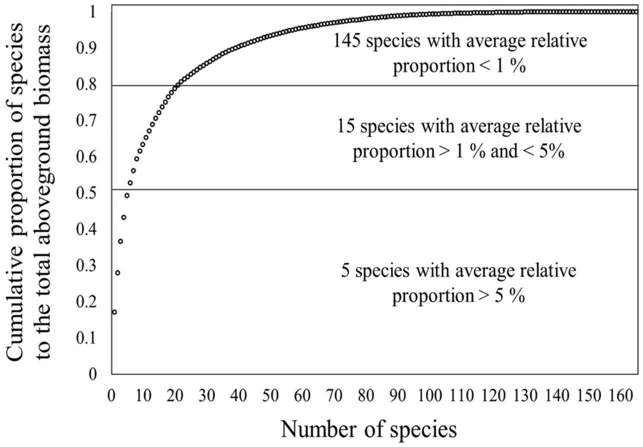

Fig. 3. The cumulative proportion of s-AGB to the *t*-AGB. See Table S-2 (Supplementary material) for details.

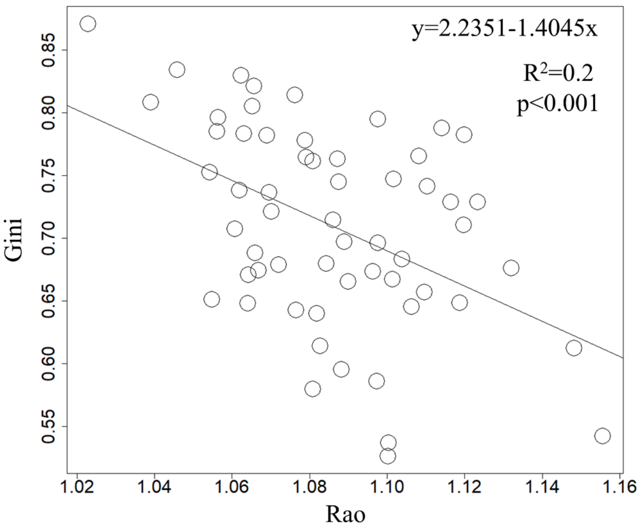

Fig. 4. Correlation between functional diversity (Rao) and biomass inequality among species (Gini).

3.2. Species responses to environmental and management factors

Explanatory variables explained 22.1 % (R^2 adj 16.3 %) of the total variation in s-AGB data (Fig. 5A, B). The impact of four explanatory variables on s-AGB was found significant after the application of forward selection and the FDR correction of the *p*-values. The most influential variable on s-AGB data was pH (39.8 % of the total variation explained; pseudo-F = 5.4; p(adj) = 0.003). Land management contributed 31.2 % (pseudo-F = 4.5; p(adj) = 0.004), temperature 16.7 % (pseudo-F = 2.5; p (adj) = 0.009), and precipitation 12.2 % (pseudo-F = 2.5; p(adj) = 0.017) to the total variation explained. None of the explanatory variables from the explanatory group topography, nor vegetation parameters, were selected in the stepwise selection of variables.

The *t*-value biplots showed positive and negative correlations of s-AGB to particular explanatory variables (Fig. 6A–D). The highest number of correlations was found for soil pH and land management. Increasing pH was positively related to the grasses (*A. elatius*, *E. repens*, *P. compressa*, *P. trivialis*, *S. pratensis*, and *T. flavescens*), the short and tall forbs (*A. vulgaris*, *C. arvensis*, *C. aromaticum*, *C. biennis*, *G. mollugo*, *G. rivale*, *O. vulgare*, *R. polyanthemos, S. jacobea,* and *T. officinale*), and the legumes (*M. lupulina* and *V. sepium*). Several grass species (*A. capillaris*, *F. rubra*, and *H. mollis*) and a tall forb (*H. maculatum*) were negatively correlated with increasing soil pH. Twice as many species were found positively correlated with the mown grasslands than with abandoned ones. A positive correlation to mowing management was found for the grasses (*A. odoratum, F. rubra, P. trivialis, S. pratensis*, and *T. flavescens*), the short forbs (*C. fontanum* subsp. *vulgare*, *C. biennis, P. lanceolata, R. acris, R. minor, R. acetosa,* and *T. officinale*), and the legumes (*T. pratense* and *T. repens*). A negative relationship between s-AGB and mown grasslands (positive with abandonment) was found for the grasses (*A. elatius* and *H. mollis*) and the tall forbs (*A. podagraria, C. aromaticum, G. mollugo, S. nemorensis*, and *U. dioica*). Increasing precipitation was positively correlated with *A. capillaris*. There were no significant relationships found for s-AGB and precipitation.

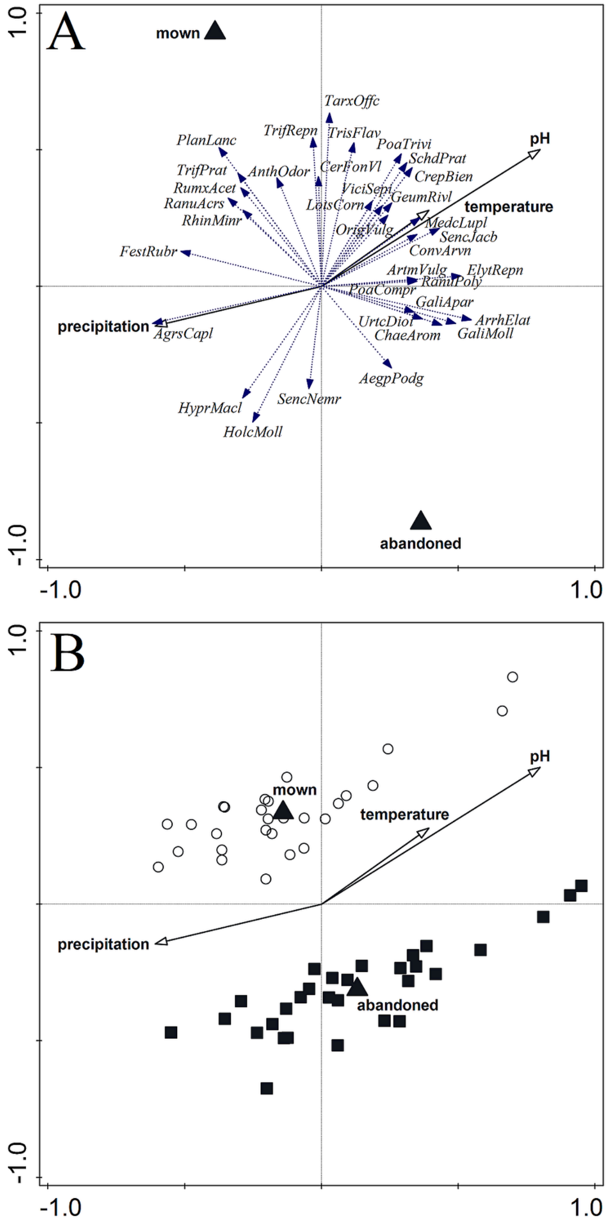

Fig. 5. The redundancy analysis (RDA) of s-AGB data. Significant and non-collinear explanatory variables (solid arrows and filled triangles) were plotted. The RDA diagram with 35 best-fitted species (dotted arrows) (A) and ordination of plots representing mown (open circles) and abandoned grasslands (filled squares) (B) are shown. Constrained RDA axis 1 (horizontal) explained 11.1% of the total variation in s-AGB data, and RDA axis 2 (vertical) explained 6.1% of the total variation in s-AGB data. Species abbrevations: AegpPodg – *Aegopodium podagraria*; AgrsCapl – *Agrostis capillaris*; AnthOdor – *Anthoxanthum odoratum*; ArrhElat – *Arrhenatherum elatius*; ArtmVulg – *Artemisia vulgaris*; CerFonVl – *Cerastium fontanum* subsp. *vulgare*; ChaeArom – *Chaerophyllum aromaticum*; ConvArvn – *Convolvulus arvensis*; CrepBien – *Crepis biennis*; ElytRepn – *Elytrigia repens*; FestRubr – *Festuca rubra*; GaliApar – *Galium aparine*; GaliMoll – *Galium mollugo*; GeumRivl – *Geum rivale*; HolcMoll – *Holcus mollis*; HyprMacl – *Hypericum maculatum*; LotsCorn – *Lotus corniculatus*; MedcLupl – *Medicago lupulina*; OrigVulg – *Origanum vulgare*; PlanLanc – *Plantago lanceolata*; PoaCompr – *Poa compressa*; PoaTrivi – *Poa trivialis*; RanuAcrs – *Ranunculus acris*; RanuPoly – *Ranunculus polyanthemos*; RhinMinr – *Rhinanthus minor*; RumxAcet – *Rumex acetosa*; SchdPrat – *Schedonorus pratensis*; SencJacb – *Senecio jacobaea*; SencNemr – *Senecio nemorensis*; TarxOffc – *Taraxacum officinale*; TrifPrat – *Trifolium pratense*; TrifRepn – *Trifolium repens*; TrisFlav – *Trisetum flavescens*; UrtcDioi – *Urtica dioica*; ViciSepi – *Vicia sepium.*

4. Discussion

4.1. Contributions of species and species groups to the aboveground biomass

This study found a differing relative contribution of common and rare species to the *t*-AGB and high biomass inequality between coexisting species; as expected, it shows that widely distributed plant species

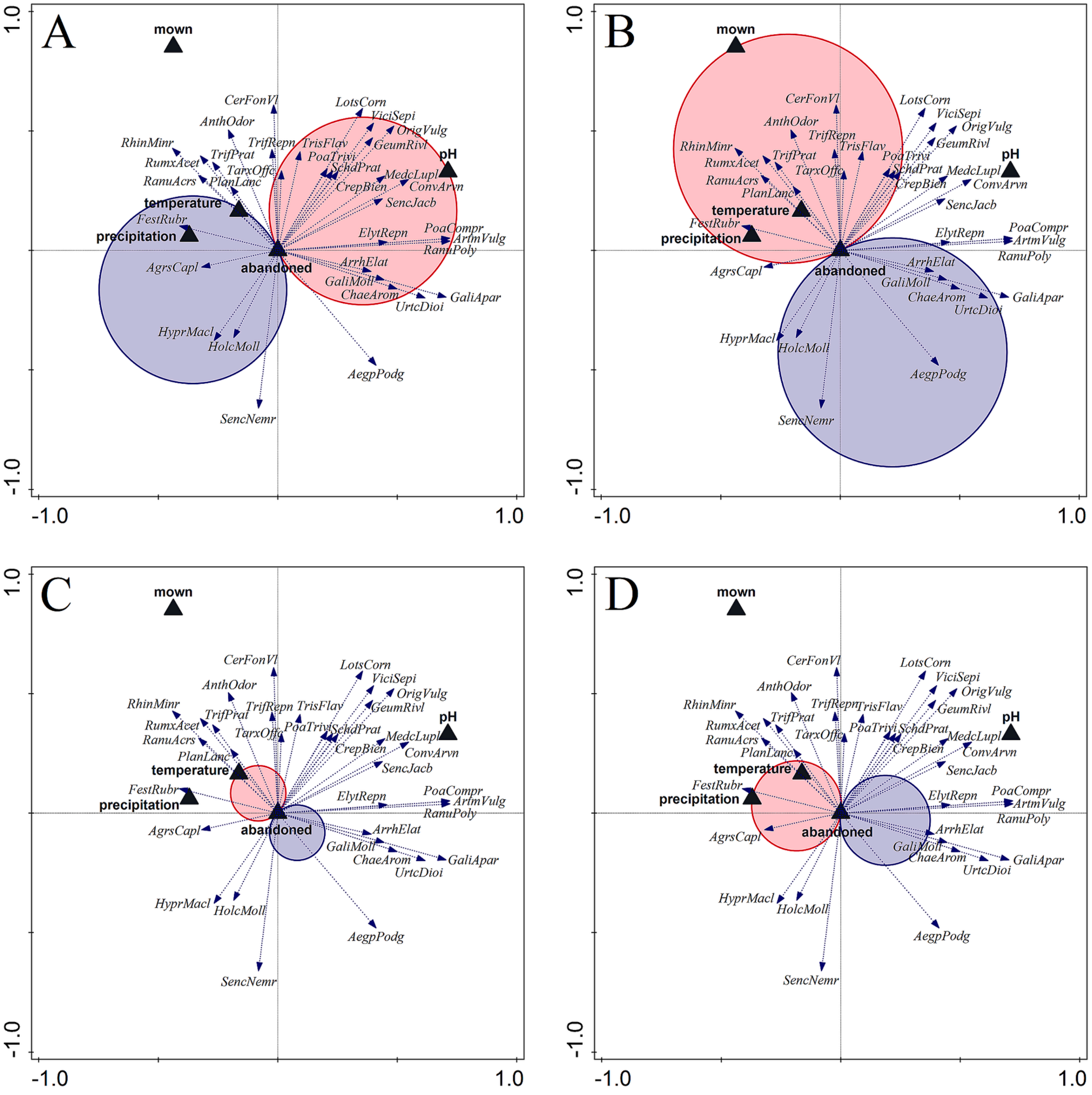

Fig. 6. *T*-value biplots of redundancy analysis (RDA) with Van Dobben circles drawn for pairwise relationships between s-AGB data and explanatory variables pH (A), land management (B), temperature (C), and precipitation (D). The s-AGB data (response variables) are displayed as dashed arrows. Explanatory variables are displayed as triangles. See Fig. 5 for species abbreviations.

are indeed most important in terms of biomass production in semi-natural grasslands, but the role of rare species should not be underestimated. Worth noting is that rare species constituted about three-fourths of all species recorded in this study. This study and others have shown that various forbs (also legumes) contribute significantly to grassland biomass and are indicative of high diversity in grassland communities (Li et al., 2016; Pokorny et al., 2004). It has been postulated that a variety of forbs is largely responsible for the taxonomic, phylogenetic, and functional diversity of grassland biome (Bråthen et al., 2021) and are crucial for the diversity of pollinators (Biesmeijer et al., 2006). Forbs contribute greatly to the richness of grass-dominated ecosystems worldwide across a wide range of climate regimes, including, for instance, prairies in North America; savannas in Africa; temperate European grasslands; Mongolian steppes; pampas, campos and cerrados in South America (see Table 1A, Supplementary material; Bråthen et al., 2021). Soliveres et al. (2016) underlined that rare species are the most important component of diversity because these species ensure ecosystem multifunctionality. Moreover, Schaub et al. (2020) underlined the importance of species-rich grasslands in forage production since high species diversity is positively correlated with increased biomass yields at rather constant forage quality. The balance between preserving high plant diversity and profitable yields in semi-natural grasslands should be prioritized in modern agriculture and nature conservation policies.

The relatively high values of the Gini coefficient found in the studied grasslands indicate an overall high biomass inequality among coexisting species. Biomass inequality can be ascribed to the five most widespread and most abundant grass species, which constituted on average about 49.2 % of the *t*-AGB. All of them are widespread grassland species in Western and Central Europe; thus, their dominance in grassland biomass can be expected in the entire range of plant communities they form (Preislerová et al., 2022; Rodríguez-Rojo et al., 2017). The fact that grasses were found to have the highest relative proportion to the *t*-AGB is not surprising since this group of species is evolutionarily best adapted to open landscape habitats with continuous disturbance (Linder et al., 2018; Strömberg, 2011). According to the mass ratio hypothesis, ecosystem functioning is predominantly determined by the dominant species and their functional traits (Grime, 1998). However, it is equally important to highlight that nearly a half of the *t*-AGB was dependent on 160 species. Among them, there were 145 species with a very low relative proportion to the *t*-AGB (< 1 %). Non-dominant species can be of different sizes and have various functional traits and life strategies, and varying abilities to compete for resources. This study shows that the inequality in biomass distribution among species decreases with increasing functional diversity of the community. The distinctions in resource use between different plants (high niche differentiation) ensures the coexistence of less competitive species with the dominants by the variety and complementarity of species' functional traits (Hector et al., 1999; Jiang et al., 2020; Maire et al., 2012; Padullés Cubino et al., 2022; Tilman et al., 1997). The result of this study supports the belief that mass ratio hypothesis and niche complementarity in semi-natural grasslands are complementary to each other rather than mutually exclusive (Diaz et al., 2007; Maire et al., 2012; Mouillot et al., 2011). The complementarity of the mass ratio hypothesis and niche complementarity is also well supported by a number of pairwise positive correlations identified between dominant and non-dominant species (Table 2, Table S-3, Supplementary material). In contrast, many interactions between dominants and weak competitors could not be detected due to stochasticity in species distribution being affected by dispersal, environmental filtering, colonization, and successful competition.

4.2. *Species responses to environmental and management factors*

The highest portion of the variation in the s-AGB data was explained by the soil pH gradient. Soil pH has been indicated as one of the most important predictors of plant species composition in multiple studies based on species coverage data from wet grasslands (Hájek and Hájková, 2004; Zelnik and Čarni, 2008), dry mesic grasslands (Dvořáková et al., 2014), acidic grasslands (Stevens et al., 2011), and various different grassland types (Merunková and Chytrý, 2012). This study fills the gap of knowledge related to the effect of pH on s-AGB. In mountainous areas, changes in topographical features heavily impact pH, which is reflected in vegetation composition (Furley, 1974b, 1974a). The soil pH is typically lower on steep convex slopes exposed to weathering and higher in flat and concave areas (Merunková and Chytrý, 2012). In this study, the pH gradient was very wide, with a predominance of strongly acidic soils (47 % of samples had pH of < 4.5). The soil pH was negatively correlated with increasing precipitation, which positively correlated with increasing altitude, as there is a strong linear relationship between these factors in the Sudetes Mountains. The study found that there is a strong turnover in species composition along the pH gradient, and many more species correlated positively rather than negatively with increasing soil pH. Species with a negative correlation to pH (positive correlation to low pH), including *A. capillaris*, *F. rubra*, *H. mollis*, and *H. maculatum*, are diagnostic for nutrient-poor habitats on acidic bedrock (Chytrý et al., 2007; Kącki et al., 2021). These species are the most important in terms of productivity at higher elevations, possibly due to their physiological adaptations related to acidification. Alternatively, species with a positive correlation to pH are mostly lowland species that also thrive in low altitude grasslands in more nutrient-rich and less acidic habitats (Chytrý et al., 2007; Kącki et al., 2021). The limited abundance of these species in low pH habitats could be related to high phytotoxicity and nutrient deficiency (Tyler, 1996).

Land use management was found to be the second most important explanatory variable, and it accounted for about one-third of the variation explained in s-AGB. Short period of time since abandonment did not have as strong an effect as soil chemistry (pH in this case). With further successional changes it can probably be expected that abandonment will have an overriding role over the soil properties on the community structure and composition.

This and other studies documented a positive relationship between nitrogen-fixing legumes (here *T. pratense* and *T. repens*) and mowing management, while negative with abandonment (Ribeiro et al., 2014; Rudmann-Maurer et al., 2008). These results may indicate the low competitive ability of legumes in relation to the increasing dominance of strong competitors such as clonal grasses and tall forbs in the absence of mowing. This study also observed that mowing facilitates the development of less competitive plant species, especially low-productive short forbs, which are the core of the diversity in semi-natural grasslands (Pykälä et al., 2005). The results presented here show that the dominance of indigenous species may persist despite the cessation of mowing over a period of 5–15 years. Lepš (2004) highlighted that the high stability of dominant species is a property of semi-natural plant communities that have a naturally developed dominance structure. A similar role was found for less abundant species (Lyons & Schwartz, 2001). Pokorny et al. (2005) found that the dominance of indigenous species and their maximized niche complementarity is important in invasion resistance This could explain why alien species common in the Sudetes Mountains such as *Solidago gigantea*, *S. canadensis* and *Lupinus polyphyllus* (Czarniecka-Wiera et al., 2019) were poorly represented in abandoned grasslands (Table S-1, Supplementary material). Expansive species with high competitive abilities produce high amounts of biomass that can considerably exceed the productivity of non-invaded grassland ecosystems (McLeod et al., 2016; Teixeira et al., 2020). Abandonment of semi-natural grasslands is also often followed by the expansion of native tall forbs (Galvánek and Lepš, 2012; Pavlů et al., 2013), which was also found to be the case in this study (*A. podagraria*, *C. aromaticum*, *G. mollugo*, *S. nemorensis* and *U. dioica*). These species have their optimum in nutrient-rich and species-poor fringe communities. The progressive expansion of these species may lead to the exclusion of species with life-history strategies developed under mowing and grazing management.

Nutrient levels have been previously reported as one of the major determinants of species composition (Hejcman et al., 2007; Pavlů et al., 2022; Titěra et al., 2020) and productivity in grasslands with indications that phosphorus and nitrogen are limiting factors (Hejcman et al., 2010; Pavlů et al., 2013). This study found a wide range of nutrient levels, and therefore it is very difficult to generalize their effect on s-AGB. The lack of a unitary effect from nutrients could also be influenced by the predominant role of pH, which determines nutrient availability to plants (Heyburn et al., 2017; Tian et al., 2017).

The gradient in climatic variables is heavily dependent on altitude and mirrors that of pH. The significant response of s-AGB is the result of a wide gradient in mean annual temperature (6.3 °C-9.6 °C) and precipitation (721–1600 mm), but as individual variables both were weaker predictors of s-AGB than pH and land use management. This is reflected by a small number of correlations of individual species with these controlling variables. Two climatic variables together accounted for almost a third of the total variation explained in s-AGB data. The most pronounced effect of climatic factors on productivity was observed in macroecological studies carried out analyzing macro-climatic continentality and altitudinal gradients (Ni, 2004; Yang et al., 2009). Neither topography-related nor vegetation parameter variables were selectively significant in the model. The lack of any significant impact due to topography is most likely due to the wide and overlapping environmental requirements of mesic grassland species in relation to water availability (TWI), thermal conditions (DAH), and heterogeneity of the landscape (TRI).

5. Conclusions

From these findings it can be concluded that semi-natural grasslands consist of a number of species with a differing relative contribution to the total aboveground biomass. It was found that just a few grass species made up half of the total biomass, on average. However, less frequent and less abundant species (especially short forbs) combined to play an important role in the production of biomass. What is crucial is that they are the core of diversity in semi-natural grasslands. This study showed overall high biomass inequality among coexisting species, and that it is decreasing with increasing functional diversity of the community. These findings support the mass ratio hypothesis on one hand, but on the other hand they highlight the essential role of niche differentiation which ensures the coexistence of less competitive species with the dominants by the variety and complementarity of functional traits. This study identified pH as the most important predictor of s-AGB, followed by land management (mowing versus abandoned) and climatic explanatory variables. Soil and climatic conditions are important environmental filters that shape species composition in plant communities. However, mowing (or other disturbance regimes such as grazing) is essential for the conservation of high species and functional diversity in semi-natural grasslands. Regular biomass removal suppresses competitor species, thus preventing the competitive exclusion of multiple subordinate species which are an important component of grasslands productivity and diversity. The maintenance of species diversity in grasslands should be prioritized in nature conservation policies to ensure the sustainability of ecosystem functioning and services.

CRediT authorship contribution statement

Grzegorz Swacha: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Supervision. **Mateusz Meserszmit:** Conceptualization, Investigation, Methodology, Writing – review & editing. **Lenka Pavlů:** Investigation, Writing – review & editing. **Vilém V. Pavlů:** Investigation, Writing – review & editing, Supervision. **Klára Kajzrová:** Investigation, Writing – review & editing. **Teowdroes Kassahun:** Investigation, Writing – review & editing. **Małgorzata W. Raduła:** Formal analysis, Writing – review & editing. **Jan Titěra:** Investigation, Writing – review & editing. **Zygmunt Kącki:** Conceptualization, Methodology, Investigation, Writing – review & editing, Supervision.

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.

Data availability

Data will be made available on request.

Acknowledgments

This work was funded by the European Union from the European Regional Development Fund under Interreg VA Czech Republic-Poland from the project 'Grassland biomass as a renewable energy source-Biodiversity-Biomass-Biogas' (CZ.11.4.120/0.0/0.0/16_026/0001092). We thank Tomasz Szymura and Magdalena Szymura for valuable suggestions.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.109740.

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