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Multi-aspect analysis of biomass production concerning taxonomic and functional trait composition of vegetation on heaps

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Abstract: Studies on biodiversity and biomass productivity in ecosystems indicate that species richness and functional diversity drive ecosystem processes, including biomass productivity. Various models, such as unimodal, negative, and neutral, including complementarity and mass-ratio hypotheses, propose relationships between biodiversity and biomass. Despite numerous studies in natural and seminatural ecosystems, factors affecting biodiversity and biomass relationships remain controversial. This study analyses taxonomic and functional diversity as drivers of above-ground biomass and explores mechanisms influencing biomass production in spontaneous vegetation in post-mining mineral habitats. The study reveals that in the coal mines' mineral novel ecosystems, the highest biomass in spontaneous vegetation is not significantly correlated with high diversity in vegetation species composition. Harsh conditions in mineral material habitats are reflected in plant species and the functional diversity of spontaneous vegetation. Successional development on post-coal mine heaps exhibits non-analogous species composition. Biotic and abiotic conditions shape gradients along which vegetation species composition is distributed, influencing functional and taxonomical diversity, and ultimately impacting biomass quality, quantity, and ecosystem function. Contrary to expectations, higher biomass is not linked to vegetation types with greater species composition diversity. Regardless of diversity measurement, areas with lower species diversity show higher accumulated biomass. This paradox suggests that factors beyond species diversity significantly impact biomass quantity in ecosystems. These findings challenge assumptions, emphasising the need for further research into specific mechanisms regulating biomass quantity in different vegetation types to refine our understanding of ecosystem dynamics.

Keywords: biomass, diversity indices, non-analogous species assemblages, primary productivity, taxonomic and functional diversity

INTRODUCTION

Understanding the relationship between the above-ground biomass (AGB) and the vegetation plant species composition diversity drives the mechanisms of ecosystem functioning processes, which are at the core of community ecology. This relationship has been intensively studied in different vegetation types and ecosystems. The forest inventory data suggest a positive relationship between AGB and community species diversity (Gamfeldt *et al.*, 2013; Vargas-Larreta *et al.*, 2021). Other studies have presented the antagonistic relationships between AGB and community species diversity (Reich *et al.*, 2004). The research conducted by Wang *et al.* (2012) revealed a unimodal relationship. In comparison, Wang *et al.* (2012) and Grace *et al.* (2016) reported null relationships.

Two main hypotheses have been considered to understand the relationship between biodiversity, community species composition, and the related below and above-ground organisms on ecosystem processes. The mass-ratio hypothesis was presented by Grime (1998), and a complementarity hypothesis was presented by Tilman *et al.* (1997). According to the complementarity hypothesis, species richness and diversity represent the variety of resource use strategies. The limited overlap of niches along the nutrient provision axes enhances the ecosystem functioning due to the partition of the niches. In natural and semi-natural ecosystems, the abundance of species diminishes as resource availability declines. A few species can survive under the reduced nutrient provision in the habitats. At high productivity, the abundant nutrient availability and competition for space and light cause the competitive exclusion of species. In such competitive conditions, only a few plant species can become dominant. Grime (1998) suggests that the productivity of a vegetation community and, consequently, the ecosystem depends on the abundance of the particular functional traits presented by the individuals of dominant species to the plant biomass. Based on the above, ecosystem properties including biomass, can be assessed from the weighted mean community values (CWM) traits of species assembled in the analysed community.

Some aspects have to be underlined to emphasise the need to present a multi-aspect analysis of biomass amount establishment concerning taxonomic and functional traits of vegetation plant species composition on the mineral habitats of post-coal mine heaps. Plant species individuals with particular functional traits, that assemble in vegetation patches on the mineral habitats of post-coal mine heaps might present distinctive biomass's chemical and biochemical composition, that are released and comprise the resources at the individual and ecosystem levels (Díaz *et al.*, 2007). The plant species composition of the spontaneous vegetation patches recorded on the mineral of post-coal mine heap habitats is based on the presence of the dominant plant. The non-analogous species composition of the Novel Ecosystem vegetation on post-coal mine heaps is characterised, and identified by the dominance of individuals of one, dominant species, accompanied by many species of low abundance (Kompała-Bąba *et al.*, 2020). The role of dominant species in vegetation and ecosystems functioning has been observed e.g., by Grime. In particular, Grime's hypothesis suggests that functional traits of the dominant species have a more significant influence on ecosystem processes due to the few competitive species, which decrease complementary processes and decrease the functional diversity. This mechanism is still being discussed (Kirby and Potvin, 2007; Schumacher and Roscher, 2009; Cheng *et al.*, 2018). The spontaneous processes that can be observed and analysed in the ecosystem developing on habitats established due to human activity give us additional data related to the multi-aspect analysis of the biomass amount concerning the taxonomic and functional trait's composition of vegetation on post-coal mine spoil heaps (Kompała-Bąba *et al.*, 2020).

Species richness is a commonly used diversity measure that reflects the fundamental aspects for understanding the relationship between species diversity and biomass concerning ecosystem productivity (Díaz and Cabido, 2001). Species richness provides a measure of diversity that is strictly related to many processes that regulate ecosystem functioning. However, based only on species richness, it is challenging to relate particular ecosystem processes to each species and determine their contributions to ecosystem functioning and productivity. The formula used for species richness calculation assumes that all species are equivalent. The functional differences among species are not accounted for in the calculation. Functional diversity is the crucial determinant of ecosystem functioning (Díaz and Cabido, 2001; Loreau *et al.*, 2001). For this reason, the functional analysis performed for the spontaneous vegetation, that presents an additional aspect of diversity, can be supportive in understanding the diversity biomass relationship.

Analysing biomass production concerning the taxonomic and functional vegetation plant species trait composition on the mineral habitats of post-coal mine heaps is important for many reasons: The post-coal mine spoil heaps are areas that require effective ecosystem re-establishment. Understanding which plant species are best adapted suited to colonise these challenging conditions and the functional traits that enable them to do so is crucial. Different plant species and their functional traits influence the rate of biomass establishment. Identifying these species and traits can help to select the most efficient plants for novel ecosystem re-establishment.

Most studies on the relationship between biomass and diversity of vegetation plant species composition have been conducted in relatively non-complex ecosystems, such as poor in-species grasslands and forest monocultures. Regardless of the uncertainty about the biodiversity-biomass relationship in natural and semi-natural ecosystems, human-induced environmental change is occurring globally and, therefore, ecosystem properties are altered directly through changing abiotic conditions and indirectly by modifying community composition.

However, when human activity causes transformations that cross the ecological threshold, a novel ecosystem develops (Hobbs, Higgs and Harris, 2009; Hobbs, Higgs and Hall, 2013; Dyczko, Jagodziński and Woźniak, 2022). The novel ecosystems evolve under anthropogenically derived conditions frequently on the habitats established de novo by humans and are referred to as novel ecosystems (Hobbs *et al.*, 2006; Prach and Hobbs, 2008; Morse *et al.*, 2014; Bierza *et al.*, 2023; Woźniak *et al.*, 2023). Hobbs *et al.* (2006) found that in novel ecosystems, the primary production depends on vegetation assemblages composed of plant species not known in any natural or semi-natural vegetation. The non-analogous species composition is emerging in habitats and environments not known in natural and semi-natural conditions (Williams and Jackson, 2007). The non-analogous plant species assemblages cause the non-analogous composition of the above- and below-ground organisms related to the primary producer to differ (Williams and Jackson, 2007; Błońska *et al.*, 2019).

Due to the specific habitat conditions of the post-mining mineral material, the organisms are gathered according to new habitat constrains and unknown pathways of ecosystem development. A defined aspect of the successional development of herbaceous vegetation on post-coal mine heaps is the emergence of unique assemblages of non-analogous plant species. The spontaneous vegetation development on the heap habitats is reflected as a mosaic of distinctive, one species dominated, vegetation patches. The spontaneous herbaceous vegetation growing on post-coal mine heaps consists of a mosaic of patches dominated by species confined to a wide range of microhabitats (Błońska *et al.*, 2019; Kompała-Bąba *et al.*, 2019). The herbaceous vegetation that spontaneously emerges on post-coal mine heaps forms a patchwork of areas primarily governed by species adapted to diverse microhabitats (Frouz *et al.*, 2008; Woźniak, 2010; Kompała-Bąba *et al.*, 2019). The recorded vegetation patches are composed together of species known as typically growing in very different vegetation types, including the aquatic and marsh habitats, along with dry meadow and other grassland communities, stony gravel communities, and ruderal habitats (Kompała-Bąba *et al.*, 2023). The most accurate description of the vegetation growing spontaneously on post-mineral mining sites is the presence of dominant species. The dominant species drive the physiognomy and functionality of a given vegetation patch (Chmura *et al.*, 2011; Kompała-Bąba *et al.*, 2020; Ryś *et al.*, 2023). Understanding the mechanisms that influence the spontaneous vegetation plant species composition developed under habitat and environmental conditions created by humans is crucial for the efficient management of urban-industrialised areas (Hobbs, Higgs and Hall, 2013; Rotherham, 2017). This understanding is essential for sites where the knowledge about the ecosystem functioning processes and environmental habitat conditions, from the natural or semi-natural habitats, cannot be used (Frouz *et al.*, 2009; Collier and Devitt, 2016). Based on the current knowledge about the relationship between the vegetation plant species diversity and the amount of biomass in natural and semi-natural habitats, the objectives of this study have been elaborated. The intricate interplay of species dynamics within these non-analogous assemblages presents an intriguing avenue for exploring novel ecological paradigms and informs strategies for sustainable ecosystem management in anthropogenically disturbed landscapes (Collier and Devitt, 2016). Based on the overall characteristics of the vegetation diversity, understanding how this diversity is influencing the novel ecosystem functioning processes is the next step in the identification of the ecosystem functioning mechanisms. Analysing biomass production in relation to taxonomic and functional vegetation plant species trait composition on the mineral habitats of post-coal mine heaps is important for many reasons: The post-coal mine spoil heaps are areas that require effective ecosystem re-establishment. Understanding which plant species are best suited to colonise these challenging conditions and the functional traits that enable them to do so is crucial. Different plant species and their functional traits influence the rate of biomass establishment. Identifying these species and traits can help to select the most efficient plants for novel ecosystem re-establishment.

The aim is to assess the relationship between the taxonomical and functional diversity of the spontaneous vegetation species composition under the impact of biomass of dominant species in the spontaneous vegetation of the novel ecosystems of coal mine heaps that reflect the habitat condition diversity. Based, on current knowledge, we have hypothesised that the more diverse taxonomically and functionally vegetation types will be characterised by less biomass amount. The dominant species and species identity of the dominant species have no significant effect on the biomass amount on the poor mineral habitats of post-coal mine heaps. Analysing biomass amount in relation to taxonomic and functional vegetation plant species trait composition on the mineral habitats of post-coal mine heaps is important for many reasons: The post-coal mine heaps are areas that require effective ecosystem re-establishment. Understanding which plant species are best suited to colonise these challenging conditions and the functional traits that enable them to do so is crucial. Different plant species and their functional traits influence the rate of biomass establishment. Identifying these species and traits can help to select the most efficient plants for novel ecosystem re-establishment.

STUDY MATERIALS AND METHODS

SITE DESCRIPTION

The study area comprised spoil heaps of carboniferous barren rock located in the Silesian Upland: Zabrze (50°16'22" N, 18°44'43" E), Katowice (50°11'04" N, 19°00'33" E), Murcki (50°11'21" N, 19°02'07" E), and Mysłowice (50°10'28" N, 19°05'44" E).

The study has been carried out on heaps set up from mineral material being the by-product of deep black coal mining. The research area comprises four post-coal mining spoil heaps: "Sośnica-Makoszowy", "Kostuchna", "Murcki Boże Dary" and "Wesoła". These studied objects belong to the overburden heaps and stand out distinctly from their surroundings. They were started to be formed between 1900 and 1906 due to intensive coal mining in the Silesia region. The "Sośnica-Makoszowy" heap, covering an area of 170 ha, is an active heap located in the southern district of Zabrze. It has two settling ponds for mine water – a smaller "freshwater" and a larger "brackish" lake. The heap reaches a height of over 30 m. It is situated near the international A4 highway and the "Sośnica-Makoszowy" coal mine. It attracts tourists by offering breathtaking views and numerous trails for cycling and motorsports enthusiasts. The "Kostuchna" heap is located in the southern part of Katowice, in Kostuchna. It covers an area of 32 ha, with a heap height of approximately 62 m. It has been inactive since 1995 when mineral material deposition from the Murcki Coal Mine ceased. Reclamation work was completed in 2007. The area of the spoil heap is mainly covered with non-forest and scrub vegetation. The "Murcki Boże Dary" heap is located in Katowice – Murcki, near the Tychy–Katowice express road, covers about 14 ha with a volume of 1.7 mln m^3. It's adjacent to forests on the west and south and residential buildings on the northeast. Formed by mineral material from the "Murcki" coal mine, it underwent technical reclamation and is now largely covered with non-forest vegetation. It's used for tourism and cultural activities. The "Wesoła" heap, spanning 58 ha in Mysłowice, has been inactive since 1994 when mineral material deposition by the Mysłowice Wesoła Coal Mine ceased. It reaches a maximum height of 389 m a.s.l. and is predominantly covered in non-forest vegetation and scrub, with landscape reclamation efforts undertaken. The stored material is non-toxic.

The post-coal mine heaps' habitats represent unique sites characterised by pure mineral substrates. The habitat conditions on these heaps exhibit extreme abiotic conditions, including substantial variations in humidity and daily temperatures, high salinity, absence of soil, susceptibility to erosion, substrate instability, dusting, and unconventional chemical composition, along with the aforementioned thermal activity (Błońska *et al.*, 2019; Kompała-Bąba *et al.*, 2019; Prach and Walker, 2020). These conditions, both temporally and spatially variable, fluctuate with substrate depth resulting in a high degree of microhabitat variability. Beyond abiotic factors, the biotic parameters contribute to the unique ecology of these sites (Błońska *et al.*, 2019; Kompała-Bąba *et al.*, 2019; Prach and Walker, 2020). The habitat gradient in this study refers to the variety in abiotic and biotic mineral microhabitat conditions spotted across the coal mine spoil heaps where the research was conducted. This gradient encompasses environmental factors such as mineral material texture, salinity, water availability, organic matter content, and temperature fluctuations, which show significant differences across the studied sites. In particular, post-mining habitats are characterised by unique conditions resulting from mineral soil substrates, contributing to harsh abiotic features like high salinity, limited organic content, and unstable substrate. These factors play a crucial role in shaping diversity and plant species composition of spontaneous vegetation in newly established ecosystems. The surface, particularly at noon in summer, can experience extreme temperatures, reaching up to 50°C. Internally, elevated temperatures persist throughout the year due to coal-burning (Chmura and Molenda, 2012). This distinct thermal profile sets these sites apart from their surroundings, although precipitation levels remain consistent.

Beyond abiotic factors, the biotic parameters contribute to the unique ecology of these sites. In particular, the initial lack of a seed bank and nutrient deficiencies in the mineral soil substrate define the characteristics of these habitats. These conditions shape the specificity of the flora and give rise to vegetation types that are non-analogous, and capable of tolerating the harsh environmental conditions in these post-mining areas. Despite the challenging constraints, diverse vegetation has spontaneously developed on these sites. The term "biological deserts" has been applied to describe these areas due to the unique combination of factors. The recorded dynamics of the novel ecosystem development on the post-mining sites indicate that the term is not justified. Conversely, the mineral, post-mining sites become refugee habitats for endangered oligotrophic species (Tropek *et al.*, 2012). It is noteworthy that technical and other management practices have been implicated in reducing the biological diversity of post-mineral excavation heaps (Tropek *et al.*, 2012). Nonetheless, the spontaneous development of varied vegetation on these post-coal mine heaps underscores the resilience and adaptability of plant life in the face of extreme environmental challenges.

FIELDWORK METHODS

Field vegetation sampling

In our study, the methodology employed for vegetation sampling aimed at capturing the intricate details of land cover within designated research plots strategically positioned in areas showcasing uniform vegetation patches, predominantly characterised by the presence of the dominant species. In the presented study, the attention was focused on herbaceous non-forest vegetation. The size of the circular studied plots was unified by the 3 m radius. In order to identify and analyse the whole diversity, each of the physiognomically different vegetation patches has been recorded. The research was conducted during the growing season between 2018 and 2022 on 324 study plots. No special sampling arrangement has been adopted. Due to the dominant species presence, the patches representing different vegetation types are possible to recognise. To ensure a systematic approach, circular research plots with a consistent 3-metre radius were configured for data collection. Each circular research plot served as a microcosm for detailed vegetation assessment. The choice of a circular shape allowed for a balanced representation of the surrounding environment. The diameter of 3 m was selected to strike a harmonious balance between capturing localised plant diversity and minimising potential edge effects. The plot size was optimised to facilitate efficient and comprehensive data collection. Within each research plot species composition and coverage were meticulously documented. A systematic survey was conducted employing a ten-point scale to quantify the abundance of each vascular plant species. This scale ranged from less than 1% to increments of 10% up to 100%, facilitating a nuanced understanding of the dominance and distribution of plant species within the plots. This detailed assessment method allowed us to capture subtle variations in species abundance, contributing to a thorough characterisation of the vegetation landscape. The collected vegetation data formed the foundation for computing various diversity indices within the analysed area. Phytosociological investigations played a crucial role in this process.

Field soil sampling

During field research on designated 324 study plots, mineral material sampling was conducted. From each plot, a composite mineral material sample was collected for abiotic and biotic analysis performance and characteristics. To ensure representativeness, each sample consisted of a mixture of 3 (approximately 1.5 kg each) random points from the designated plot. Each sample was meticulously labelled, taking into account its precise location. Upon arrival at the laboratory, samples were air-dried and sieved to ensure uniformity for subsequent analyses.

The physicochemical parameters were measured as follows: soil pH was determined with a glass electrode in both water and 1 M KCl solution; electrical conductivity (*EC*) was measured using an electrode; soil organic carbon (SOC) was quantified using the Tiurin method; total nitrogen (TN) was analysed via the Kjeldahl method; available phosphorus (P_2O_5) was assessed by the Egner-Riehm method, and available magnesium (MgO) concentration was determined using the Schachtsabel method. Exchangeable cations (K^+, Na^+) were measured through atomic absorption spectroscopy, and soil moisture content was evaluated by comparing the mass of soil samples before and after drying.

Enzyme activity in the soil was also assessed, specifically targeting dehydrogenase, urease, and phosphatase as indicators of soil biological activity. Dehydrogenase activity was quantified based on formazan production per unit of soil mass over a specified period (Schinner *et al.* (eds.), 1996). Urease activity was evaluated following a modified method of Zantua and Bremner (1975), and phosphatase activity was measured through the quantification of p-nitrophenol released after soil incubation with buffered sodium p-nitrophenyl phosphate solution at varying pH levels.

Field biomass sampling

In the course of our study, we executed a meticulous procedure for biomass collection within predefined study plots. Employing a circular pattern with a 3-metre radius, we targeted the dominant plant species that significantly occupied the designated plot, surpassing the surrounding vegetation in cover. Inside each vegetation 3 m radius sampling plot, a smaller 50×50 cm subsampling plot has been selected in order to assess the biomass amount. The subsampling plots were selected in such a way to represent the proportion between the dominant and non-dominant plant species in the particular vegetation patch. In this way, the plants fresh and dry biomass weight reflected the ratio of biomass of dominant and non-dominant plants in the total biomass of the studied vegetation patch.

After collection, we ensured the preservation of sample integrity through precise packaging using labelled bags. On-site, the harvested plants were meticulously weighed, yielding crucial data on the fresh biomass of both the dominant species and coexisting flora in the proximity. The selection of study plots was guided by the utilisation of representative quadrats encapsulating the dominant species, thereby optimally representing the entire study area. Within these squares, we conducted assessments of the dominant species' coverage and quantitatively analysed its interactions with other co-occurring plants. The side length of these squares was standardised at 0.5 m, facilitating a precise evaluation of the dominant species' impact on the overall vegetation within the area. Based on the biomass of species present we calculated the biomass of the dominant species and assigned it as BiomDom. Based on the biomass of remaining species we calculated a fraction of biomass for each species, calculating total cover of species, fraction of cover of a species in a total cover and finally using proportion a proxy of biomass of remaining species were computed.

DATA ANALYSIS

To examine species-environment relations double CCA was applied on the basis of biomass of remaining species. Double CCA is a three-table ordination method proposed by Lavorel *et al.* (Lavorel *et al.*, 1998; Lavorel and Richardson, 1999; Lavorel, Rochette and Lebreton, 1999). In the classical context, canonical correspondence analysis (CCA) is used to link tables L and R to ordinate the community data in the light of the environmental variables (Kleyer *et al.*, 2008). The main task of CCA is to predict community data by environment and to ordinate the predicted values. Ojeda, Arroyo and Marañón (1998) performed an unusual CCA in which the ordination of L is constrained by the species traits table Q. Lavorel *et al.* (Lavorel *et al.*, 1998; Lavorel, Rochette and Lebreton, 1999) proposed combining these two CCA approaches in one analysis that was named as a double CCA (Lavorel *et al.*, 1998; Ojeda, Arroyo and Marañón, 1998; Lavorel, Rochette and Lebreton, 1999). This approach ordinates L by taking the effects of R and Q simultaneously into account (Lavorel and Richardson, 1999). Double CCA also encompasses two steps: (1) prediction of community data by both environmental variables and species traits and (2) ordination of predicted values (Kleyer *et al.*, 2008). In the present study, we used the R script provided by Kleyer *et al.* (2008) with a new function dbcca() and the packages "ade4", "vegan", "cluster", "ggplot2" and the others. Based on used plant traits Rao's quadratic entropy index (*RaoQ*) was calculated (Botta-Dukát, 2005). This index is a measure both of functional richness and functional divergence (Botta-Dukát, 2005). Apart from this, alternative approach was done i.e. community-weighted means (CWM) of plant traits were calculated. Detrended correspondence analysis (DCA) was run to examine whether CWM biomass of dominants and *RaoQ* significantly explain species composition. The passive projection using the "vegan" function envfit() was applied to examine the statistical significance of these factors in explaining the diversity of species composition. A Monte Carlo test with 999 permutations was undertaken. The Monte Carlo test in DCA involves generating simulated data sets by randomly shuffling the species data concerning the environmental or functional trait variables. By comparing the variation in the results obtained from the simulated data sets to the actual observed data, the Monte Carlo test helps to determine whether the observed relationship between species and environmental or functional trait variables is statistically significant. If the observed results are unlikely to occur by random chance alone, it suggests a significant relationship between species composition and environmental gradients. The Monte Carlo test is a valuable tool for assessing the significance of ecological patterns revealed through DCA, helping to understand the importance of environmental or functional trait variables in driving species composition. The species were grouped into functional groups called clusters based on the species responses in double CCA (Kleyer *et al.*, 2012). The distances were computed on the first two axes of the RLQ analysis distances among species and Ward's hierarchical clustering. The clusters were obtained from the dendrogram and the optimal number of functional groups was determined using the Calinsky-Harabasz stopping criterion (Tab. 1). The correlation ratios

Table 1. The list of traits of species that were included in analysis

Name of trait	Code	Type	Description
Height	height	continuous	a continuous trait measuring the plant's height from base to highest point, serving as a key indicator of structural and developmental characteristics
Leaf area	le_area	continuous	a continuous trait representing the leaf surface area, which determines the plant's photosynthetic capacity
Bud Height	BudHeight	ordinal (0 – T, 0.12 – G, Hy, 0.25 – H, 0.5 – Ch, 0.75 – N, 1 – M)	an ordinal trait indicating relative bud heights, establishing rank without precise distance measurement
Beginning of flowering	flw_early	integer	an integer trait indicating the timing of the onset of flowering
End of flowering	flw_late	integer	an integer trait indicating the timing of the end of flowering
Pollination by animals	poll_zoo	binary	a binary trait indicating whether pollination occurs via animals
Self-pollination	poll_self	binary	a binary trait indicating the presence or absence of self-pollination

cont. Tab. 1

Name of trait	Code	Type	Description
Wind pollination	poll_wind	binary	a binary trait indicating whether pollination occurs via wind
Medium seed weight	medium_seed_wght	continuous	a continuous trait measuring the average weight of seeds, indicating reproductive investment
Propagation by seed	seed	binary	a binary trait indicating the presence or absence of reproduction through seeds
Vegetative propagation	veg	binary	a binary trait indicating the presence or absence of vegetative reproduction
Presence of mycorrhiza	Myc	binary	a binary trait indicating whether the plant has a symbiotic relationship with mycorrhizal fungi
Anemochory	Anem	binary	a binary trait describing wind-based seed dispersal (anemochory)
Zoochory	Zoochory	binary	a binary trait describing animal-based seed dispersal (zoochory)
Barochory	Barochory	binary	a binary trait describing gravity-based seed dispersal (barochory)
Competitiveness	Comp	ordinal (1 – C, 0.5 – CR, CS, 0.33 – CSR)	an ordinal trait reflecting the plant's ecological competitiveness
Stress	Stress	ordinal (1 – S, 0.5 – CS, SR, 0.33 – CSR)	an ordinal trait indicating the plant's level of tolerance to environmental stress
Ruderality	Rude	ordinal (1 – R, 0.5 – CR, CS, 0.33 – CSR)	an ordinal trait describing the plant's ability to thrive in disturbed habitats
Ellenberg value for light	L	integer (0–9)	an integer trait indicating the plant's light preference, based on Ellenberg's ecological indicator scale
Ellenberg value for temperature	T	integer (0–9)	an integer trait indicating the plant's temperature preference, as per Ellenberg's scale
Ellenberg value for moisture	F	integer (0–12)	an integer trait reflecting the plant's moisture preference, following Ellenberg's ecological indicators
Ellenberg value for soil reaction	R	integer (0–9)	an integer trait indicating the plant's soil pH preference, according to Ellenberg's scale
Ellenberg value for nitrogen	N	integer (0–9)	an integer trait indicating the plant's nitrogen requirement, based on Ellenberg's ecological indicator scale

Source: own elaboration.

(median values) were calculated to measure the relationships between the obtained cluster and significant species traits and to determine any differences among the distinguished groups (Kleyer *et al.*, 2012). Only significant plant traits in the fourth corner analysis were subjected to this analysis. The Kruskal-Wallis test was used to test the significance of differences in *RaoQ* among dominants.

RESULTS

Key diversity metrics, including the Shannon-Wiener diversity index *H*, Evenness uniformity, and Simpson's dominance index, were calculated. These indices provided a nuanced and quantitative perspective on the vegetation structure, offering insights into both the richness and evenness of plant species. Importantly, this analysis focused solely on vegetation components.

According to the data presented in the table, the vegetation type characterised by the highest biomass are not the richest in species (Tab. 2). The habitat features *Calamagrostis epigejos* (type 1) a tufted grass common in grassy areas, and *Centaurea rhenana* (type 2), a meadow species. *Chamaenerion palustre* (type 3) is associated with wetland areas, while *Daucus carota* (type 4) grows in dry, sunny environments. *Eupatorium cannabinum* (type 5) prefers moist habitats, contributing to wetland plant diversity. Grasses from the *Festuca* group (type 6) appear across varied grassy sites. *Lotus corniculatus* (type 7) is characteristic of meadow habitats, and *Melilotus albus* (type 8) thrives in well-drained, disturbed soils. *Phragmites australis* (type 9) dominates wetland areas, providing essential structure and habitat. *Poa compressa* (type 10) is common on nutrient-poor soils, while *Solidago gigantea* (type 11) is a robust, ruderal species. *Tripleurospermum inodorum* (type 12) often occupies disturbed ruderal habitats, and *Tussilago farfara* (type 13) is commonly found in moist conditions. These vegetation types have been characterised based on their typical habitats, species composition, and ecological functions, providing insight into the varied environmental conditions across the study sites.

According to double CCA, both first and second axes totalled 59.84% (43.56% on the first axis and 16.29% on the second axis respectively). Some plant traits were correlated on the first axis (BudHeight, Zoochory, poll_wind) and on the second axis (Rude, Barochory, F). Amongst environmental factors soil enzymes, pH, and Ca were correlated with the first axis whereas Nematode, K, and Na were correlated with the second axis (Fig. 1).

Amongst plant traits, 12 variables were significantly associated with 9 environmental factors. There were, amongst

Table 2. The list of vegetation types and the value of main diversity parameters

Vegetation type and code	Dominant plant	Number of species			Biomass of the dominant dry mean	Biomass of the non dominant dry mean	Sum of the dry biomass of the patch mean
		max.	min.	mean	g		
1 (CE)	*Calamagrostis epigejos*	**22**	3	12	98.71	13.42	**112.13**
2 (CR)	*Centaurea rhenana*	20	7	11	85.31	11.91	97.23
3 (CP)	*Chamaenerion palustre*	16	8	11	76.41	12.99	89.40
4 (DC)	*Daucus carota*	20	7	13	81.81	12.87	94.68
5 (EC)	*Eupatorium cannabinum*	12	7	9	69.97	6.56	76.54
6 (F)	*Festuca* group	15	3	9	92.55	9.51	102.06
7 (LC)	*Lotus corniculatus*	16	9	12	113.67	12.22	125.89
8 (MA)	*Melilotus albus*	16	8	13	47.51	21.32	68.83
9 (PA)	*Phragmites australis*	**10**	3	7	172.70	14.70	**187.40**
10 (PC)	*Poa compressa*	19	8	14	87.42	15.34	102.76
11 (SG)	*Solidago gigantea*	**22**	6	13	110.93	14.96	**125.89**
12 (TI)	*Tripleurospermum inodorum*	21	8	13	81.34	13.24	94.58
13 (TF)	*Tussilago farfara*	18	1	8	67.00	9.85	76.85

Note: bold numbers indicate the patches of communities with the highest and lowest average number of species and corresponding the sum of the dry biomass.
Source: own study.

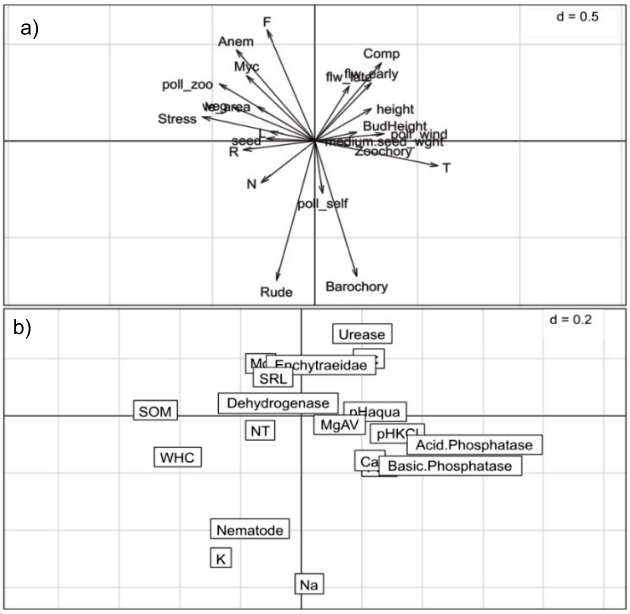
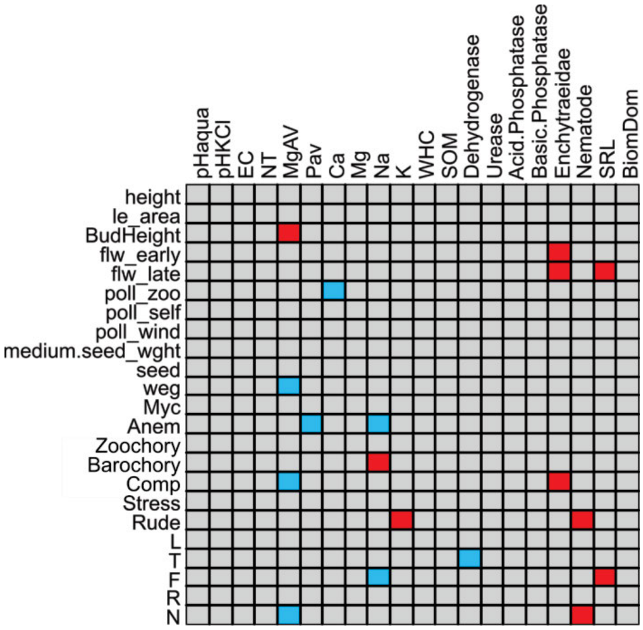


Fig. 1. The ordination of double canonical correspondence analysis (double CCA): a) plant traits, b) soil variables (physicochemical parameters, soil enzymes) and relationships amongst them; d = value in the upper right corner is the scale of the graph given by a grid, codes as in Tab. 1; source: own study



	pHaqua	pHKCl	EC	NT	MgAV	Pav	Ca	Mg	Na	K	WHC	SOM	Dehydrogenase	Urease	Acid.Phosphatase	Basic.Phosphatase	Enchytraeidae	Nematode	SRL	BiomDom
height																				
le_area																				
BudHeight					🟥															
flw_early																	🟥			
flw_late																	🟥		🟥	
poll_zoo							🟦													
poll_self																				
poll_wind																				
medium.seed_wght																				
seed																				
weg					🟦															
Myc																				
Anem						🟦			🟦											
Zoochory																				
Barochory									🟥											
Comp					🟦												🟥			
Stress																				
Rude										🟥								🟥		
L																				
T													🟦							
F									🟦										🟥	
R																				
N					🟦													🟥		

Fig. 2. Relationships between plant traits and environmental factors based on the fourth corner analysis; associations at $p < 0.05$: red cells = positive and significant, blue cells = negative and significant, grey cells = not significant, codes as in Tab. 1; source: own study

others, positive associations between available magnesium and BudHeight sodium content and Barochory, potassium and ruderal species, SRL, and weighted cover of Ellenberg F value. As far as negative associations are concerned, there were significant relationships between available magnesium content in vegetative reproduction, competitiveness and nitrogen value of plants, sodium content, and anemochory and moisture value for plants (Fig. 2).

Based on the responses of plant species through their traits in double CCA ordination space, 4 groups were distinguished. The list of clusters with species present is in Table 1. The most distinct group is a group D which contains eight species: *Lathyrus tuberosus*, *Lepidium campestre*, *Petrorhagia prolifera*, *Securigera varia*, *Senecio vulgaris*, *Sonchus asper*, *Tussilago farfara*, *Viola tricolor* (Fig. 3). The remaining groups are more similar to each other.

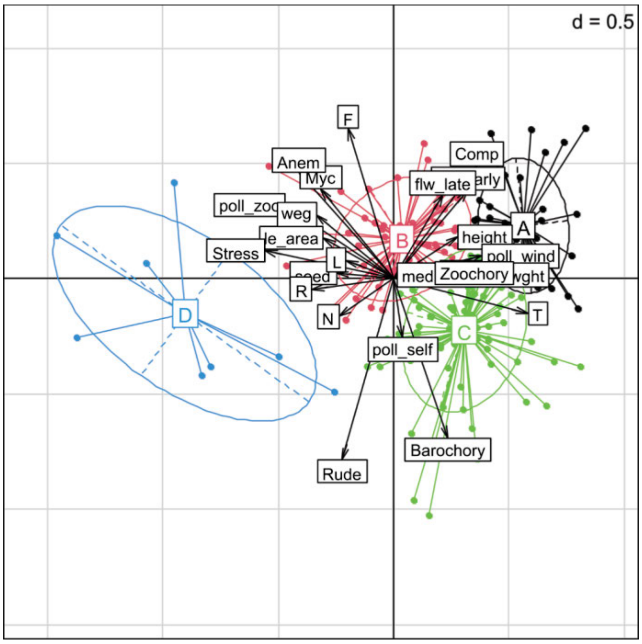


Fig. 3. The clusters of vegetation species composition in double CCA ordination space along with the gradients presented by the analysed plants' functional traits; *d* = value in the upper right corner is the scale of the graph given by a grid, codes as in Tab. 1; groups A to D reflect the similarity of the analysed traits and convergent responses of the species through their traits to the variability of habitat conditions revealed in the double CCA analysis; source: own study

According to DCA 22 plant traits explain species composition of vegetation on coal mine heaps. Only the values for late flowering and medium seed weight were non-significant (Fig. 4). The highest functional richness and divergence measured by Rao's quadratic entropy index (*RaoQ*) was revealed in *Triplospermum inodorum* and the lowest was in *Phragmittes australis* vegetation patches (Fig. 5).

The analysis of the median values of the plant traits revealed differences between the compared vegetation groups. The height of the bud is a trait that is different in groups A and D. The traits of early and late flowering are different in groups A and D either. The plant's ability to spread vegetatively and anemochory are influenced by trait diversity within groups B and E (Fig. 6). Barochory is higher in groups A and D while pollination by animals is important in all groups except for C. Taking into account competitiveness there is a positive gradient from group A to D and for ruderality there is a reverse trend (Fig. 6).

The comparison of Ellenberg's indicator values revealed there are no important differences among groups; however, these traits were associated with some environmental factors.

The detrended correspondence analysis (DCA) ordination analysis shows the distribution of the recorded vegetation patches along the functional traits' gradients (Tab. 3). The first axis is determined by the functional traits of plant species that present the mycorrhizal status, preference for acid soils, and stress while with the second axis zoochory trait, competition, height, ruderality. The biomass of dominant is associated with the first axis likewise *RaoQ* index.

Plant functional traits that appear most often in the vegetation patches distribution are the value of leaf area, animal pollination, the spreading by seeds, the presence of mycorrhiza, Barochory, and T Ellenberg indicator.

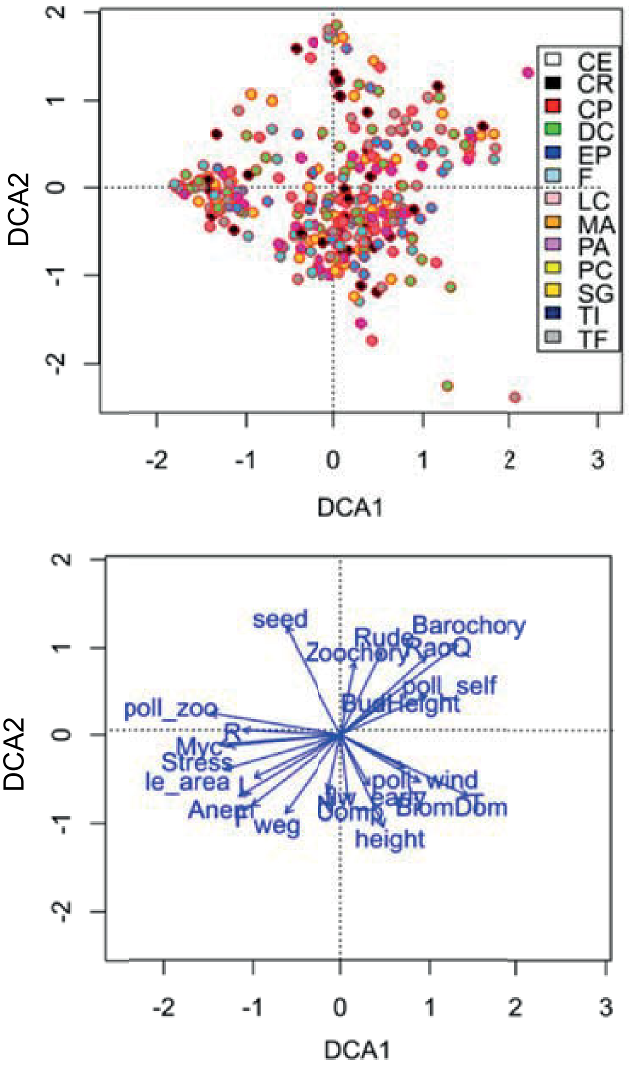


Fig. 4. The detrended correspondence analysis (DCA) with a passive projection of plant traits and functional diversity, *RaoQ* = Rao's quadratic entropy index, CE = *Calamagrostis epigejos*, CR = *Centaurea rhenana*, CP = *Chamaenerion palustre*, DC = *Daucus carota*, EP = *Eupatorium cannabinum*, F = *Festuca* group, LC = *Lotus corniculatus*, MA = *Melilotus albus*, PA = *Phragmites australis*, PC = *Poa compressa*, SG = *Solidago gigantea*. TI = *Tripleurospermum inodorum*, TF = *Tussilago farfara*, codes as in Tab. 1; source: own study

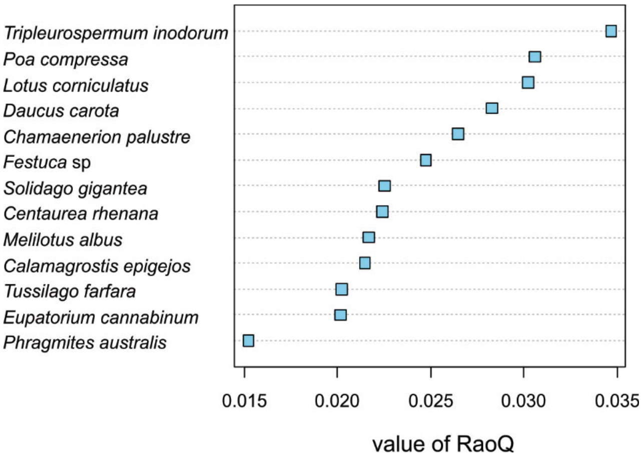


Fig. 5. The value of Rao's quadratic entropy index (*RaoQ*) analysis calculated for the recorded species composition of the distinguished vegetation types; source: own study

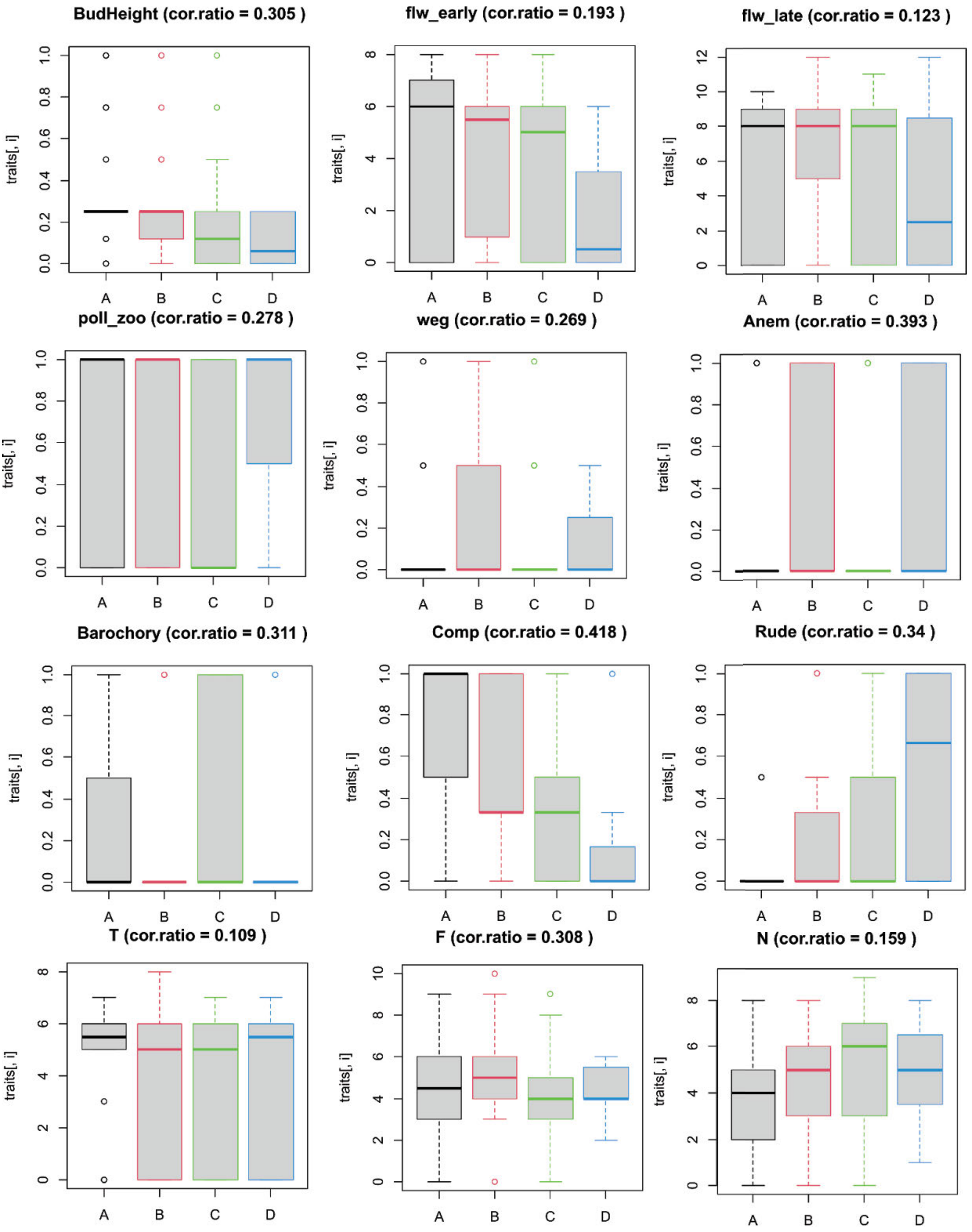


Fig. 6. The comparison of the median values of the plant traits among the distinguished functional groups of plants; cor.ratio = correlation ratios, codes as in Tab. 1; groups A to D reflect the similarity of the analysed traits and convergent responses of the species through their traits to the variability of habitat conditions revealed in the double CCA analysis; source: own study

Rao's quadratic entropy analysis has been performed to calculate Rao's diversity index. It is a measure of diversity used in community ecology. It is based on the concept of entropy from information theory and is used to quantify the diversity of a community by considering the relative abundance or proportion of different species within that community. Rao's diversity index provides a way to measure both richness (the number of different species) and evenness (how equally abundant those

Table 3. The *p*-values of the Monte-Carlo test in DCA to assess the significance of the relationship between species abundance and environmental or functional variables driving the space of gradients in which the plots are distributed

Name of trait	DCA axis 1	DCA axis 2	r^2	*p* value
RaoQ	0.73029	0.68314	0.3279	0.001
height	0.43447	−0.90069	0.2421	0.001
le_area	−0.95877	−0.28419	0.3547	0.001
BudHeight	0.80641	0.59136	0.0723	0.002
flw_early	0.50193	−0.86491	0.0790	0.001
poll_zoo	−0.98506	0.17222	0.4191	0.001
poll_self	0.90433	0.42683	0.2128	0.001
poll_wind	0.89044	−0.45509	0.1195	0.001
seed	−0.45054	0.89276	0.3549	0.001
weg	−0.58070	−0.81412	0.2224	0.001
Myc	−0.99744	−0.07145	0.3488	0.001
Anem	−0.85944	−0.51124	0.3347	0.001
Zoochory	0.18955	0.98187	0.1362	0.001
Barochory	0.78405	0.62070	0.5197	0.001
Comp	0.12608	−0.99202	0.0995	0.001
Stress	−0.99528	−0.09701	0.3084	0.001
Rude	0.43461	0.90062	0.2141	0.001
L	−0.89908	−0.43778	0.2242	0.001
T	0.90267	−0.43033	0.4672	0.001
F	−0.78363	−0.62123	0.3122	0.001
R	−0.99828	0.05863	0.2326	0.001
N	−0.20927	−0.97786	0.0777	0.001
BiomDom	0.86205	−0.50682	0.2015	0.001

Note: only significant variables are shown.
Explanations: r^2 = squared correlation coefficient, *RaoQ* = Rao's quadratic entropy index, codes as in Tab. 1.
Source: own study.

species are) within a community. The index takes into account the abundance of different species and provides a single value that represents the overall diversity of the community. This analysis revealed that the highest value of Rao's diversity index is recorded for the *Tripleurospermum inodorum*-dominated patches. This vegetation type indicates the initial stages of vegetation colonisation. A high value of Rao's diversity index typically indicates a higher level of diversity within a community. It suggests that the community contains a greater variety of species and that those species are more evenly distributed in terms of their abundance. The high value suggests that the community has a richer and more evenly balanced composition of species, which can be an indication of a healthy and well-functioning ecosystem. The lowest value of Rao's diversity index has been calculated for the *Phragmites australis* vegetation type. This vegetation type is characterised by the intense domination of the *Phragmites australis* individuals.

As presented in Table 4 the biomass of dominant plant species play a crucial role in the biomass amount of particular vegetation patch types. In Table 4 the number of species in relation to dominant and non-dominant biomass is presented.

DISCUSSION

THE CURRENT KNOWLEDGE ON THE RELATIONSHIP BETWEEN BIODIVERSITY AND BIOMASS AMOUNT

The relationship between plant diversity and the vegetation plant species biomass amount has been considered in some papers. There are some studies focused on this relationship (Frouz and Nováková, 2005; Frouz *et al.*, 2009; Pan *et al.*, 2016; DeMalach and Kadmon, 2017; Cheng *et al.*, 2018; Kompała-Bąba *et al.*, 2021; Ryś *et al.*, 2023). Many of the studies are conducted in forest ecosystems and managed forests, or based on the meta-analysis of data obtained from forest vegetation plant species composition and the amount of biomass. Plant biomass production has been studied and discussed in many papers in recent decades (e.g., Willig (2011), Grace *et al.* (2016)). The most crucial questions about the plant productivity–plant diversity relationships are

Table 4. The relations between the biomass of the dominant and non-dominant plant species in the analysed vegetation patches

Vegetation type	Dominant plant	Biomass of the dominant dry	Biomass of the non-dominant dry	Sum of the dry biomass of the patch	Biomass of the non-dominant dry (weight)		
		mean			max	min	mean
		g					
1 (CE)	*Calamagrostis epigejos*	98.71	13.42	112.13	28.38	1.13	13.42
2 (CR)	*Centaurea rhenana*	85.31	11.91	97.23	21.39	8.01	11.91
3 (CP)	*Chamaenerion palustre*	76.41	12.99	89.40	16.89	9.31	12.99
4 (DC)	*Daucus carota*	81.81	12.87	94.68	20.39	6.88	12.87
5 (EC)	*Eupatorium cannabinum*	69.97	6.56	76.54	12.33	0.12	6.56
6 (F)	*Festuca group*	92.55	9.51	102.06	15.19	3.98	9.51

cont. Tab. 4

Vegetation type	Dominant plant	Biomass of the dominant dry	Biomass of the non-dominant dry	Sum of the dry biomass of the patch	Biomass of the non-dominant dry (weight)		
		mean			max	min	mean
		g					
7 (LC)	*Lotus corniculatus*	113.67	12.22	125.89	16.93	9.53	12.22
8 (MA)	*Melilotus albus*	47.51	21.32	68.83	43.83	2.21	21.32
9 (PA)	*Phragmites australis*	172.70	14.70	187.40	28.48	6.45	14.68
10 (PC)	*Poa compressa*	87.42	15.34	102.76	23.17	9.16	15.34
11 (SG)	*Solidago gigantea*	110.93	14.96	125.89	24.79	8.16	14.96
12 (TI)	*Tripleurospermum inodorum*	81.34	13.24	94.58	21.36	7.06	13.24
13 (TF)	*Tussilago farfara*	67.00	9.85	76.85	20.11	4.32	9.85

Source: own study.

those regarding (a) a hump-shaped relationship, which assumes that the species richness and species number increases, and then become reduced with increasing plant productivity (Fraser *et al.*, 2015), (b) the concept of a monotonic relationship, according to which plant species numbers are negatively or positively linked to the amount of plant biomass (Niklaus *et al.*, 2001; Tilman *et al.*, 2001; Ruijven van and Berendse, 2005; Spehn *et al.*, 2005; Emmett Duffy, Godwin and Cardinale, 2017), and (c) the in-between concept assuming that the hump-shaped relationship is non-significant and alternatively the monotonic relationship explains the biodiversity-biomass relationships (Waide *et al.*, 1999; Li, W. *et al.*, 2015; Li *et al.*, 2018).

The studies that have led to the above concepts were conducted on multiple sites and included large-scale measurements. It is suggested that different aspects of the indices of plant species diversity should be considered when studying the relationship between biomass productivity and diversity at different sites and at different scales (Willig, 2011; Fraser *et al.*, 2015). The plant species biomass amount changes with other varied components of the **taxonomic and functional dimension** of biodiversity measurements of species richness, including e.g., species diversity, dispersion, or evenness (Chalcraft *et al.*, 2009). In our study, the spontaneous vegetation plant species composition, and its biomass, that has developed on post-coal mine heaps novel ecosystems reflect the specific habitat conditions. Due to the specific habitat conditions, the organisms are gathered according to new rules and unknown pathways of ecosystem development. A characteristic feature of the herbaceous vegetation successional development on post-coal mine heaps is the non-analogous species composition of the vegetation patches. This unique assembly of plant species manifests as a result of adaptation to conditions specific to post-exploitation areas.

While this study examines the unique habitat conditions and successional processes on mining heaps in the area under investigation, it is noteworthy that parallels in species composition and dominance types can be found in existing literature concerning spoil heaps in Germany, the Czech Republic, and Hungary. In Germany, for instance, research by Grüttner and Heinze (2003) have identified *Calamagrostis epigejos* as a dominant species in post-industrial sites, including spoil heaps, flotation tailings ponds, and mining dumps. This finding is consistent with our own, as *Calamagrostis epigejos* frequently dominates vegetation patches, particularly in the early stages of succession. Similarly, research conducted by Prach and Pyšek (2001) in the Czech Republic has shown that ruderal species like *Solidago gigantea* are commonly found in post-mining areas. Some authors highlighted *Phragmites australis* as a predominant species on mining heaps, emphasising the crucial role of local hydrological conditions in determining species composition (Mingyang *et al.*, 2022). Despite these similarities, our study highlights the distinctive nature of the ecosystems we investigated. The vegetation patches recorded on post-coal mining heaps feature novel assemblages of species that are uniquely adapted to the specific microclimatic and habitat constraints of these environments. Factors such as soil salinity, pH, and organic matter content significantly influence species establishment and dominance, closely linked to mining depth, the chemical composition of the excavated substrate, and the historical processes involved in heap formation. Furthermore, the dominance of species like *Calamagrostis epigejos* in our research is not merely a consequence of ecological redundancy, but rather a testament to unique adaptations to extreme abiotic conditions. The high salinity and nutrient-poor soils present significant challenges for colonising vegetation. However, species such as *Calamagrostis epigejos* thrive in these conditions due to their clonal growth form and competitive abilities, which enable them to stabilise the substrate and outcompete other species (Mingyang *et al.*, 2022).

Additionally, the successional trajectories observed on these heaps differ from those documented in similar habitats. The mosaic-like arrangement of vegetation patches, influenced by microhabitat variability, leads to greater spatial heterogeneity than what is typically seen in natural or semi-natural ecosystems. This spatial diversity fosters the development of non-analogous species assemblages, reflecting a unique ecological paradigm in post-mining landscapes. These findings underscore the need for further comparative research to enhance our understanding of how local and regional factors impact vegetation dynamics in these novel ecosystems. Integrating data from long-term monitoring studies across Europe could offer deeper insights into the ecological processes that govern these habitats, ultimately aiding in the formulation of effective management and restoration strategies.

The observed biological diversity on these mining heaps may result from the adaptation of organisms to challenging soil conditions, microclimatic variations, and other environmental factors. The existing relationships between plant traits and canonical analysis axes may indicate specific adaptive mechanisms or habitat preferences. The post-coal mine heaps mineral soil conditions are significantly different from those that have been studied previously. In the presented study, the habitat factors that influenced the differences in habitat conditions are related to salinity, lack of water nutrients, and organic matter. These conditions shape the vegetation plant species diversity and amount of biomass.

THE RELATIONSHIP BETWEEN BIODIVERSITY AND ECOSYSTEM BIOMASS PRODUCTION IN NATURAL AND SEMI-NATURAL HABITATS

The selected ecosystem functioning processes e.g., the amount of biomass production that is recognised and identified in novel ecosystems such as the post-mining sites can be compared only with natural and semi-natural ecosystems. Numerous studies have documented the relationships between biodiversity and ecosystem biomass production in natural and semi-natural ecosystems with quite different conclusions, including positive, negative, hump-shaped, or null-type relationships (Adler *et al.*, 2011). Some authors, including Lehman and Tilman (2000), and Barrufol *et al.* (2013), suggested that plant species diversity increases along with the amount of biomass in the community. Conversely, Kenkel *et al.* (2001) demonstrated that augmenting the diversity of plant species composition has no effect on the quantity and amount of biomass in forests. The meta-analysis, which included about 50 studies, performed by Zhang, Chen and Reich (2012) revealed a monotonic growth of forest biomass along with a plant species diversity increase. The study performed in **forests** revealed a positive relationship between woody productivity and species richness in different habitat conditions in Spain (Vilà *et al.*, 2007). Despite the high amount of research, it is not possible to present one pattern for the biomass-biodiversity relationship (Corral-Rivas *et al.*, 2019). The most recent meta-analyses, performed in different natural and semi-natural biomes, revealed a positive effect of high biodiversity on biomass by increasing the amount of established organic matter in different types of forests (Liang *et al.*, 2016).

The research undertaken examining community plant species composition, including the influence of biomass on ecosystem processes and ecosystem functioning, has used communities that have been composed of random, artificial sets of plant species assemblages. Such **experiments** are seriously simplified and focused on selected isolated relationships between plant species or functional groups and overall ecosystem functioning properties. The findings of a controlled experiment are not transferable to natural communities (Huston, 1997; Melendez Gonzalez, Crofts and McLaren, 2019). Some research considering the biodiversity-biomass relationships have used the **removal experiments approach**, where the community plant species composition impact on ecosystem functioning and properties was assessed by removing individuals of particular plant species (Díaz *et al.*, 2003; Melendez Gonzalez, Crofts and McLaren, 2019). The applicability of the results of the removal experimental approach to the conditions of the novel ecosystem mineral soil substrate conditions of post-mineral mining sites is even less appropriate (Woźniak *et al.*, 2023).

In our study, all of the data about plant diversity and the amount of biomass have been obtained from the real existing spontaneously developed vegetation patches in post-mining novel ecosystems. These unusual habitat circumstances allow the establishment of a type of living field laboratory. Studies on real-world spontaneous vegetation communities and ecosystem functioning processes, and the biomass production, in a specific environment (living laboratory location) integrates research and experimentation into everyday life, allowing for a more holistic and contextual understanding of the complex systems of ecosystem functioning and biodiversity-biomass relationships.

The vegetation community plant species composition is reported to drive primary production (McLaren and Turkington, 2010; Pan *et al.*, 2016), to influence the soil nutrient availability (Gundale, Wardle and Nilsson, 2010; Pan *et al.*, 2016), and determine the soil microbial community composition (Long de *et al.*, 2016) in many ecosystems. The plant species composition and the related biotic below and above-ground communities, abiotic environments, and their interactive effects control the magnitude and stability of ecosystem properties (Chapin *et al.*, 2000; Diekmann and Falkengren-Grerup, 2002; Melendez Gonzalez, Crofts and McLaren, 2019). In our study, among the identified vegetation types, the grass-dominated and herbaceous species-dominated communities were identified (Kompała-Bąba *et al.*, 2023) on the mineral coal mine habitats that have been analysed regarding their abiotic and biotic conditions.

Grasses and the vegetation types dominated by grass species are characterised by shallow root systems (Ravenek *et al.*, 2014) with a greater total root length than other functional root groups (Köchy and Wilson, 2000) which leads to high water uptake, particularly in initial soil conditions (McLaren, Wilson and Peltzer, 2004). Grass tissue presents a high C: N ratio when compared with other groups of plant species (Wardle, Bonner and Nicholson, 1997). The differences in the C: N ratio might be related, and negatively correlated with decomposition rates (Wardle, Bonner and Nicholson, 1997; Silver and Miya, 2001), although in this ecosystem we found the dominant forbs decomposed more slowly than the grasses (McLaren and Turkington, 2011b).

The significant effects of graminoids in McLaren and Turkington's (2010) removal experiment have not yet explained the mechanisms affecting the loss of biomass in this treatment (McLaren and Turkington, 2011a). The short-term experiment's responses to the dominant species removal have indicated the necessity for longer studies (Vargas-Larreta *et al.*, 2021). There are also studies presenting potentially damaging and long-lasting effects of biodiversity loss on community structure and function (Li, W. *et al.*, 2015). Li, J. *et al.* (2015) comments on effects such as declines in biomass production, ecosystem productivity, net carbon exchange, and respiration. However, the removal experiments that last for a long time may be especially informative and important in northern ecosystems where growing seasons are short, the temperatures are lower, and soil microbial activity can be limited (Wijk van *et al.*, 2003; Melendez Gonzalez, Crofts and McLaren, 2019).

THE SIGNIFICANCE OF THE STUDY RESULTS FOR UNDERSTANDING FUTURE CHALLENGES

Understanding the mechanisms of the plant species composition of spontaneous vegetation development under habitat and environmental conditions established by humans is of high impact on the success of management plans and practices in urban-industrialised landscapes (Frouz *et al*., 2008; Hobbs, Higgs and Hall, 2013; Rotherham, 2017). It is particularly important for sites for which knowledge about the ecosystem structure and functioning is different from that obtained for the natural or semi-natural habitats (Frouz *et al*., 2009; Hobbs, Higgs and Harris, 2009; Collier and Devitt, 2016). Biodiversity decrease and increase assessments have frequently focused on geographically large ecosystems (Sala *et al*., 2000; Garcia *et al*., 2014). At the same time, plant biodiversity, and related heterotrophic and saprophytic diversity, is developing in insular ecosystems, i.e., small, isolated patches of unique habitat. Such conditions often support disproportionately large numbers of rare species (Collins, White and Imm, 2001; Loehle, 2006). Examples of insular ecosystems are rock outcrops, sinkhole wetlands, high-elevation balds, springs, bogs, glades, and, for example, oligotrophic mineral coal mine heaps (Noss, 2013; Cartwright, 2019).

Our study presents the unique relationships that develop during the establishment of novel ecosystems. The novel ecosystems that develop are based on the non-analogous species composition of the herbaceous vegetation. In our study, the examples of the specific herbaceous vegetation types are patches dominated by individuals of one dominant plant, which are accompanied by single individuals of other species representing different taxa and functional groups.

Moving from large-scale to experimental scale, as in our study design, the diversity and distribution of the spontaneous vegetation communities are dependent on the selection potential of the mineral habitat conditions. In such a challenging environment, many factors that vary with species diversity should be considered (Hooper *et al*., 2005). Experimental research at small scales can control many of these confusing parameters and provide additional information about diversity–function relationships. The amount of biomass productivity-richness relationship (PRR) research has been focused on the relationship and links between plant species richness and diversity and its impact on above-ground plant biomass. Plant biomass, and its biochemistry, is a major part of soil organic carbon. The various forms of soil organic carbon are crucial in regulating the soil heterotrophic soil organisms carbon sequestration (Bessler *et al*., 2009). The understanding of the mechanisms of the plant diversity–plant biomass productivity relationship is fundamental and can enhance the understanding of the links between the impact of abiotic and biotic factors in soil and community plant species diversity (Bessler *et al*., 2009).

Moreover, examining the relationship between community plant biomass amount and plant species diversity in mineral habitats of coal mine novel ecosystems can support the theoretical knowledge for maintaining ecosystem services in those human-established habitats. The biomass establishment by autotrophic organisms initiates the matter and energy cycle in any ecosystem and is the primary ecosystem service.

CONCLUSIONS

The presented study has revealed that in the coal mine, mineral novel ecosystem the highest amount of biomass of the spontaneous vegetation type is not significantly correlated with the high diversity of the vegetation species composition.

The harsh conditions of the mineral material habitats of the coal mine heaps are reflected in the novel ecosystem of plant species and the functional diversity of the spontaneous vegetation. A characteristic feature of the diversity of the herbaceous vegetation successional development on post-coal mine heaps is the non-analogous species composition of the vegetation patches. The vegetation's functional and taxonomical species composition diversity are shaped and distributed along biotic and abiotic gradient conditions. While the different aspects of the vegetation diversity influence the biomass quality and quantity, and ecosystem function.

Contrary to our expectation, and our hypothesis, the higher amount of biomass is not related to the vegetation types characterised by higher species composition diversity. Regardless of the analysed diversity measurement, the highest amount of biomass is related to the vegetation type of low diversity parameters.

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CONFLICT OF INTERESTS

All authors declare that they have no conflict of interests.

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