Taxonomic and functional diversity along successional stages on post-coalmine spoil heaps

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Coal is the most abundant fossil fuel in Europe, but the excavation of hard coal has covered large areas with disposed rock waste, and turned the natural habitats into disturbed novel ecosystems with harsh conditions differ in time and space. To examine the spontaneous complex successional gradient, we studied a large number of post coalmine heaps in Upper Silesia, which differ in vegetation type and age. Cluster analysis based on plant community composition (367 species in total) separated all surveyed plots on coal mining spoil heaps with herbaceous vegetation from Late Stage (LS) forests aged 14−56 years. Furthermore, the herbaceous vegetation was sub-grouped to three stages: Initial Stage (IS) aged 2−5 years, Early Stage (ES) aged 3−8 years and Mid-Stage (MS) aged 5−12 years. MS vegetation was characterised by the highest species richness and diversity (47 and 2.79) compared to ES (30 and 2.18) and IS (9 and 1.6), but higher species number and a similar diversity index occurred in LS (37 and 2.81). Functional diversity (FD) and community weighted mean (CWM) of nine functional traits showed higher (23.1) functional richness, higher (0.72) functional divergence, higher (4.5) functional dispersion, and higher value (24.4) of Rao's quadratic entropy in LS compared to those calculated from the first three stages. Species at the initial successional stage (IS) were characterised by lower canopy height, seed mass, higher lateral spread, and specific leaf area (SLA). Additionally, the lowest (0.22 mg CO_2 per hour per square metre) soil respiration (Sr) rate was recorded from IS compared to (0.53, 0.82 and 1.00) from ES, LS and MS, respectively. The soil water content (SWC) was the most important factor affecting the soil respiration, while the soil temperature (St) did not follow the well-studied relationship between soil respiration and soil temperature. Our spatial and temporal analyses illustrated changes in plant community assembly processes in the course of spontaneous vegetation succession on post coalmine

spoil heaps. The importance of trait mediated abiotic filtration in community assembly in initial-, early-, and mid-stages of succession with an increase in competitive exclusion at the late successional stage was emphasized.

1 Introduction

Succession as an ecological process of changes in the plant community over time following natural or anthropogenic disturbance, has been one of the main areas of scientific interest for a long time (Meiners et al., 2015; Prach and Walker, 2020). In most studies researchers underlined that succession is directed by three main factors: niche availability, species availability to colonise a newly established site and species performance, enabling them to interact with other species or to respond to environmental factors and abiotic stresses (Booth et al., 2003). Theoretical studies suggest that environmental filtering is the crucial assembly rule driving species composition in the early stages of development. It depends on the species pool (geographical, regional) that occurs in the surrounding areas and dispersal modes that enable species to reach a given site. In further stages other mechanisms such as competition between species, facilitation, tolerance and inhibition might become the most important factors (Purschke et al., 2013; Batalha et al., 2015; Chang and HilleRisLambers, 2019).

Newly established coalmine spoil heaps are successfully and quickly colonised by plant species and other organisms (Bierza et al., 2023). The harsh abiotic and biotic conditions force the colonising organisms to assemble according to new rules during the spontaneous succession from pioneer herbaceous vegetation communities to newly developed woodlands. As a result, non-analogous plant species assemblages are formed that differ from natural and semi-natural habitats (Hobbs et al., 2006; Keith et al., 2009). Some research investigated the dynamic changes in floristic composition of patches over time, as well as species selection by functional traits during succession or along environmental gradients (Prach and Bohemia, 1987; Schleicher et al., 2011; Bierza et al., 2023).

The most frequent aspect of studying plant diversity is the taxonomic approach, although species richness as a commonly used diversity measure is unable to relate particular ecosystem processes to each species and determine their contributions to ecosystem functioning and productivity (Lavorel et al., 2007). The formula used for species richness calculation assumes that all species are equivalent and the functional differences among species are not accounted for. Functional diversity is the crucial determinant of ecosystem functioning (Tilman et al., 1996; Grime, 1998; Díaz and Cabido, 2001; Dequéant et al., 2006), with a few highly competitive, dominant species having a more significant influence on ecosystem processes (Grime, 1998; Kirby and Potvin, 2007; Zhang et al., 2012; Isbell et al., 2015; Schuldt et al., 2015). A decrease of functional diversity due to environmental filtering has been suggested (Mouchet et al., 2010). In plant ecology, changes in the vegetation along gradients of habitat stressors are the most studied patterns (Peltzer et al., 2010). Functional diversity indicators can be used to reveal the processes of

GRAPHICAL ABSTRACT
Changes in spontaneous vegetation succession in time.
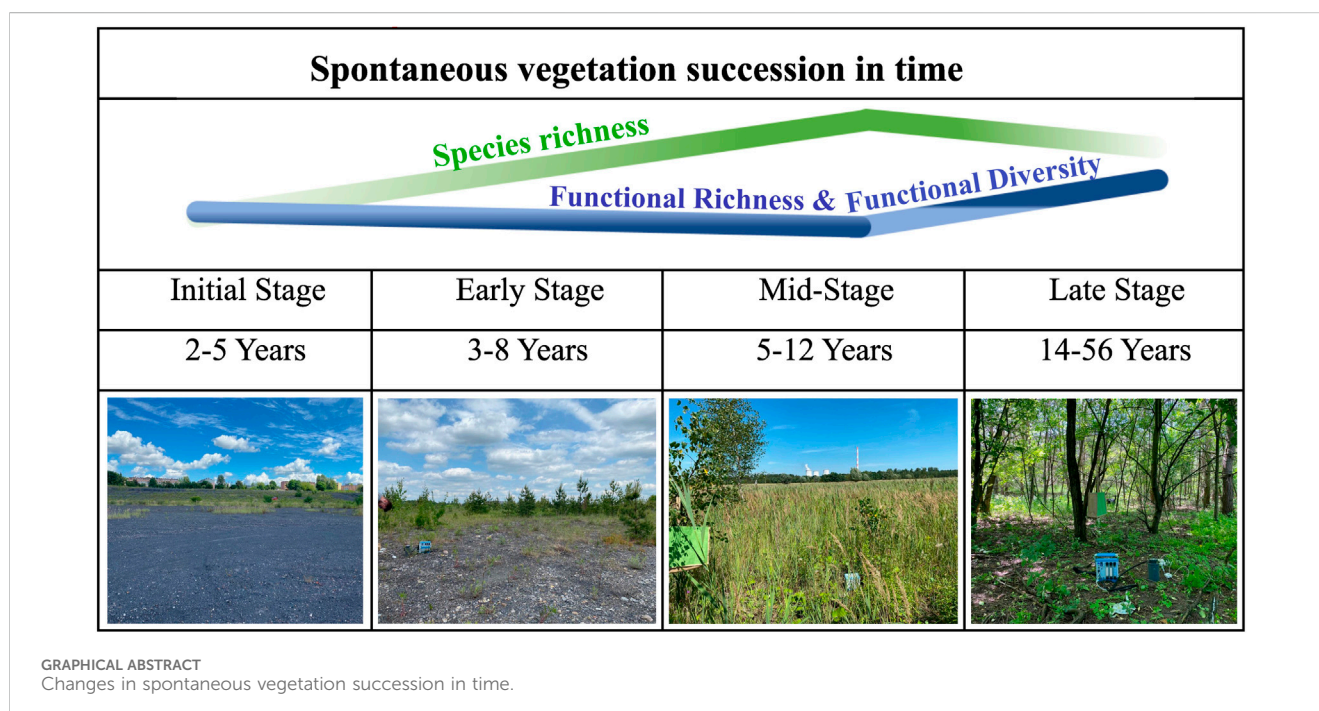
vegetation community assembly (Botta-Dukát, 2005; Mason et al., 2008). Recommended indicators include functional richness (FRic) to remove any trivial effects of species richness, and two mathematically very close indices (RaoQ and FDis) to measure the functional divergence (Botta-Dukát, 2005; Mason and Pavoine, 2013).

The substrate of coalmine spoil heaps is rock waste mineral material, inert with no buffering capacity, lacking organic matter and seed bank; it has low capacity to hold water and high thermal conductivity (Kompała-Bąba et al., 2020; 2021). Despite all the abiotic and biotic constraints and difficulties, species diaspores enter the area, germinate, and species start to grow on the *de novo* ecosystem mosaics (Bradshaw, 2000; Prach et al., 2013). The spontaneous succession process offers an opportunity for novel flora and fauna to re-colonise the new disturbed sites (Hobbs et al., 2006; Kowarik, 2011).

In this work, we aimed to show different patterns of initial, early, mid and late vegetation successional stages by characterizing the taxonomic and functional diversity. Additionally, to inspect the hypothesis predicting increasing of functional diversity along with taxonomic diversity during the spontaneous successional stages. Finally, we tested the response of soil respiration to abiotic factors and changes in plant diversity.

2 Material and methods

The studied coalmine heaps are scattered in the urban-industry landscape, providing poor mineral environmental islands. Plot locations on the coalmine spoil heaps were selected randomly and in advance by a computer algorithm, followed by field visits to exclude plots reclaimed and/or affected by human activities to guarantee that all plots exhibit natural spontaneous vegetation succession. The mineral materials gathered on heaps as the by-product of black hard coal excavation are different in terms of time of deposition, and how a given heap was built. In this way, the coalmine heaps that have been established for decades provided the opportunity to investigate a large-scale experiment and created habitats that differed in plant community composition (Anibaba et al., 2023).

2.1 Description of the study site

Upper Silesia is an industrial region in Poland and one of the most affected by human activity, specifically the hard coal mining industry. Hard coal mining has impacted the local ecosystem and directly affected more than 20 square kilometres of urban land (Szczepańska, 1987). Large amounts of rock composed of Carboniferous sediments on Precambrian crystalline rocks, mudstones and sandstones, and small coal particles left are brought to the surface that differ drastically from the soil covered, creating hundreds of spoil heaps piled up on the ground (Cabala et al., 2004).

All the 32 coalmine sites considered in this work are located in the south-western region of Upper Silesia in Poland. The region has a climate that is favourable for forest vegetation, transitory between oceanic and continental, with annual rainfall of 600–700 mm and a mean annual temperature of 8 °C (Kosmala, 2013). To ensure the

spontaneity of the succession process, reclaimed sites were excluded and only seres started on bare ground were considered. The origin, nature, properties, and environmental stresses caused by the disposed rock waste were previously described in detail (Rahmonov et al., 2020).

To avoid the subjectivity of preferential sampling, a computer algorithm was used for the random sampling and determining the vegetation type depending on light reflectance and photo imaging, followed by a hierarchical cluster analysis using a set of dissimilarity values of the plant communities based on species composition (Zelený, 2022). Both methods distinguished four successional stages with some mismatches that were corrected by a field visit, resulting in 94 plots, including: Initial Stage (IS) 17 plots aged 2–5 years, Early Stage (ES) 28 plots aged 3–8 years, Mid-Stage (MS) 25 plots aged 5–12 years, and Late Stage (LS) 24 plots of forests aged 14–56 years. In total 94 plots were investigated. The different number of plots among different successional stages is due to the site availability.

2.2 The vegetation sampling

The plant cover representing a spectrum of different vegetation and successional stages was examined in June-September 2021. Each plot was 140 m² in area, and consisted of five subplots (radius 3 m, area 28 m²) were established in a cross-design pattern, with a central subplot and four subplots at distances of 50 m in north, east, south and west directions (470 subplots in total; Figure 1). In each of the sampled subplots, all the vascular plant species with their abundances (visually estimated as cover of all individuals of recorded species) were recorded along with their percentage cover class (1%, 2%, 5%, 10% and every 10%–100%) (Kompała-Bąba et al., 2021; Woźniak et al., 2021). Scientific names of species were from (Mirek et al., 2020) checklist. The occurrence and abundance of species were recorded in all spatial layers (tree, shrub, and herbaceous) distinguished in vegetation patches.
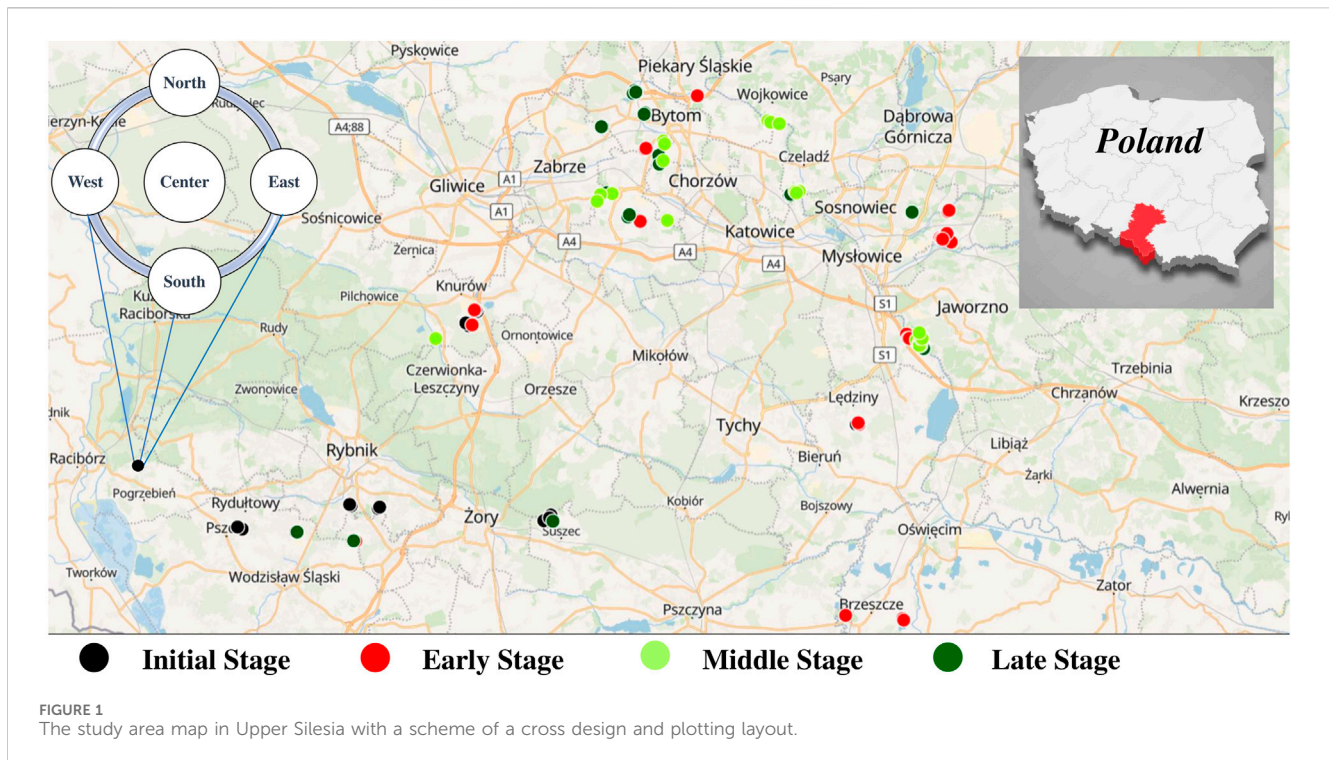
2.3 Substrate parameters

Substrate samples for the physicochemical analyses were collected from the organic horizons (the top 20 cm) representing the densest rooting layer for all cross-designs in fivefold repetition. Samples were air-dried in the soil laboratory to a constant weight at room temperature. A random 120–150 g (substrate up to 500 g) of dry soil sample was collected and ground in a mortar. Then the sample was sieved through a 2 mm mesh sieve to separate the skeletal from non-skeletal parts and weighed on a scale. The proportion of fine parts <2 mm (PM < 2.0) from each sample was calculated (Kompała-Bąba et al., 2019).

All samples were weighed before drying in oven at 105 °C for 24 hours then they were submerged in water overnight to percolate and weighed again to calculate the percentage of water holding capacity (WHC) using the following equation:

$$WHC \ (\%) = \frac{[saturated \ weight \ (g) - dried \ weight \ (g)]}{saturated \ weight \ (g)}$$

At the same time of measuring the substrate respiration (described below in section 2.4) and in three consecutive seasons,

FIGURE 1
The study area map in Upper Silesia with a scheme of a cross design and plotting layout.

the soil temperature (St) and the volumetric water content (SWC) records were taken from the same depth of the substrate. The thermometer DT1 Z Sonda ST01-1300 was used to measure the temperature, while the soil water content was measured by the moisture metre Delta-T HH2 (Delta-T Devices, England).

The substrate was mixed in a 1:2.5 substrate/distilled water for 24 hours, then the pH was measured by a glass electrode, while the electrical conductivity (EC) was measured in 1:5 substrate/distilled water ratio. The modified Simakov Turin method (Hristov et al., 2016) was used for total carbon determination and the Kjeldahl (Rutherford et al., 2006) method was used for the total nitrogen content. For Na extraction 1 Mol neutral ammonium acetate solution was used and the determination of Na was done by AAS (López-Marcos et al., 2018). Available K, Ca, P, and Mg were extracted by the Mehlich-3 (1:10 soil/solution ratio) solution (Mehlich, 1984; Ziadi and Tran, 2008), while K and Ca were determined by flame photometry method, P was determined by spectrophotometer and Mg was determined by the atomic absorption spectrometry (AAS).

2.4 Soil respiration (Sr)

A soil respiration chamber SRC-2 was linked to a TARGAS-1; PP system (Amesbury, MA, United States) to measure the CO_2 efflux from 78 cm^2 of the substrate surface attached to the chamber. The closed chamber is made of rugged PVC ending with a stainless-steel ring to seal and prevent gas leakage. The chamber relies on an internal fan to mix and flush the air accumulated to an external infrared gas analyser, where changes in CO_2 concentrations are recorded in time. To adapt to the surrounding conditions and sustain the impulse of the carbon dioxide, the PP system uses an auto-zero mechanism to guarantee robust and precise readings.

2.5 Functional traits

The functional approach was based on a set of traits that have significant ecological implications for plant species dispersal, establishment, competitive ability, and stress tolerance. We used only functional traits that were available in the open databases (Supplementary Appendix S1) such as LEDA (Kleyer et al., 2008), BIEN (Maitner et al., 2018), Pladias (Wright et al., 2005; Chytrý et al., 2021), BioFlor (Klotz et al., 2002) and TRY Global Plant Traits Database (Kattge et al., 2011). Specific leaf area (SLA) and leaf dry-matter content (LDMC) serve as proxies of species status on the leaf economic spectrum (Pérez-Harguindeguy et al., 2013). High LDMC and low SLA unveil a conservative approach with resistance to the harsh abiotic stress in the mineral material of post-coalmine heaps, while low LDMC and high SLA infer the increased importance of an acquisitive strategy by plant species (Westoby et al., 2002; Pérez-Harguindeguy et al., 2013) used the canopy height as an approximation of plant competitive ability. Species with lower seed mass has been found on younger post-coalmine spoil heaps and *vice versa*, therefore the ability of species to colonise a new habitat can be explained through the seed mass (Piekarska-Stachowiak et al., 2014). Dispersal strategies were based on a combination of dispersal modes (e.g., *autochory* and *epizoochory*; *autochory*; *anemochory* and *autochory*) (Sádlo et al., 2018). For plants functional traits this study included only species with a high frequency, excluding in the analyses those with a frequency less than 0.25% of all plots.

2.6 Data analysis

To classify the sample plots, a hierarchical cluster analysis was used following the average agglomeration method in the vegan package in R

software (Allaire, 2011). The test grouped the 94 cross-design plots sampled into four plant communities based on their overall plant community composition and following the dissimilarity among all plots and along all habitats. The average silhouette method (Rousseeuw, 1987) was used to determine the optimal number of clusters. Clusters (groups) were described in terms of diagnostic, constant as well as dominant species. Diagnostic species were based on fidelity, which is a measure of species concentration in vegetation units (clusters). The phi coefficient of associations was used to calculate fidelity. This measure is useful when comparing fidelity values among differently sized data sets and vegetation units. Its value ranges from −1 to 1 (multiplied by 100). Constant species were distinguished based on their frequency in a given cluster (as a threshold, we chose the occurrence of a species in at least 50% of plots in a given cluster), and dominant species were distinguished by taking into account their cover-abundance.

To find the main factors affecting the studied communities along the gradients, samples were arranged in the DCA biplot using the detrended correspondence analysis (Oksanen and Minchin, 1997), then the direction of plant diversity, functional, and community weighted means (CWM) variables along the gradient was visualised using the veganenvfit () function. Alpha taxonomic diversity indices: H'- Shannon Wiener Index, S - Species richness, E – Evenness obtained using the R Vegan package (Oksanen et al., 2022), and the function dominance () in the {abdiv} package were used to calculate the D-value of the dominance ($0 < D \leq 1$), Simpson index. The impact of the studied abiotic habitat parameters on the distribution of the recorded vegetation patches was performed by canonical component analysis CCA. To fit the environmental factors onto the CCA ordination, the envfit function was used and insignificant vectors were eliminated by the (p.max = 0.5) function.

Rao's quadratic equation index (Botta-Dukát, 2005), community weighted mean (Lavorel et al., 2008), functional dispersion index (Laliberte and Legendre, 2010) and other functional diversity indices based on functional traits have been used, which make up for the deficiency of functional-group approach. Plants functional traits (Supplementary Appendix S1) were used to compute the CWM following (Garnier et al., 2004). Functional diversity (FD) indices: FDis, FDiv, FEve, FRic, and RaoQ entropy were quantified and calculated based on the species function traits using dbFD () function in the FD package (Laliberté and Shipley, 2011).

Shapiro-Wilk multivariate normality test (Royston, 1995) was used to check the normal distribution of the samples, and independent variables were compared using the linear model (Wheeler, 2010) with permutation test in the {lmPerm} package. Variables failed to meet the normality test induced by the non-parametric test (Kruskal–Wallis). To visualise the relationship and its direction between different variables, Pearson correlation (Becker et al., 1998) was used and their significance was calculated with 999 iterations of a permutation test.

3 Results

3.1 Classification of vegetation patches based on their floristic criteria

A total of 376 vascular plant species from 245 genera and 54 families were recorded in 94 vegetation sample plots on coalmine spoil heaps. Based on the floristic criteria, the average silhouette method for the optimal number of clusters suggested two main groups of vegetation patches (Figure 2 "topright"). The first group is represented by spontaneously developed forest on post-coal mining spoil heaps at late stage (LS, framed in red) and the second group by non-forest vegetation. The hierarchical cluster analysis based on the dissimilarities of all plots further divided the non-forest vegetation into three sub stages: initial stage (IS), early stage (ES), and mid-stage (MS) as illustrated in Figure 2. These stages of succession differed in terms of diagnostic, constant as well as dominant species.

There were no diagnostic species in the initial stage (IS), while constant species were *Calamagrostis epigejos*, *Polygonum aviculare*, *Atriplex prostrata*, *Puccinellia distans* and *Chenopodium rubrum*. Only 60 species were recorded in initial stage patches as a whole.

Tussilago farfara was the only diagnostic species in early stage (ES). The species composition included ruderal species (*Conyza canadensis*, *Oenothera biennis*, *Tussilago farfara*), species of necrophilous fringe communities (*Eupatorium cannabinum*, *Solidago gigantea*), meadow species (*Daucus carota*, *T. sec. Taraxacum*). *C. epigejos* and *Phragmites australis* were the dominants among 168 species found in patches of the ES group (Supplementary Appendix S2).

The mid-stage (MS) had 16 diagnostic species including meadow species (*Achillea millefolium*, *Dactylis glomerata*, *Galium mollugo*, *Lotus corniculatus*, *Plantago lanceolata*, *Trifolium pratense*), and ruderal species (*Melandrium album*, *Picris hieracioides*, *Tanacetum vulgare*). *C. epigejos*, *P. australis*, *P. lanceolata*, *S. gigantea* reached up to 20% in some patches. MS was the richest successional stage with 238 species that occurred in all patches (Supplementary Appendix S3).

Forests in late stage (LS) had 12 diagnostic species including shrubs and trees that constitute tree and shrub layers, e.g., *Acer pseudoplatanus*, *Betula pendula*, *Populus tremula*, *Robinia pseudoacacia*, *Tilia cordata*, *Padus serotina*, *Sambucus nigra*, *Crataegus monogyna* and some forbs *Geum urbanum*, *Impatiens parviflora*. In total 135 vascular species were recorded in all forests in the LS that developed on coalmine spoil heaps (Supplementary Appendix S3).

3.2 Distribution of samples in environmental and diversity space

Among all fifteen habitat environmental factors, substrate parameters, fine particles (PM < 2.0 mm), water holding capacity (WHC), soil water content (SWC), soil temperature (St), and pH constrained the plant species distribution in the ordination space in the CCA ordination the most (10.80%). Substrate parameters: SWC, WHC, St, and pH were significant at ($p \leq 0.0001$) alpha level, while the PM < 2.0 was significant at ($p = 0.019$) alpha level (Table 2).

A higher share of fine particles affected the water holding capacity and soil water content and decreased the substrate temperature on coalmine spoil heaps with MS and heap forest LS. On the contrary, patches in IS were characterised by very low SWC, WHC, and higher substrate temperature. As one of the most important soil parameter, the pH was higher in heap forests LS, which in turn positively correlated with the soil calcium content, total nitrogen, and total carbon (Figure 3).
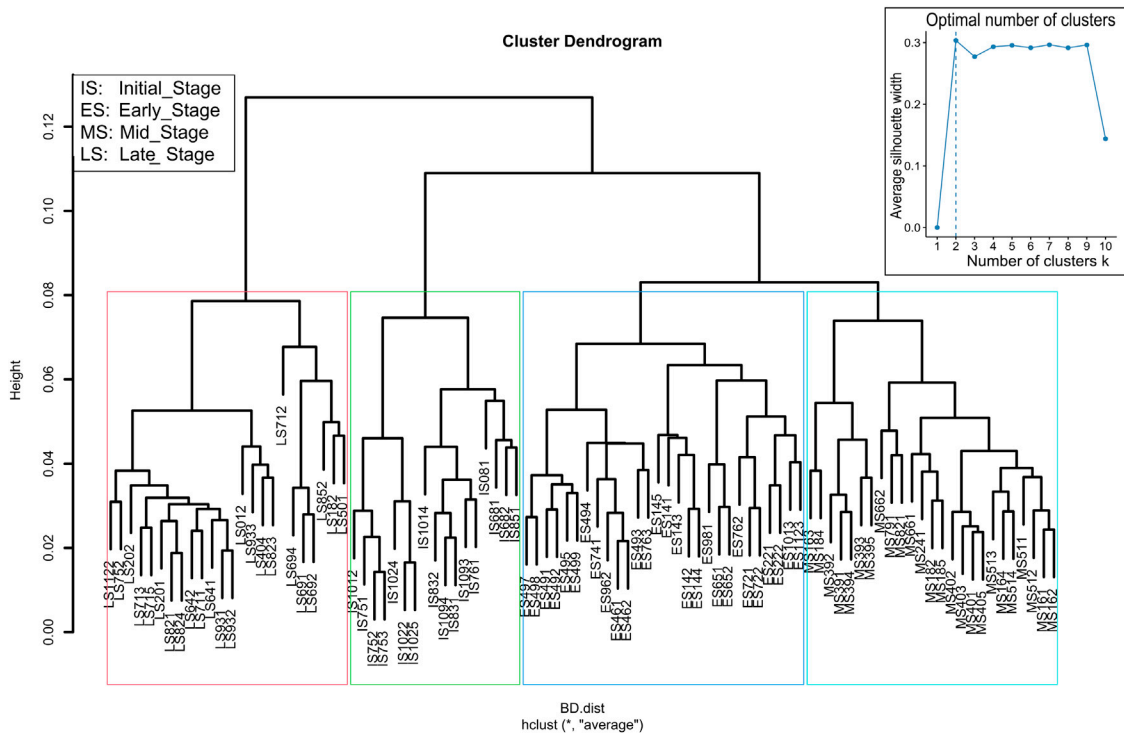
FIGURE 2
Hierarchical clustering of different vegetation patches developed on coalmine spoil heaps based on their floristic composition. The optimal number of clusters is indicated by the Average Silhouette method "top right".
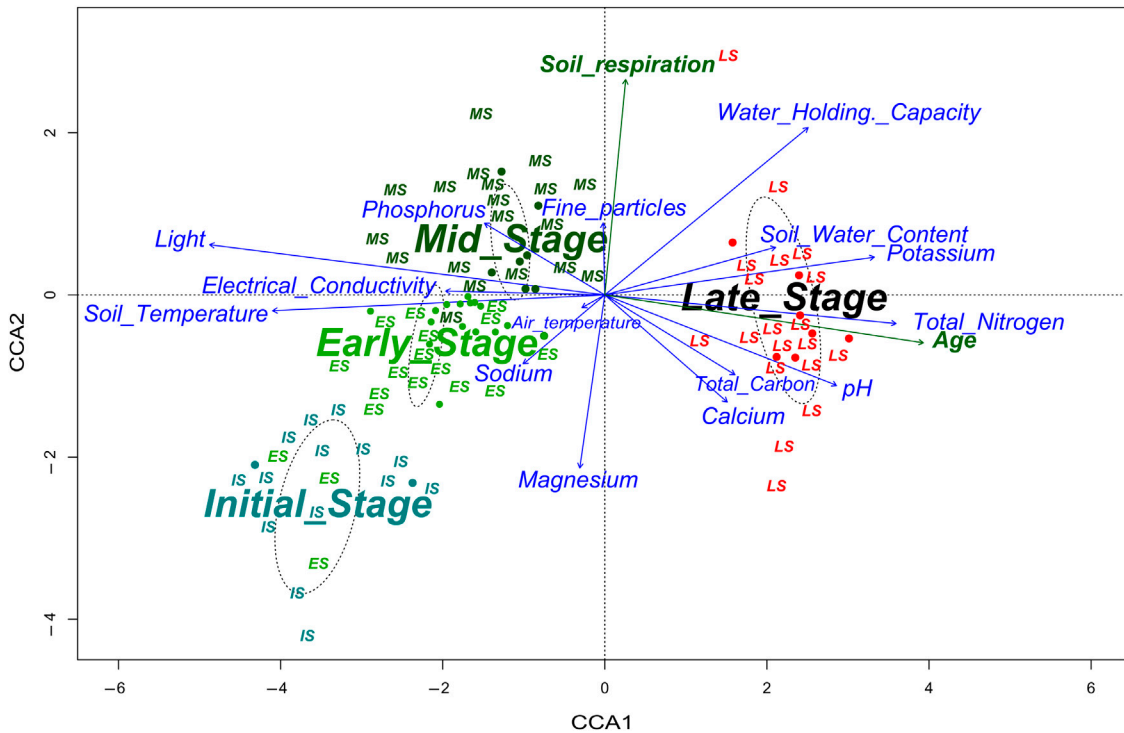
FIGURE 3
The CCA ordination biplot illustrates significant differences in the substrate parameters on species composition. Soil respiration and age are projected not constrained (green arrow).

FIGURE 4
Detrended Correspondence Analysis (DCA) displays the correspondence of succession stages in the ordination space. Only significant variables are shown.
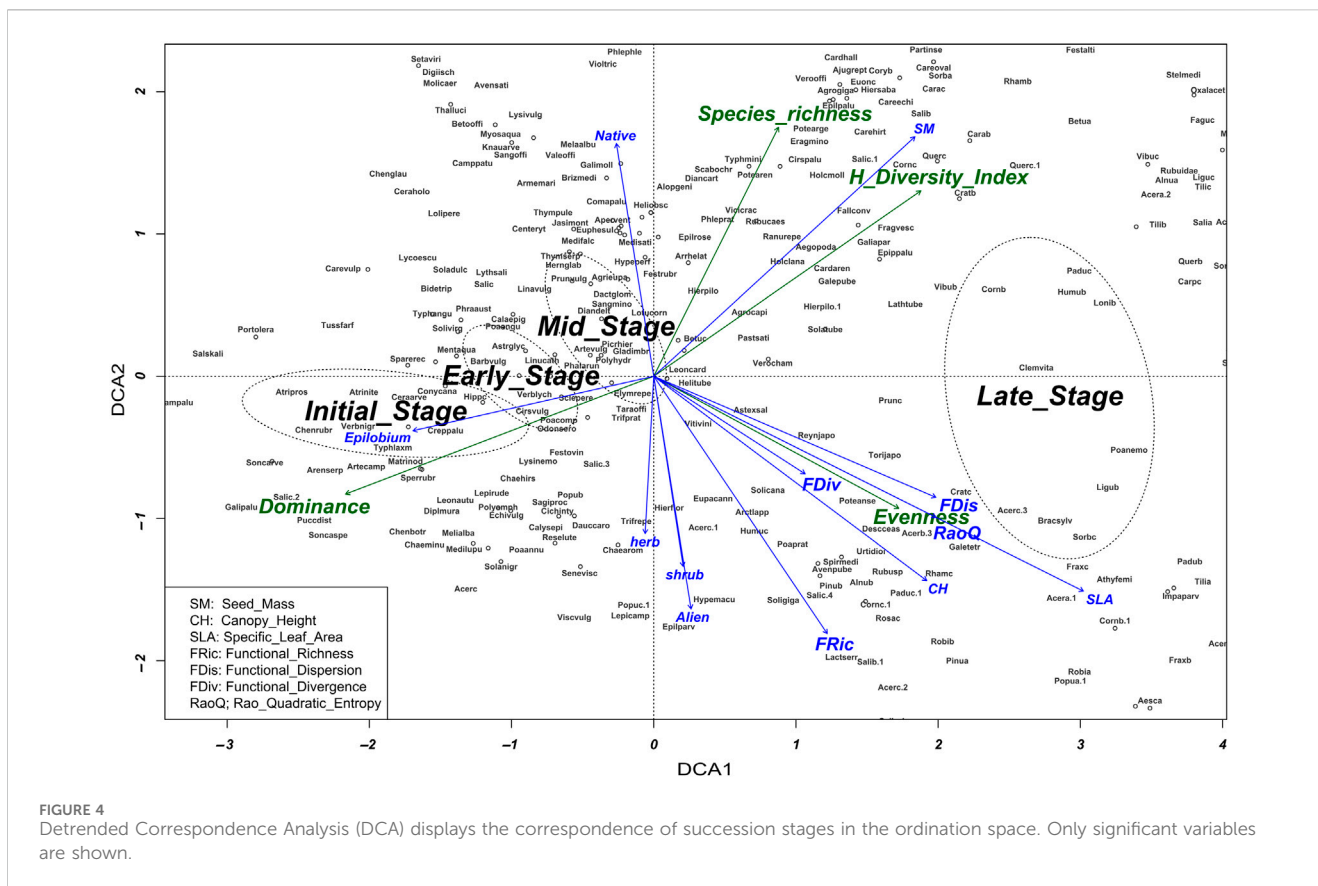
Patches in the MS group were species-rich, and had the highest values of Shannon-Wiener diversity index and the vegetation mainly consisted of native species, mostly grasses (e.g., *Arrhenatherum elatius, Briza media, D. glomerata, Festuca rubra, Phleum pratense*).

The IS stage was species-poor and dominated by some single species (e.g., *T. farfara, C. epigejos, A. prostrata, Chamaenerion palustre,* and *P. distans*). Additionally, the IS was characterised by higher functional evenness, while other functional indices such as FRic and RaoQ entropy are more pronounced in forests developed on coalmine spoil heaps in the LS stage (Supplementary Appendix S2). Woodlands in the LS group were species rich with a well-developed tree, shrub, and herb layer, higher canopy height, and specific leaf area (Figure 4).

The diversity of spontaneous vegetation assemblages established during succession reflected the variety of each successional stage condition (Graphical abstract). As it is illustrated in the Graphical abstract, a steady increase in species number occurred from the start until the mid-stage of succession with a decline at the late stage. On the other hand, the opposite trend suggested an increase of functional diversity at late stage due to the replacement of redundant individuals by species that are more different.

Apart from the numerical analysis and the impact of the factors tested by using the permutation tests, the quantitative test of the subsequent successional stages showed significant differences. The comparison of the species richness between the four studied successional stages revealed that the highest number of species (47) was recorded in the mid-stage, followed by late stage (37), early stage (30), and finally the least number of species (9) was found in initial stage patches. The highest values of the Shannon-Wiener diversity

index were recorded in MS and LS groups compared to other ones. Values of Shannon-Wiener diversity index were much higher than in IS, but did not reach a statistically significant level (Table 1).

Forests developed at the late stage had higher functional richness (23.1) and Rao's quadratic entropy (24.4), followed by mid stage (FRic 14.0; RaoQ 15.5), early-stage (FRic 8.96; RaoQ 12.0), and initial stage (FRic 3.48; RaoQ 12.2). The functional divergence index value of the ES group was low and varied in others, while the functional dispersion was the highest (4.5) in LS forests and followed the same trend as RaoQ entropy (Table 1).

Soil water content and water holding capacity followed a gradual increase along the successional stages with time, while the substrate temperature took the opposite path. The gradual increase of soil respiration (Sr) form (0.22 mg-CO_2 per hour per square metre) in IS to (0.53, 0.82 and 1.00) in ES, LS and MS respectively, was mainly derived from soil water content (SWC) and soil temperature (St), and vegetation species composition (Table 2). Moreover, the highest values of pH (6.25), total Nitrogen (0.46%), available potassium (210 mg kg^{-1}), and available Calcium (1770 mg kg^{-1}) were recorded from the forest soils in LS.

Soil respiration was positively affected by substrate water holding capacity, water content, fine particles portion, plant diversity, functional richness, and to a lesser extent functional diversity (WHC; r = 0.62***, SWC; r = 0.59***, PM < 2.0; r = 0.57***, H; r = 0.50***, and RaoQ; r = 0.33**) respectively (Figure 5).

Except for the correlation between the total carbon (r = −06 ns), pH, and RaoQ, which did not reach significant levels, all other

TABLE 1 The comparison of successional stages in terms of taxonomic diversity, functional diversity, and community weighted mean (CWM). Normally distributed variables subjected to ANOVA, Kruskal−Wallis test (with asterisks) for variables failed to meet the ANOVA assumption test; Df is 3.

Diversity indices and community weighted mean traits	Initial stage	Early stage	Mid-stage	Late stage	*p*-Value
Species richness	9.4[days]	30.3[c]	47.4[a]	37.4[b]	2.2×10^{-16}
Shannon-Wiener Diversity Index	1.60[b]	2.18[b]	2.79[a]	2.81[a]	6.5×10^{-10}
Dominance Index	0.34[a]	0.24[a]	0.13[b]	0.10[b]	0.000***
Evenness Index	0.76[a]	0.65[b]	0.73[ab]	0.79[a]	0.001**
Functional Evenness	0.68[a]	0.53[b]	0.48[c]	0.54[b]	4.4×10^{-7}
Functional Richness	3.48[c]	14.0[a]	8.96[b]	23.1[a]	0.000***
Functional Divergence	0.64[a]	0.53[b]	0.64[a]	0.72[a]	4.4×10^{-4}
Functional Dispersion	3.0[b]	3.4[b]	3.2[b]	4.5[a]	0.000***
Rao's Quadratic entropy	12.2[bc]	15.5[b]	12.0[c]	24.4[a]	3.8×10^{-9}
Specific Leaf Area (mm^2 mg^{-1})	17[c]	17[c]	20[b]	34[a]	0.000***
Seed Mass (mg)	0.98[b]	2.72[b]	1.69[b]	87.0[a]	0.000***
Canopy Height (m)	3.4[b]	2.4[b]	1.0[c]	6.1[a]	0.000***
Lateral Spread (m/y)	0.04[b]	0.09[a]	0.07[a]	0.06[b]	0.001**

The Means of variables with the same letter are not statistically significant. Symbolic codes (ns = p > 0.05, *p < 0.05, **p < 0.01, ***p < 0.001).

TABLE 2 The comparison of successional stages in terms of environmental parameters. Normally distributed variables subjected to ANOVA, Kruskal−Wallis test (with asterisks) for variables failed to meet the ANOVA assumption test; Df is 3.
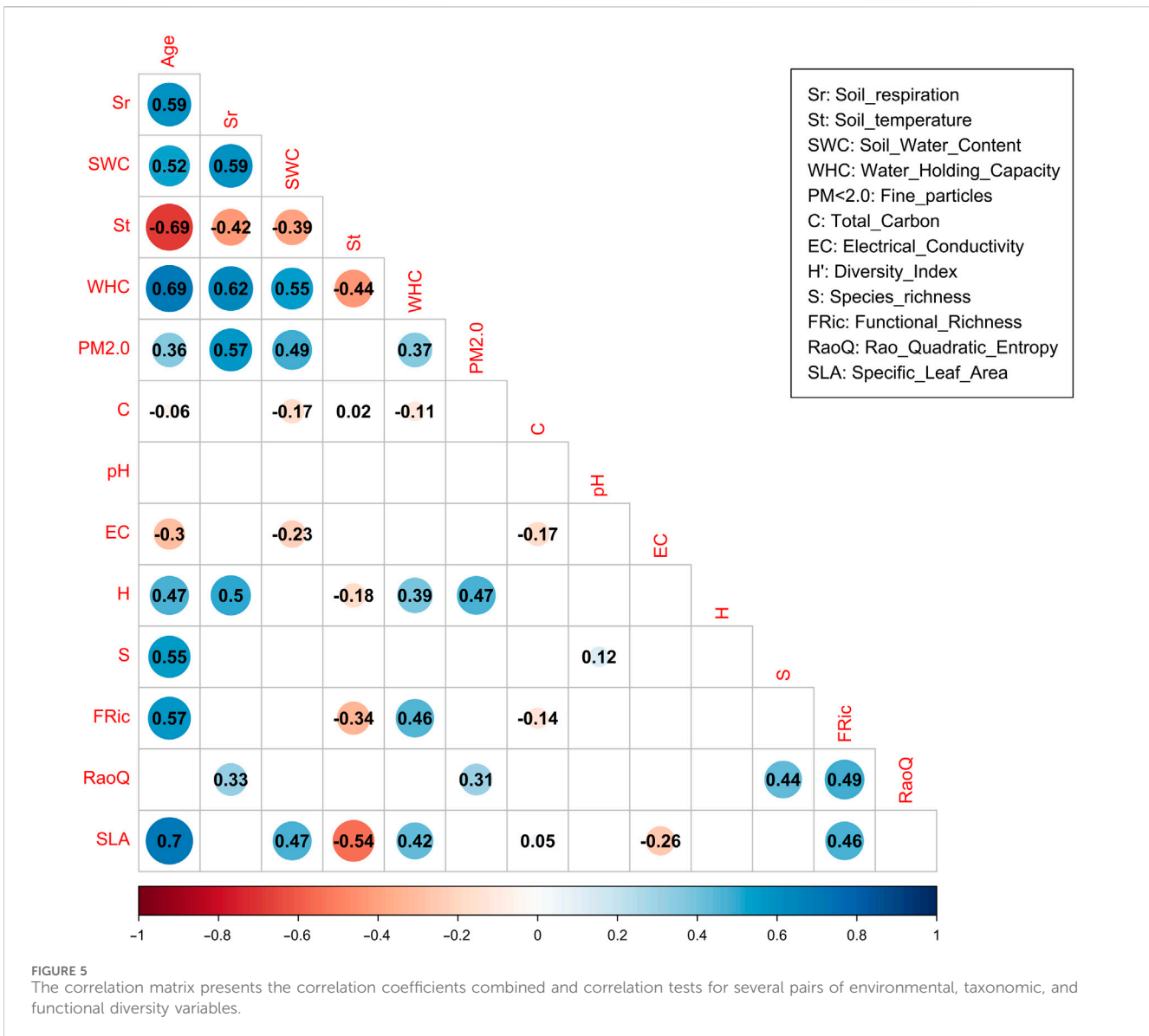
Environmental parameters	Initial stage	Early stage	Mid-stage	Late stage	*p*-Value
Soil Water Content (%)	11[b] ± 4	12[b] ± 2	17[a] ± 4	18[a] ± 6	0.000***
Water Holding Capacity (%)	21[d] ± 2	27[c] ±4	30[b] ± 4	33[a] ± 4	3.1×10^{-13}
Fine particles PM < 2.0 (%)	27[c] ± 7	32[bc] ± 7	44[a] ± 1	37[b] ± 1	2.2×10^{-7}
Substrate temperature (°C)	11.9[a] ± 2	12.5[a] ± 2	11.8[a] ± 2	10.7[b] ± 1	6.2×10^{-11}
pH	6.12[bc] ±0.2	6.02[c] ±0.1	6.10[b] ± 0.1	6.25[a] ±0.2	3.6×10^{-6}
EC (mS cm^{-1})	5.9[ab] ±0.1	6.00[a] ±0.1	5.8[a] ±0.1	5.5[b] ± 0.1	1.0×10^{-3}
Total C (%)	12.7[a] ±6	10.6[a] ±5	6.27[b] ± 4	12.3[a] ±6	0.000***
Total N (%)	0.27[b] ± 0.07	0.27[b] ± 0.07	0.25[b] ± 0.1	0.46[a] ±0.1	0.000***
P$_{ava.}$ (mg P$_2$O$_5$ kg^{-1})	44[ab] ± 23	37[ab] ± 16	45[a] ± 20	33[b] ± 11	0.152ns
K$_{ava.}$ (mg kg^{-1})	167[a] ± 47	126[b] ± 52	170[b] ± 45	210[a] ±60	0.001**
Ca$_{ava.}$ (mg kg^{-1})	1709[a] ± 1296	771[b] ± 373	1685[a] ± 981	1775[a] ± 947	0.000***
Na$_{ava.}$ (mg kg^{-1})	62[a] ± 32	39[b] ± 31	33[bc] ± 24	23[c] ± 8	0.000***
Mg $_{ava.}$ (mg kg^{-1})	190[a] ± 39	189[a] ± 53	180[a] ± 71	171[a] ± 54	0.659ns
Age (year)	2.6[d] ± 2	5.5[c] ± 2	8.4[b] ± 3	34[a] ± 12	2.3×10^{-15}
Soil respiration (mg CO$_2$ h^{-1} m^{-2})	0.22[d] ± 0.1	0.53[c] ± 0.3	1.00[a] ± 0.2	0.82[b] ± 0.2	0.000***

The Means of variables with the same letter are not statistically significant. Means are ±sd. Symbolic codes (ns = P > 0.05, *p < 0.05, **p < 0.01, ***p < 0.001).

parameters were correlated with age, either positively or negatively. Substrate temperature declined with age (St; r = −0.69***), the electrical conductivity decreased (EC; r = −0.30***), and other positive effects of aging were reflected positively and significantly the ability of the substrate to hold water (WHC; r = 0.69***), increased the soil water content (SWC; r = 0.52***), higher fine particle fraction (PM < 2.0 mm; r = 0.36***), higher number of species (S; r = 0.55***), higher plant diversity (H: r = 0.47***), higher

FIGURE 5
The correlation matrix presents the correlation coefficients combined and correlation tests for several pairs of environmental, taxonomic, and functional diversity variables.

functional richness (FRic: r = 0.57***) and higher specific leaf area (SLA: r = 0.70***). The specific leaf area correlated positively with the soil water content (SWC; r = 0.47***), water holding capacity (WHC; r = 0.42***), and functional richness (FRic; r = 0.46***).

4 Discussion

4.1 Changes in taxonomic and functional diversity along the successional stages

The four distinguished stages of succession differed in species richness, species diversity, and cover of a dominant species. Woody species rarely occurred at the beginning of the succession while seedlings of woody species started to appear just from the second stage. Pioneers such as *A. prostrata*, *C. rubrum*, *P. distans*, *P. aviculare* and *T. farfara* on steep slopes prone to erosion, were the first to colonise the newly disposed of mineral material on moist

coal mine spoil heaps. In other studies on coal mine sites, initial plant communities in sedimentation pools were also dominated by one or two forbs (*A. prostrata*, *P. distans*) or more species in their floristic composition occurred with varied cover/abundance and that were distributed more evenly (*C. rubrum*, *C. glaucum*) (Kompała-Bąba et al., 2023). Along with the succession, both the number of species and their abundance increased, which resulted in higher values of Shannon-Wiener diversity index. In all vegetation classes studied and out of 376 species surveyed, 238 species were found in herbaceous vegetation patches that developed within a decade of heap formation and increased in abundance before reaching a more stable level in the mid-successional stage and started to decrease with development of woody species at the late successional stage. *C. epigejos* grows on sites with a wide range of nutrient availability, and can overcome extreme surplus and scarcity of water. The fact that *C. epigejos* cannot tolerate shade (Rebele and Lehmann, 2001), was probably the cause of its decline when forests developed on the coal mine sites. In further stages of succession on

coal mine sedimentation pools, some perennial, tall forbs started to dominate, among them both native (*T. vulgare*, *C. epigejos*) or alien species (*S. canadensis*) (Błońska et al., 2019). The main direction of the successional stages considered in this study was towards the establishment of a woodland, which is typical potential vegetation in the study area (Řehounková et al., 2018).

In our study, the non-analogous species composition of the novel ecosystems established on mineral habitats of the coalmine heap environmental sites revealed that the taxonomic diversity indices were significantly different between the spontaneous vegetation successional stages distinguished in the classification analysis. The analysis of variance revealed significant differences in values of Shannon-Wiener diversity index between initial stage and early stage as compared to higher values in mid-stage and late stage vegetation. In the opposite direction, the dominance index followed an opposite trend, higher in both initial and early stages than in mid and late stages.

Species richness and diversity showed a fast gradual growth with time from initial stage to early stage reaching their peaks in mid-stage then changes were more related to plant species rather than growth in numbers (Table 1). On coalmine heaps, the absence of a light barrier is in the favour of plant diversity until canopy closure by dominant trees during the late successional stage, which accounts for the strongest environmental filter in forests (Sheil and Burslem, 2003). We observed that the stages representing the dynamic successional processes are significantly different, increasing the plant taxonomic diversity with time until reaching a certain level of herbaceous development and when forests are established. In late stage where forests developed on coal mine heaps, the canopy closure played a critical role in decreasing the species richness and the plant diversity.

In comparison to species diversity, functional diversity reflects a different approach that estimates the distribution and the range of organisms in communities and ecosystems and thus assesses the complementarity and redundancy of the co-occurring species (Tilman et al., 1996; Hulot et al., 2000; Díaz and Cabido, 2001; Heemsbergen et al., 2004; Petchey and Gaston, 2006) Functional richness and functional divergence detected changes in the plant assembly processes along our proposed stress gradients; higher calculated values of functional richness and functional divergence occurred when forests developed on coalmine spoil heaps at the late stage. This indicates higher ecological resilience of woodlands developed on coalmine spoil heaps to the environmental stressors, and better maintenance of ecosystem functioning (Hooper et al., 2005).

4.2 Environmental conditions, species diversity changes and vegetation development during the succession process

Environmental filtering is the most recognized abiotic mechanism that acts as a sieve to select species that can establish and persist in a given habitat condition from those that fail due to species-specific environmental needs (Keddy, 1992). Underlying this approach is the assumption that species, often unrelated, share similar adaptations to harsh habitat conditions that lead to a higher similarity concerning functional traits (traits convergence).

Fine particles, water holding capacity, water content, temperature, and the pH of the substrate were the most crucial environmental factors that decide which species pass through environmental filters and cope with harsh abiotic conditions. This is the logical result of the niche differentiation idea that assumes that plant species in a particular location must display differences in resource acquisition to co-exist (Macarthur and Levins, 1967; Angert et al., 2009). Apart from the above concepts, the novel ecosystem conditions bring new dimensions into habitat-diversity relationships.

The current results regarding shifts in diversity patterns during succession are inconclusive (Helsen et al., 2012), while other results were ambiguous (Schleicher et al., 2011; Chang and HilleRisLambers, 2019), concluding that there are no consistent changes in community assembly processes along successional gradients.

The process of plant colonization on newly open mineral habitats depends primarily on the type of the material and its properties (Tang et al., 2003; Alday et al., 2011). In our study, the soil water content turned out to be the most important variable that influenced the colonisation pattern on post-coal mine spoil heaps. Moreover, fine particles (smaller than 2 mm) of the substrate played an important role in vegetation development and increased substrate water holding capacity and soil water content. The mineral rock with a significant amount of nutrient elements and soil small or medium particle fractions associated with high water holding capacity and aeration promotes the colonisation of vegetation (Rahmonov et al., 2020).

The total carbon measured from the rock substrates was higher in initial and late stages. Higher values of parameters such as total nitrogen, available potassium, and calcium were mainly due to the decomposition of dead roots and above-ground dead biomass in forests developed on heaps (Shannon et al., 2022). The release of different elements from the organic matter, especially the calcium to the organic layer affected the pH, which was higher in substrates of forests developed on coalmine spoil heaps. The Na concentration declined along the successional gradient, reaching its lowest levels in heap forests; with time soluble salts washed out and the electrical conductivity decreased.

4.3 Soil respiration as the functional aspect parallel to vegetation diversity

The carbon dioxide released from the substrate differs remarkably in different vegetation and ecosystem types due to specific assembly rules of the plant community depending on the habitat filtering concept (Kraft et al., 2014). Our study confirmed that carbon release differs on coalmine spoil heaps and higher soil respiration in the mid-stage of succession due to differences in vegetation composition and habitats. In woodlands at late succession, the carbon is stored in below and above-ground living biomass, deadwood, and leaf litter (Shannon et al., 2022), following the sequestration through the products of photosynthesis.

Studies lacking the seasonal variability and inter-annual records for soil respiration rely on how the diversity of plant communities stabilise carbon dynamic (Korrensalo et al., 2017) to explain the role of plant richness in the carbon cycle especially if different species reach their optimal performance at different times. We measured the

soil respiration in spring, summer and autumn to avoid seasonal variation of respiration. Our results showed an increase of the respiration rate by two folds shifting from the initial to the early stage and another two folds more in mid-stage which counts as an evident proof that the species richness played the main role. This is in line with results suggesting significant differences between vegetation types and the role of environmental filtering in plant community assembly (Kraft et al., 2014).

5 Conclusion

Considering that the harsh conditions of post-coalmine spoil heaps persist for decades after their abandonment, we detected four development stages during the spontaneous succession depending on the plant community composition and the age of the heap. The taxonomic diversity showed a different pattern than the functional diversity during succession; heap forest had the highest functional diversity, whereas the herbaceous vegetation, especially in the mid-stage, was richer in species number and species diversity. Native plant species that can cope with hostile habitats such as heaps and mounds of technological wastes, and saline habitats, were the first and the most abundant species recolonizing such *de novo* habitats. Their rapid development is clear evidence that spontaneous succession is the most suitable process to restore the altered site due to coal excavation in the temperate zone. More studies are needed to investigate the carbon dynamics on post-coalmine spoil heaps and whether such novel ecosystems act as a carbon storage pool.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author.

Author contributions

JB: Conceptualization, Formal Analysis, Investigation, Methodology, Resources, Software, Validation, Writing–original draft, Writing–review and editing. AK-B: Conceptualization, Formal Analysis, Investigation, Methodology, Resources, Validation, Writing–original draft, Writing–review and editing.

WB: Conceptualization, Investigation, Methodology, Resources, Validation, Writing–original draft, Writing–review and editing. DC: Formal Analysis, Software, Validation, Writing–review and editing. AH: Data curation, Investigation, Project administration, Resources, Validation, Visualization, Writing–review and editing. AB: Investigation, Resources, Validation, Writing–review and editing. TN: Validation, Writing–review and editing. FM: Validation, Writing–review and editing. AMJ: Funding acquisition, Writing–review and editing, Validation. GW: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing–original draft.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2024.1412631/full#supplementary-material

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