Factors driving plant diversity in the spontaneous vegetation of the novel ecosystem of post-coal mining spoil heaps and their relationship with soil respiration

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Abstract: The subject of the paper is the analysis of the relationship between spontaneous vegetation diversity and soil respiration in novel post-coal mine ecosystem. In the natural and semi-natural ecosystems, soil respiration process (Rs) is a crucial ecosystem function regulating terrestrial ecosystems' carbon cycle. Soil respiration depends on the quality and quantity of the soil organic matter (SOM), the soil microbes' activity, and root metabolism. The listed factors are directly related to the composition diversity of vegetation plant species (biochemistry). For many years, soil respiration parameters have been studied in natural and seminatural vegetation communities and ecosystems. However, there still need to be a greater understanding of the relationship between vegetation plant species diversity and soil respiration as a crucial ecosystem function. Plant species diversity has to be analysed through both the taxonomic diversity and the functional diversity. These approaches reflect the composition, structure, and function of plant species communities. We hypothesise that the diversity of the spontaneous vegetation species composition shapes the amount of soil respiration in a post-coal mine novel ecosystem. The soil respiration differs significantly along the vegetational types driven by habitat gradients and is significantly higher in highly functional richness and dispersion vegetation patches. Contrary to our expectation, soil respiration was the highest in the less diverse vegetation types – both taxonomical and functional evenness were non-significant factors. Only functional dispersion is weakly negative correlated with soil respiration level (SRL).

Keywords: coal mining heaps, disturbed sites, functional diversity mineral habitats, non-analogous species composition, soil respiration, spontaneous vegetation species composition, taxonomic diversity

INTRODUCTION

Soil respiration (Rs) is a crucial ecosystem function, regulating terrestrial ecosystems' carbon cycle (Chen and Chen, 2019). It depends on the quality and quantity of the soil organic matter (SOM), soil microbes' activity, and root metabolism. The aboveground and below-ground ecological processes are connected by soil respiration (Wang *et al.*, 2021). Soil respiration, as one of the key processes in ecosystems, is related to ecosystem productivity, soil fertility, and the regional and global carbon cycle. As the global carbon cycle regulates climate change, soil respiration is also relevant to climate change, carbon trading, and environmental policy. In the natural and semi-natural ecosystems, soil respiration is now a multidisciplinary issue of interest to ecologists, soil scientists, microbiologists, agronomists, and climate scientists. Soil is one of the largest carbon reservoirs on Earth, storing more carbon than the atmosphere and terrestrial vegetation combined. Therefore, the mechanism of soil respiration

is of great importance to the Earth's carbon balance and ultimately to the rate of climate change. It is also important to understand to what extent the factors influencing, and the relations driving, soil respiration are different in novel ecosystems.

The interest in how plant diversity influences ecosystem function (Newbold *et al.*, 2020) has increased recently. For a long time, many ecosystem functions have focused on productivity and biomass quantity (McKee, 1970). The second commonly studied aspect of ecosystem functioning is soil nutrient cycling (Duffy, Godwin and Cardinale, 2017). Both productivity and decomposition are related to respiration parameters (Handa *et al.*, 2014). However, until now, less attention has been paid to understand how plant diversity can affect soil respiration amount. The relationship between plant species diversity and soil respiration can be direct or indirect through soil factors (such as soil water content, temperature, SOM parameters, and nutrients) (Metcalfe *et al.*, 2011).

The direct effects of plant species diversity on soil respiration in natural and near-natural vegetation communities is still limited, however the understanding of the relationship between plant species diversity and ecosystem function such as soil respiration is crucial (Loreau and Hector, 2001; Hillebrand and Matthiessen, 2009). Plant species diversity has to be analysed in a few dimensions. Plant species diversity has to be analysed through both the taxonomic diversity and the functional diversity perspective. The varied diversity aspects are reflected in plant species communities' composition, structure, function, and relations with the associated and heterotrophic and saprophytic organisms.

However, for different species, the taxonomic diversity in a community often exhibits different physiological-ecological and adaptive processes, so considering taxonomic diversity alone does not reveal the full spectrum of plant diversity and its impact on *Rs* (Arnan, Cerdá and Retana, 2015). An additional aspect of plant diversity is the variety of functional traits. The functional plant attributes are closely related to species growth, reproduction, and competition and can better represent the direct influence of species on ecosystem function (McGill *et al.*, 2006). In recent years, functional diversity has become a mainstream approach in studying plant diversity and ecosystem function (McGill *et al.*, 2006). Recently, the understanding of the negative impacts of plant diversity loss on ecosystem functions has increased, including the understanding of net primary production (Liang *et al.*, 2016; Duffy, *et al.*, 2017), carbon sequestration (Tilman, Hill and Lehman, 2006) and nutrient cycling (Handa *et al.*, 2014). However, how plant diversity loss affects *Rs* and its components remains uncertain. Regardless of the uncertainty in natural and seminatural ecosystems in human-disturbed habitats, additional factors influence crucial processes, including respiration.

Human activity have very strong impact on environment especially when it is area which was it was heavily exploited and destroyed as a result of his activities. Habitat transformations are sometimes so substantial (e.g., on sites of post-mineral excavation) that the emerging system resulting from natural succession processes meets the criteria set for defining novel ecosystem (Hobbs, Higgs and Harris, 2009). Vegetation composition also undergoes significant changes. The abiotic and biotic parameters are unknown from natural or seminatural systems, and the main feature of the biotic background is non-analogous species composition (Keith, Mackey and Lindenmayer, 2009; Morse *et al.*, 2014; Rotherham, 2017).

This study aims to identify the environmental gradients that influence the diversity expressed as taxonomical and functional vegetation community composition and, based on the identified gradients, analyse the relationships between different measures of vegetation diversity and soil substratum respiration parameters.

We hypothesise that the diversity of the spontaneous vegetation species composition shapes the amount of soil respiration in a post-coal mine novel ecosystem. The soil respiration differs significantly along the vegetational gradient and is significantly higher in vegetation patches of high functional diversity. In particular, evenness and divergence and low functional richness and dispersion.

MATERIAL AND METHODS

STUDY AREA

The study area is in the Katowice Upland – a central part of the Silesian Upland (southern Poland). This region is under a temperate climate, with annual rainfall of 600–800 mm and the highest mean temperature of 14–16°C in July. In the Silesian Upland, western winds dominate. The number of days with mists ranges from 30 to over 100, and cloud cover is around 60–80%. Field studies were carried out in the mineral habitats of the spoil heaps of the coal mines at (Zabrze, 50°16'22"N, 18°44'43"E; altitude: 255 m); "Kostuchna" (50°11'04"N, 19°00'33"E; altitude: 324 m); Murcki (50°11'21"N, 19°02'07"E; altitude: 314 m); and "Wesoła" in Mysłowice (50°10'28" N, 19°5'44" E; altitude: 281 m). The sites analysed are areas with environmental conditions that differ from natural ones. The sites were created by human activity during fossil fuel extraction, and the mounded material comes from a depth of 0.5–1.0 km. These new anthropogenic forms are unique habitats because they are depleted in nutrients such as nitrogen, carbon, sulphur, phosphorus, etc., and are devoid of organic matter.

CALCULATION OF SPECIES DIVERSITY

To measure biodiversity, the following biodiversity indices were implemented: the number of all species present (S), Shannon–Wiener index (H), Shannon evenness (H/log(S)), evenness uniformity, and Simpson's dominance index. The detailed measurement procedure is described in Radosz *et al.* (2023).

SPONTANEOUS VEGETATION ON COAL MINE SPOIL HEAPS

The mosaic of habitats occurring on coal mine sites affects the species diversity of vegetation patches that are created by ruderal, grassland, meadow, psammophilous, rush, and even saltmarsh species (Woźniak, 2010; Markowicz *et al.*, 2015). In the structure of plant communities that developed spontaneously on coal mine spoil heaps, the role of dominants and co-dominants is played by expansive, perennial grasses (e.g., *Calamagrostis epigejos*, *Phragmites australis*), legumes (e.g., *Melilotus alba*, *Medicago lupulina*, *M. sativa*) or other herbaceous plants (*Tussilago farfara*, *Centaurea stoebe*, *Chamaenerion palustre*), which give the patches a specific physiognomy (Błońska *et al.*, 2019; Kompała-Bąba *et al.*, 2020). In further stages of succession, alien species (e.g., *Solidago gigantea*) can also be found in the composition of patches.

FUNCTIONAL DIVERSITY

During the fieldwork, GPS devices were used, 324 plots were established on the analysed site, and vegetation and soil substrate samples and data were collected. In the test plot, a representative square was determined to contain the dominant species and best represent the entire patch (the coverage of the dominant species and quantitative responses between the dominant and co-occurring species). The test field had a side length of 0.5 m.

The taxonomy focuses on plant species composition, measured primarily by species richness. The functional diversity has been based on some selected plant species' functional traits. The chosen traits represent the plants' productivity potential, propagation, and competition ability. **Height:** this is a continuous characteristic that describes the height of the plant. **Leaf area:** this continuous characteristic describes the plant's leaf area. **Bud height:** this is an ordinal trait that describes the height of the plant's bud. Ordinal (0 – T, 0.12 – G, Hyd, 0.25 – H, 0.5 – Ch, 0.75 – N, 1 – M; T = therophytes, G = geophytes, Hyd = hydrophytes, H = hemicryptophytes, Ch = chamaephytes, N = nanofanerophytes, M = megaphanerophytes). **Beginning of flowering** and **End of flowering:** these total traits describe the plant's flowering period. **Pollination by animals, Self-pollination,** and **Wind pollination** are binary traits that describe different plant pollination methods. **Medium seed weight:** this is a continuous trait that describes the average seed weight of a plant analysed. **Propagation by seed and vegetative propagation:** these are binary traits that describe different methods of plant propagation. **Presence of mycorrhiza:** this binary trait describes whether a plant has mycorrhiza. **Anemochory, Zoochory, Barochory:** these are binary traits that describe different plant-spreading methods. **Competitiveness, Stress tolerance,** and **Ruderality:** these are ordinal traits that describe different ecological aspects of the plant. **Ellenberg values:** the Ellenberg ecological indices are indicators used to assess plant species' ecological characteristics and habitat requirements (Cornelissen et al., 2003).

SUBSTRATE PHYSICOCHEMICAL ANALYSES

Soil samples weighing approximately 1 kg were taken at five points at 0–15 cm depth at each sampling site. In addition, soil bulk density, total soil porosity, and maximum water-holding capacity were measured. These data will help the understanding of the soil samples physicochemical properties during observation. The detailed measurement procedure is described in research undertaken by Bierza et al. (2023). The substrate samples for physicochemical analyses underwent several stages of preparation. First, they were air-dried, ground, and sieved to a fraction smaller than 2 mm.

The substrate samples were then analysed for several physicochemical parameters including: pH – determines the acidity or alkalinity of the soil; electrical conductivity (EC) – measures the ability of the soil to conduct electricity; soil organic carbon content (SOC) – indicates the amount of organic matter in the soil; C loss on ignition– indicates the loss of organic carbon during the combustion process; total nitrogen (TN) is the sum of nitrate (NO_3), nitrite (NO_2)), organic nitrogen and ammonia; content of available forms of phosphorus (P_2O_5) – indicates the amount of available phosphorus; available magnesium concentra-tion (MgO) – measures the amount of magnesium in the soil; exchangeable cations (K^+, Na^+, Ca^{2+}): measures the concentration of exchangeable cations in the soil; moisture – a percentage that determines the water content of the soil.

SUBSTRATE RESPIRATION (RS) MEASUREMENTS

Soil respiration was measured using a portable infrared gas analyzer (IRGA) connected to the soil respiration chamber. The soil respiration chamber had an area of 78 cm^2 and a volume of 1171 cm^3. The edge of the soil respiration chamber was inserted into the soil to a depth of 1–2 cm. The detailed measurement procedure is described by Woźniak et al. (2022).

DATA ANALYSIS

In order to determine the relationships between environmental factors and functional attributes of the species (Tab. 1), the RLQ ordination followed by the improved fourth-corner method (Dray et al., 2014) was used as it links three data matrix tables: table L with abundance values noted for species growing on a series of plots, table R with variables describing the plots, and table Q containing the chosen traits of particular species. Table L contained the 192 vascular plant species with their abundance in 324 studied plots. Table R contained the environmental variables, mainly soil traits (physical-chemical properties, gran-ulometric composition, pH, presence of soil enzymes, SRL).

The table Q had 23 plant traits for 192 vascular plant species found in this study. Prior to RLQ, a default option, i.e., standardised principal component analysis (PCA), was computed on the matrix of environmental variables by sites (table R) as well as for the traits-by-species matrix (table Q). For the RLQ analysis, statistical analyses were undertaken using the fourth-corner statistics in the form that (Dray et al., 2014) improved. The analysis was conducted to assess the relationship between each environmental variable and the first two axes of the RLQ and also between the traits and the axes of the RLQ. This statistical tool allowed both the quantitative and qualitative variables to be used. Finally, we analysed the bivariate associations between the variables of two matrices, R and Q. The significance was tested using a permutation procedure. For this analysis, the fourth corner was used. To examine the overall functional diversity of vascular plant composition noted in the plots, four components of functional diversity were computed: richness (FRic), evenness (FEve), divergence (FDiv), and dispersion (FDis). The default function dbFD in the FD package was used. It was assumed that FRic can be interpreted as a measure of low habitat filtering. Functional evenness (FEve), a measure of niche overlap and functional divergence (FDiv) as a degree of functional hetero-geneity, can be treated as signs of competition in a community. Apart from functional factors, taxonomical diversity was calculated: species richness (S), Shannon–Wiener index (H), evenness (E), and Simpson dominance index using "vegan" and "abdiv" packages. To assess the relationship between FD components and SRL against the species diversity, detrended correspondence analysis (DCA) with passive projection (999 permutations of Monte Carlo test) was applied. The SRL Spearman rank correlation test was used to check whether there are relationships among the functional diversity parameters.

Table 1. The list of functional traits of the recorded plant species that were analysed

Name of trait	Code	Type
Height	height	continuous
Leaf area	le_area	continuous
Bud height	BudHeight	ordinal (0 – T, 0.12 – G, Hyd, 0.25 – H, 0.5 – Ch, 0.75 – N, 1 – M)
Beginning of flowering	flw_early	integer
End of flowering	flw_late	integer
Pollination by animals	poll_zoo	binary
Self-pollination	poll_self	binary
Wind pollination	poll_wind	binary
Medium seed weight	medium seed_wght	continuous
Propagation by seed	seed	binary
Vegetative propagation	weg	binary
Presence of mycorrhiza	Myc	binary
Anemochory	Anem	binary
Zoochory	Zoochory	binary
Barochory	Barochory	binary
Competitiveness	Comp	ordinal (1-C, 0.5-CR, CS, 0.33-CSR)
Stress	Stress	ordinal (1-S, 0.5-CS, SR, 0.33-CSR)
Ruderality	Rude	ordinal (1-R, 0.5-CR, 0.33-CSR)
Ellenberg value for light	L	integer (0–9)
Ellenberg value for temperature	T	integer (0–9)
Ellenberg value for moisture	F	integer (0–12)
Ellenberg value for soil reaction	R	integer (0–9)
Ellenberg value for nitrogen	N	integer (0–9)

Explanations: contribution of Raunkiaer's forms: T = therophytes, G = geophytes, Hyd = hydrophytes, H = hemicryptophytes, Ch = chamaephytes, N = nanofanerophytes, M = megaphanerophytes. The basic classification of *CSR* plant functional types: *C* axis of competition (ability of plants to displace the other species under favourable environmental conditions); *S* axis of stress tolerance (ability to withstand long-term adverse environmental conditions); *R* axis of ruderality (ability to grow faster in disturbed sites).
Source: own elaboration.

RESULTS

In order to estimate the impact of the various aspects of diversity of the spontaneous vegetation species composition apart from the taxonomic diversity, some functional traits have been assessed. The list of the traits is presented in Table 1.

In both axes, RLQ explained 68% of total inertia. The proportion of the variance that was accounted for by the RLQ analysis was compared with the results from separate analyses of the data for the species (L), species traits (Q), and environmental data (R).

The first axis of the RLQ analysis accounted for 86.25% of the variability that was explained by the first axis of the separate environmental analysis (i.e., the ratio between the variance of the environmental characteristics in RLQ and the variance of the environmental characteristics in the separate analysis) – Table 2. The variability explained by the first axis of the separate plant trait analysis was 84.5% (Tab. 2). The eight environmental variables and plant traits are positively correlated with the first axis of RLQ, while 11 and 15 of the environmental and trait variables are correlated negatively (Fig. 1).

We considered the RLQ (R = environmental data, L = species, and Q species traits) analysis as the most suitable for examining relationships between among environment, species composition, plant traits, and four functional diversity compo-

Table 2. Decomposition of RLQ analysis

Parameter	RLQ axis 1	RLQ axis 2
Eigenvalue	1.52	0.48
Covariance	1.23	0.69
Correlation	0.39	0.39
Total variance	52.87	16.87
R/RLQ (%)	86.25	83.66
L/RLQ (%)	44.16	53.36
Q/RLQ (%)	84.50	71.92

Explanations: R = environmental data, L = species, and Q = species traits.
Source: own study.
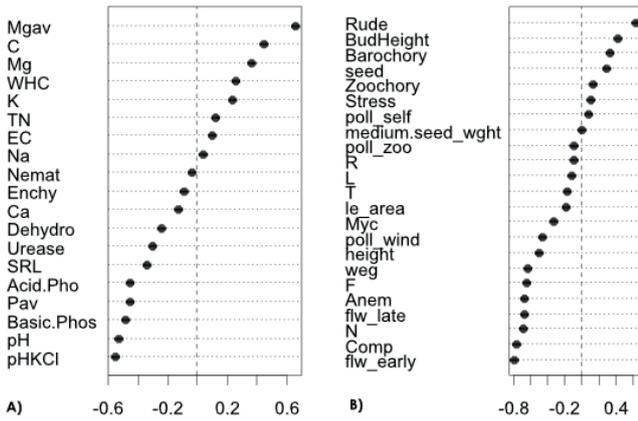
Fig. 1. The weighted correlations of environmental variables and plant traits with the first RLQ axis: A) environmental variables, B) plant traits; the weighted correlations of environmental variables and plant traits with the first RLQ axis; Mg av. = magnesium available, P av. = available phosphorus, Mg = available Mg (MgO) concentration, *WHC* – water holding capacity, K, Na, Ca = exchangeable cations, TN = total nitrogen, *EC* = electrical conductivity, Nemat = Nematoda, Enchy = Enchytraeidae, Dehydro = dehydrogenase activity, Urease = urease activity; *SRL* = soil respiration level, Acid.Pho = acid phosphatase, Basic.Phos = alkaline phosphatase, Rude = ruderality, BudHeight = bud height, Barochory = barochory, seed = propagation by seed, Zoochory = zoochory, Stress = stress; poll_self = self-pollination, medium seed_wght = medium seed weight, poll_zoo = pollination by animals, *R* = Ellenberg value for soil reaction, *L* = Ellenberg value for light, *T* = Ellenberg value for temperature, le_area = leaf area, Myc = presence of mycorrhiza, poll_wind = wind pollination, height = height, weg = vegetative propagation, *F* = Ellenberg value for moisture, Anem = anemochory, flw_late = end of flowering, N = Ellenberg value for nitrogen, Comp = competitiveness, flw_early = beginning of flowering; source: own study

nents (richness, evenness, dispersion, and divergence). The literature suggests that high soil richness is typical for species-rich ecosystems, so we assume that this parameter scores a high value in sites that represent a high functional evenness (*FEve*) and divergence (*FDiv*). The high values of these functional components indicate high competition, which usually occurs in communities with many species. High functional richness (*FRic*) and dispersion (*FDis*) values represent low habitat filtering.

The analyses that present the main gradients of the collected data show that the negative impact of some environmental parameters, such as acidity of the soil substrate, available phosphorus, phosphorus-dependent soil enzyme activity, calcium, and sodium, and determines the gradients. The environmental parameters responsible for the positive part of the gradient are sodium, electrical conductivity, total nitrogen, potassium, water holding capacity, available Mg (MgO) concentration, C loss of ignition, and magnesium availability.

While among the analysed plant traits, presenting the gradients and influencing it negatively, the following traits should be listed: early flowering, traits responsible for competitiveness, Ellenberg value for nitrogen, beginning of flowering, anemochory, Ellenberg value for moisture, vegetative propagation, height, wind pollination, presence of mycorrhiza, leaf area, Ellenberg value for soil reaction, Ellenberg value for light and Ellenberg value for temperature. Lesser plant traits are correlated with the RLQ axis shaping the gradient, including traits responsible for stress resistance and adaptivity to conditions of the ruderal part of the continuum, zoochory, barochory, and bud height.

Permutation tests of the fourth-corner analysis showed associations between the first two axes of the RLQ analysis and the environmental variables and plant traits, respectively (Fig. 2). The positively significant environmental parameter shaping the AxQ1 is the available Mg (MgO) concentration. In contrast, the negatively significant environmental parameters shaping the AxQ1 are the pH, available phosphorus, dehydrogenase activity, and alkaline phosphatase.
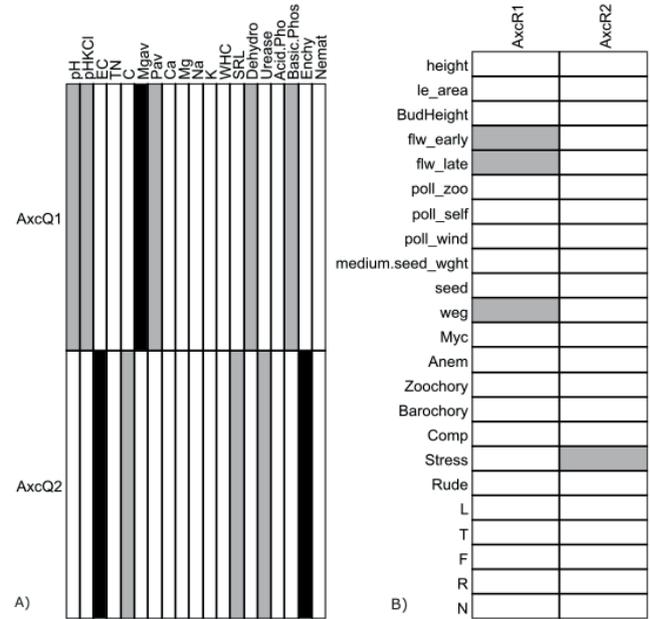
Fig. 2. The fourth-corner tests between the first two RLQ axes for the vascular plant traits (AxQ1/AxQ2) and environmental variables (A) and fourth-corner tests between the first two RLQ axes for the environmental variables (AxR1/AxR2) and vascular plant traits (B); positive and significant (*p* < 0.05) association ns are represented by black cells and negative significant ones by grey cells, while white cells indicate non-significant associations; other explanations as in Fig. 1; source: own study

The positively significant environmental parameters shaping the AxQ2 are electrical conductivity and Enchytraeidae. In contrast, the negatively significant environmental parameters shaping the AxQ1 are the C loss of ignition, water holding capacity, and urease activity.

The ordination analysis of the plant traits that are represented by species composition of the spontaneous vegetation of post-mining sites reveals that the manner of seed dispersion, the height of bud location, and ruderal traits are divided by the first axis from the species that are competitors, anemochorous and spreading vegetatively. Concerning the ordination of the environmental factors, electrical conductivity, available magnesium, and water holding capacity, together with nitrogen, carbon, and potassium content in the soil substratum, are one part of the ordination. The biotic functional traits parameters of competitiveness, zoochory, end of flowering, wind pollination, beginning of flowering, bud height, mycorrhiza, seed weight, height, Ellenberg value for temperature, self-pollination, ruderality, leaf area, and vegetative propagation is shown at the top of the chart. The second axis separates the above plant species traits from the parameters represented by plant species that possess the traits of adaptation to Stress on the far down of the functional trait distribution (Fig. 3).
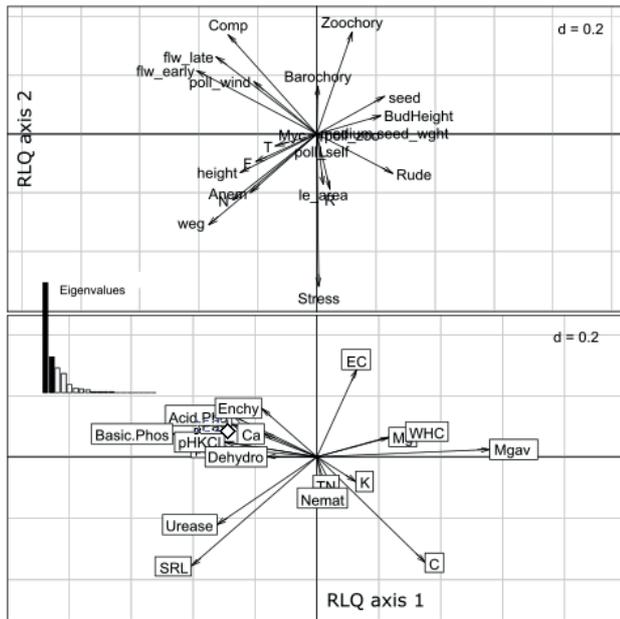
Fig. 3. The RLQ ordination, showing relationships between plant traits (upper) and environmental factors (down) along the two first axes; explanations as in Fig. 1; source: own study

The RLQ ordination was performed for environmental factors. The first axis is determined by the two extremes shaped by the available magnesium (Mg av.) and the activity of basic phosphorus and pH (in KCl). The *EC* and SRL determine the second axis. The other parameters distributed along the first axis are the water-holding capacity, calcium, dehydrogenase activity, and magnesium. Those parameters which lie, along the second axis are, C loss on ignition, urease activity, Enchytraeidae, Nematoda, and total nitrogen.

The vegetation type with the lowest number of species, *Phragmites australis*, the value of soil respiration is the highest. This result reveals that the vegetation with the higher diversity in the coal mine heaps novel ecosystem does not present a higher soil respiration value (Tab. 3).

The fourth-corner correlation analysis has shown that the soil respiration value is positively correlated with vegetation

patches in which plant species composition is represented by species characterised by vegetative spreading together with plant species that have traits responsible for adaptation to stressed habitat conditions (Fig. 4.).

The significance of functional and taxonomic diversity is apparent in the gradient for species composition (Fig. 5B). The higher functional richness, divergence, and dispersion values positively correlate with the Shannon–Wiener index and species richness. Both taxonomical and functional evenness were non-significant factors. Among functional components only and in the case of functional dispersion, it is weakly negative and significantly correlated with *SRL* (Fig. 5A).

The relationship between temperature and *SRL* is weak and positive but significant (Fig. 6). An increase in temperature is associated with a slight increase in *SRL*. The value of the correlation coefficient ($r = 0.17$) confirms this weak relationship. In addition, the p-value $= 0.0018$ indicates the statistical significance of this relationship, meaning that the probability that the observed correlation is due to chance is very low.

DISCUSSION

THE ROLE OF TAXONOMIC AND FUNCTIONAL DIVERSITY IN ECOSYSTEM FUNCTIONING

The ecosystem development on disturbed habitats such as post-mining mineral sites, follows the sequence of processes and functionality established during the natural, spontaneous vegetation process. Identifying the critical factor in a disturbed environmental situation of the structure and function affecting the biodiversity of the vegetation of the non-analogous species composition in general and the microbial communities is frequently impossible due to the complexity of the various biotic and abiotic factors (Berg and Smalla, 2009). In the presented study, we attempt to identify the environmental gradients that influence the diversity expressed as taxonomical and functional vegetation community composition and, based on the identified gradients, analyse the relationships between different measures of vegetation diversity and soil substratum respiration parameters.

Table 3. The list of spontaneous vegetation types with the biodiversity indices (maximum, minimum, and mean) along with the value soil respiration level (*SRL*) rate in the vegetation patches of the particular vegetation types

Vegetation type groups	Poa compressa	Tussilago farfara	Daucus carota	Chamaenerion palustre	Phragmites australis
Maximum number of species	19	18	20	16	10
Minimum number of species	8	1	7	8	3
Mean number of species ±SD	13.8 ±2.90	8.11 ±3.62	12.6 ± 3.00	11.5 ±2.02	10 ±5.06
The mean Shannon–Wiener diversity index ±SD	1.92 ±0.24	1.17 ±0.473	1.84 ±0.277	1.66 ±0.262	1.06 ±0.594
The mean species evenness ±SD	0.73 ±0.08	0.56 ±0.15	0.732 ±0.0605	0.685 ±0.0883	0.454 ±0.187
Maximum SRL rate ($(g\ CO_2)\cdot m^{-2}\cdot h^{-1}$)	1.21462	0.82552	0.15826	0.161759091	0.97638
Minimum SRL rate ($(g\ CO_2)\cdot m^{-2}\cdot h^{-1}$)	0.00752	0.00506	0.00158	0.0086	0.271
Mean SRL rate ($(g\ CO_2)\cdot m^{-2}\cdot h^{-1}$)	0.227	0.20173	0.0526	0.1617	0.5842

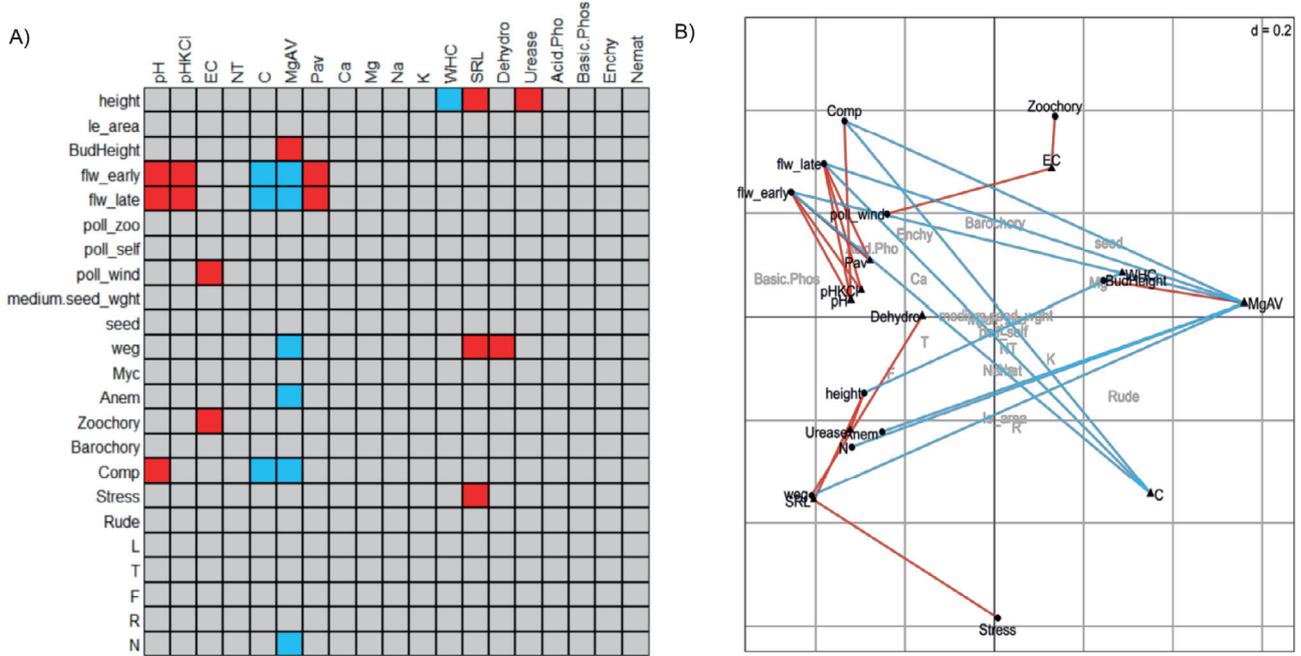Explanation: *SD* = standard deviation.
Source: own study.

Fig. 4. The results of fourth-corner analysis between environmental variables and plant traits; red and blue cells – positive and negative significant ($p < 0.05$) associations, respectively, grey cells – non-significant associations; explanations as in Fig. 1; source: own study
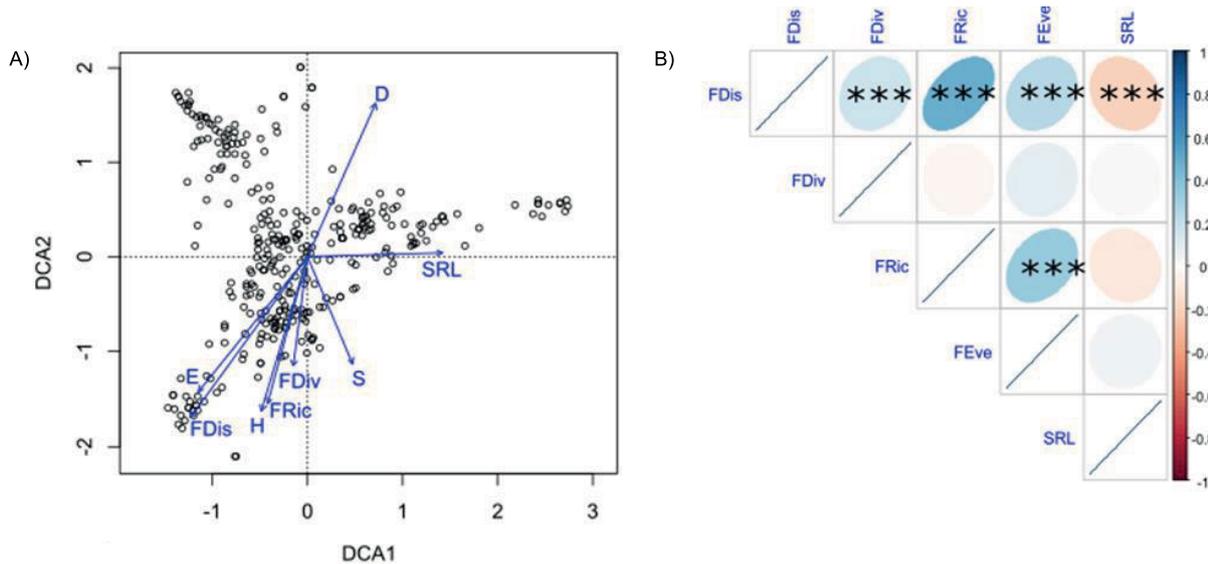

Fig. 5. Passive projection of functional and taxonomical diversity and their relations with soil respiration level (SRL): A) the ordination of DCA, B) matrix correlation; *FDis* = high functional dispersion, *FDiv* = high functional divergence, *FRic* = high functional richness, *FEve* = high functional evenness; source: own study

The taxonomic diversity analysis focuses on plant species composition and indices that measure preliminary species richness and abundance. These indices are primarily used in Europe and are based on the principle that certain plant species have specific tolerance ranges for environmental factors such as light, temperature, moisture, soil pH, and nutrient availability. In these studies, the well-known Ellenberg ecological indices are the Ellenberg indicator values (*EIVs*), which are used to evaluate the ecological preferences of plants along environmental gradients. These values are assigned to plant species based on their observed ecological behaviour in the field. Our study revealed that plant species representing different functional traits are filtered along the gradient of biotic and abiotic habitat factors. The results showed that only some traits are significant in the spontaneous vegetation on coal mine heap novel ecosystems concerning soil respiration. The low habitat filtering expressed by functional richness and dispersion was associated with relatively high functional evenness and divergence being a proxy of competition, which is not common. Soil respiration was negatively correlated with low habitat filtering and competition (not significantly, but the trend is similar). It means that under novel ecosystem conditions, such as coal mine heaps, soil respiration seems to be affected by many environmental and biotic factors but the effects are of low magnitude.
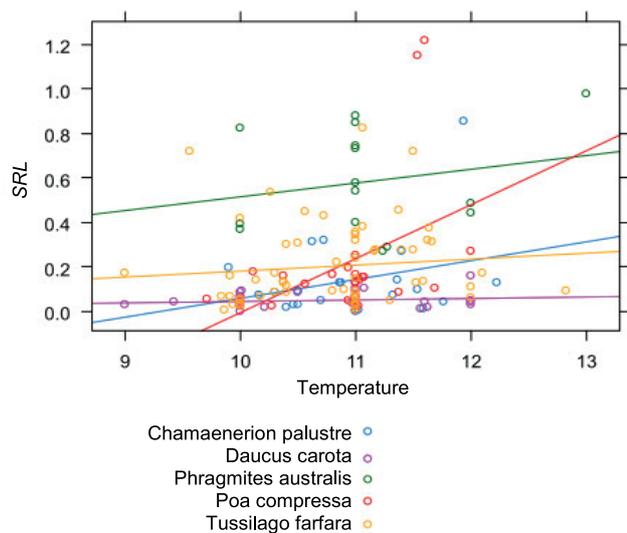
Fig. 6. The relationship between temperature and soil respiration level (*SRL*); $rs = 0.17$, $p = 0.0018$; source: own study

FACTORS AFFECTING THE TAXONOMIC DIVERSITY OF THE VEGETATION WITH REGARD TO SOIL RESPIRATION

Plant taxonomic diversity can affect soil respiration by changing the quantity and quality of organic matter supplied to the soil. Plant species can provide different amounts of leaves and other organic materials that are broken down by soil microorganisms, leading to soil respiration. Soil physicochemical properties, such as pH, water content, and nutrient content (e.g., nitrogen and phosphorus), can affect plant taxonomic diversity and soil respiration. For example, soils with low pH can reduce plant diversity and soil microbial activity, affecting soil respiration. Changes in the taxonomic diversity of plants can affect these interactions and, thus, soil respiration (Bierza *et al.*, 2023). In our study, the factors that drive the habitat gradients along which the plant species composition and vegetation types are distributed are identified. The main gradients of the collected data show that the impact of environmental parameters, such as acidity of the soil substrate, available phosphorus, phosphorus-dependent soil enzyme activity, calcium, and sodium, determine the gradients. The environmental parameters responsible for the positive aspect of the gradient are sodium, electrical conductivity, total nitrogen, potassium, water holding capacity, available Mg (MgO) concentration, C content, and available magnesium. Among the analysed plants' traits that reflect the gradients, the following traits should be listed: early flowering, traits responsible for competitiveness, Ellenberg value for nitrogen habitats parameters, beginning of flowering, anemochory, Ellenberg value for moisture, vegetative propagation, plant height, wind pollination, the ability to symbiosis mycorrhiza, the value of leaf area, Ellenberg value for soil reaction acidity of the habitat conditions, Ellenberg value for light and Ellenberg value for temperature.

Based on the primary producers' species composition, the vegetation communities and ecosystems are shaped by intense habitat conditions selection and adaptation processes dependent on the evolutionary, historical, and environmental processes (Purschke *et al.*, 2013; Stevens and Tello, 2014). Much research on the impact of plant species diversity on total soil respiration

(*Rs*) has been focused, most frequently on taxonomic diversity (Craine, Wedin and Reich, 2001). The fact that species richness can regulate *Rs* through changes in productivity showed a positive relationship between species richness and *Rs* (Craine, Wedin and Reich, 2001). In our study, vegetation patches were divided into five groups based on species composition: 1 – *Poa compressa*, 2 – *Tussilago farfara*, 3 – *Daucus carota*, 4 – *Chamaenerion palustre*, and 5 – *Phragmites australis*. The collected data indicate that the most significant group in terms of the number of species is group number 5. Group number 3 showed the highest maximum respiration value, which may indicate its high metabolic activity. Group number 2 showed the minimum number of species (1) and the minimum value for respiration, which may indicate its limited diversity and metabolic activity.

In grassland, *Rs* was related to species-specific changes (species composition). The changes in species richness were less important in influencing the *Rs* (Johnson *et al.*, 2008). These differences in results might be connected with the fact that the influence of different species on *Rs* is the same regardless of the traits of the calculated taxonomic diversity, without linking the different set of traits that particular species composition represents and might influence the value of *Rs* (Díaz and Cabido, 2001).

The uncertainty between the soil respiration and diversity parameters in varied vegetation types, grasslands, forests, and others might be connected with the dual origin of the total soil respiration. The components of total respiration *Rs* are plants' autotrophic respiration (*Ra*), which generates energy for water and nutrient acquisition, survival, and growth, and in contrast, heterotrophic respiration (*Rh*) from the activity of soil microorganisms that regulates nutrient cycling (Ryan and Law, 2005). Recently, there have been some significant advances in our understanding of the negative impacts of plant diversity loss on ecosystem functions, including net primary production (Liang *et al.*, 2016; Duffy, Godwin and Cardinale, 2017), carbon sequestration (Tilman, Hill and Lehman, 2006) and nutrient cycling (Handa *et al.*, 2014). However, how plant diversity loss affects *Rs* and its components remains uncertain (Chen and Chen, 2019). Our study focused on the total amount of respiration in the plots that represent the wide spectrum of the identified vegetation types. The range of CO_2 emissions at the analysed sites ranged from 0.00158 to 1.21462 (g CO_2)·m^{-2}·h^{-1}.

Studies suggest that the biomass created due to primary production increases with plant species diversity and trait heterogeneity due to complementary resource utilisation among constituent species in species-rich ecosystems (Hooper *et al.*, 2005; Chen and Chen, 2018). Increased litter inputs in species-rich ecosystems may lead to the accumulation of soil carbon and nitrogen pools (Fornara, Tilman and Hobbie, 2009; Lange *et al.*, 2015), which can increase microbial respiration (Hector *et al.*, 2000; Hooper *et al.*, 2005; Eisenhauer *et al.*, 2013).

FACTORS AFFECTING THE VEGETATION COMMUNITIES' FUNCTIONAL DIVERSITY REGARDING SOIL RESPIRATION

The relationship between vegetation functional diversity and soil respiration is multifaceted, involving intricate interactions between plant traits, nutrient cycling, microbial communities, and environmental conditions. Understanding these relationships is crucial for predicting how ecosystems may respond to changes in biodiversity and environmental factors, including those

associated with climate change and land-use practices. In natural and seminatural habitats, the vegetation and ecosystem diversity factors are explained by two concepts. The mass ratio hypothesis and niche complementarity hypothesis are used to consider the changes in vegetation plant species composition and ecosystem diversity, mostly about plant functional trait composition (Liu et al., 2022). The mass ratio hypothesis suggests that the characteristics of dominant species have a greater impact on ecosystem processes. In contrast, the niche complementarity hypothesis suggests that diverse communities can use resources more efficiently. In studying the spontaneous development of vegetation of novel ecosystems, the applicability of the above concepts and hypothesis needs to be tested.

Research suggests that the soil water content in the habitat and species richness influence *Rs*. As indicated by Ren et al. (2022), changes in soil microbial community structure and diversity, as well as soil carbon properties, respond to different vegetation types at different soil water levels. Soil water content and species richness also influenced *Rs*. In our study, the water holding capacity has been assessed in all study plots. The analysis showed that in the mineral habitats of post-mining areas, these parameters are responsible for the positive part of the gradient.

One of the possible aspects of the plant species' functional diversity is identified using the Ellenberg ecological indices. By using Ellenberg ecological indices, a better understanding of the ecological requirements and the environmental conditions of a particular habitat of the plant species composition is possible. This information can be valuable for conservation efforts, land management, and ecological restoration projects. In recent years, functional diversity has become a common approach in studying plant diversity and ecosystem function (McGill et al., 2006). Only temperature, soil reaction, light, and moisture in our study revealed some correlations in the Ellenberg ecological indices in the studied plots.

Among other functional traits, the leaf functional traits, such as leaf nitrogen content and specific leaf area (*SLA*), are closely related to ecosystem respiration and soil properties (Srivastava et al., 2012; Long De et al., 2019). The functional diversity based on functional traits may be more helpful in explaining *Rs*. It can provide information on those difficult-to-measure functional traits that may be closely associated with *Rs* (Cadotte et al., 2009; Stevens and Tello, 2018). There is a high degree of variability in the relationship between different dimensions of biodiversity and environmental factors. These factors may have ecosystem functions with opposing effects (Devictor et al., 2010; Bagousse-Pinguet Le et al., 2019). However, in studies based on real-world problems, the regression parameters vary across spatial locations (Wang et al., 2021). Our study analysed the nitrogen content in soil substrate as a parameter of soil respiration. Our study revealed that fewer plant traits are shaping the gradient, including traits responsible for stress resistance and adaptivity to conditions of the ruderal part of the continuum, zoochory, barochory, and bud height.

The ordination analysis of the plant traits that are represented by species composition of the spontaneous vegetation of post-mining sites reveals that the manner of seed dispersal, the height of bud location, and ruderal traits are divided by the first axis from the species that are competitors, anemochories and spread vegetatively. Concerning the ordination of the environmental factors, electrical conductivity, available magnesium, water holding capacity, nitrogen carbon, and potassium content in soil substratum are one part of the ordination. In conclusion, the ordination analysis of plant traits and environmental factors in post-mining areas shows complex relationships, which may have important implications for succession and regeneration processes.

The fourth-corner correlation analysis has shown that the soil respiration value is positively correlated with vegetation patches rich in species characterised by high plants that spread mostly vegetatively and plant species traits responsible for adaptivity to stress.

THE ENVIRONMENTAL BIOTIC AND ABIOTIC FACTORS AFFECTING SOIL RESPIRATION IN POST-MINING NOVEL ECOSYSTEMS

Using the spatial heterogeneity of natural environmental gradients to explore the response of plant diversity and ecosystem function to environmental change has become a fruitful approach in ecosystem ecology (Prager et al., 2021). Desert ecosystem biodiversity monitoring provides insight and comprehensive data on habitat conditions, vegetation, and plant community composition; in the extreme desert ecosystem, the biodiversity recordings enable the analysis of the relationships between plant diversity taxonomic, functional, soil properties, and *Rs* along a severe environmental gradient. The study of the functioning of ecosystems existing in extreme environments, e.g., post-mining sites, and desert ecosystems can enhance the understanding of the mechanisms by which *Rs* responds to relevant drivers, and may be helpful to the understanding and management of future climate change (Wang et al., 2022).

The diversity of plant composition determines the quality and quantity of the release of particular chemical substances that can recruit particular groups of microorganisms that are useful against, e.g., diseases and insect herbivory (Rudrappa et al., 2008). Releasing plant-derived metabolites that provide a carbon source attracts various microorganisms (Bais et al., 2006; Borymski et al., 2018). Plant diversity and the diversity of living organisms and their varieties (biodiversity) are the main factors driving many ecosystem functions, including the global ecosystem (Chapman and Newman, 2010; Jarzyna and Jetz, 2018; Chen and Chen, 2019). For crucial ecosystem functions like soil respiration, the relation between the individuals of plant species and the diversity and abundance of microorganisms in particular habitats is fundamental (Eisenhauer et al., 2013; Hooper et al., 2005). The presence or absence of one species in a community composition might have more significant functional implications for ecosystems than for another species, even though the species richness in both cases will be the same. However, the two species affect the assemblage functional diversity (*FD*) differently (Cadotte, Carscadden and Mirotchnick, 2011). The different species' functional attributes are crucial for understanding the dynamic processes behind the temporal and spatial species occurrence and, consequently, vegetation community assembly (Belmaker and Jetz, 2011).

CONCLUSIONS

The plant species and functional diversity of the spontaneous vegetation developing spontaneously on the mineral material of the coal mine novel ecosystem reflects the habitat's variety of biotic and abiotic conditions.

The gradient in species composition explains the functional and taxonomical diversity. The higher functional richness, divergence, and dispersion values positively correlate with the taxonomical diversity expressed by the Shannon–Wiener index and species richness. Both taxonomical and functional evenness were non-significant factors. A weak negative and significant correlation with soil respiration level (SRL) has been identified among functional components only in the case of functional dispersion.

Contrary to our expectation, soil respiration was the highest in the less diverse vegetation types. Among functional components, only functional dispersion (a proxy of low habitat filtering) is weakly negatively and significantly correlated with SRL. However, all functional diversity indices are correlated, which indicates that conditions driving community assembly on coal mine heaps act differently than on near-natural and natural ecosystems. Thus, SRL seems dependent on many abiotic and biotic factors in novel ecosystems and requires further research.

CONFLICT OF INTERESTS

All authors declare that they have no conflict of interests.

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