

Article

Plant Species and Functional Diversity of Novel Forests Growing on Coal Mine Heaps Compared with Managed Coniferous and Deciduous Mixed Forests

Jawdat Bakr ^{1,2}, Agnieszka Kompala-Bąba ², Wojciech Bierza ², Agnieszka Hutniczak ^{2,*}, Agnieszka Błońska ², Damian Chmura ³, Franco Magurno ², Andrzej M. Jagodziński ^{4,5}, Lynn Besenyei ⁶, Barbara Bacler-Żbikowska ⁷ and Gabriela Woźniak ^{2,*}

- ¹ Technical Institute of Bakrajo, Sulaimani Polytechnic University SPU, Qrga Wrme Street-327/76, Sulaymaniyah 46001, Kurdistan Region, Iraq; jawdat.bakr@spu.edu.iq
 - ² Institute of Biology, Biotechnology and Environmental Protection, Faculty of Natural Sciences, University of Silesia in Katowice, 28 Jagiellońska Str., 40-032 Katowice, Poland; agnieszka.kompala-baba@us.edu.pl (A.K.-B.); wojciech.bierza@us.edu.pl (W.B.); agnieszka.blonska@us.edu.pl (A.B.); franco.magurno@us.edu.pl (F.M.)
 - ³ Institute of Environmental Protection and Engineering, Faculty of Materials, Civil and Environmental Engineering, University of Bielsko-Biala, 2 Willowa Str., 43-309 Bielsko-Biala, Poland; dchmura@ubb.edu.pl
 - ⁴ Department of Ecology, Institute of Dendrology, Polish Academy of Sciences, 5 Parkowa Str., 62-035 Kórnik, Poland; amj@man.poznan.pl
 - ⁵ Department of Game Management and Forest Protection, Faculty of Forestry and Wood Technology, Poznań University of Life Sciences, 71D Wojska Polskiego Str., 60-625 Poznań, Poland
 - ⁶ Faculty of Science & Engineering, University of Wolverhampton, Wulfruna Str., Wolverhampton WV1 1LY, UK; lynnbesenyei@gmail.com
 - ⁷ Department of Pharmaceutical Botany, Faculty of Pharmaceutical Sciences in Sosnowiec, Medical University of Silesia in Katowice, 30 Ostrogórska Str., 41-200 Sosnowiec, Poland; bbacler@sum.edu.pl
- * Correspondence: agnieszka.hutniczak@us.edu.pl (A.H.); gabriela.wozniak@us.edu.pl (G.W.)



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Abstract: (1): The Upper Silesia region of Poland is one of the most extensively altered regions of Europe due to human activity, especially coal mining. (2): We used cluster analysis to examine the floristic composition of three classified forest communities: forests developed on post-coal mine mineral heaps (HF), mixed deciduous forests (DECI), and managed secondary coniferous forests (CON). Vegetation data were collected from 44 randomly selected plots, and plant traits connected with persistence, dispersal, and regeneration were taken from commonly used plant trait databases. (3): Higher species richness, species diversity, and evenness (36, 2.7, and 0.76, respectively) were calculated for HF plots compared with those plots from DECI (22, 1.9, and 0.62) and CON (18, 2.0, and 0.71) plots. Higher functional richness (0.173, 0.76) and functional divergence were determined for HF compared with those calculated for DECI (FRic 0.090, FDiv 0.71) and CON (FRic 0.026, FDiv 0.69). In contrast, the substrate from HF forests had significantly lower soil respiration (0.76 mg-CO₂ h/m²) compared with substrates from both CON and DECI forests (0.90 and 0.96 mg-CO₂ h/m², respectively); (4): A set of complex abiotic stresses which plants suffer from on coal mine spoil heaps shaped different patterns of taxonomic and functional diversity. These findings demonstrate the importance of investigating successional aspects and carbon dynamics of de novo forests which have developed on post-coal mine spoil heaps in urban industrial areas.

Keywords: novel ecosystem; soil respiration; community weighted mean; abiotic factors; plant functional traits

1. Introduction

Natural forest ecosystems are self-sustaining vegetation communities due to natural ecosystem processes and are known to be more resistant to different types of disturbance than secondary forests [1]. They are also effective in providing a range of ecosystem services.

Timber production forests and replanted forests are low in the biodiversity of their canopy trees and herb layer compared to a natural forest's species diversity [2,3]. The management of replanted and timber production forests, including the selection of tree species, reduces the diversity by planting only trees from selected seed banks and by damaging the herb layer, along with the upper layer of the soil, thus reducing the ability of managed forests to provide certain ecosystem services.

Forest vegetation communities in the temperate zone can dominate the terrestrial ecosystem in the northern hemisphere if there is no disturbance in the landscape [4]. In temperate zones, through natural succession, the gradual change in species assemblages and related organisms adapted to the new ecosystem conditions will finally develop into forest ecosystems. In response to the gradient of natural conditions, the development of different natural forests is reflected in most general forest groups, such as coniferous, deciduous, and mixed forests. The mechanisms of primary and secondary succession in natural and semi-natural conditions is relatively well understood [5]. During succession, in natural and semi-natural conditions, a sequential pattern of changes take place, determined by the habitat conditions, whenever a new environment is available, or after an environment is disturbed. Bare soil or rock waste can eventually become a forest with trees, understory, and herb layers, with a species composition appropriate to the habitat conditions.

The associated organisms drive changes in the successional processes of their habitat, alter its development [5]. The spontaneous vegetation succession that leads to the development of a forest is explained by several models [6–8]. The significance of random processes and unique reactions to environmental elements was demonstrated by Elias et al. [9].

Within the European temperate zone, which is extensively affected by human activities, the Upper Silesia region, like other European industrial centres, has been additionally altered by the hard coal mining industry, with direct impacts on the local ecosystems. Excavation of hard coal and the resulting post-mining mineral heaps create *de novo* habitats, which are very different from natural ecosystems. Disposing the rock waste mineral material creates extensive disturbed areas with harsh habitat conditions. These newly created novel ecosystems have developed under the habitat conditions that were established due to human industrial activities [10–13]. Nevertheless, such disturbed sites have been observed to provide opportunities for new species of plants and animals to colonise, create unique compositions, and then undergo a spontaneous succession process [10,14].

Investigations into the spontaneous processes of vegetation development and failed reclamation attempts have led to a re-evaluation of the management strategy of these new habitats [11,15]. These spontaneous successional processes can lead to long-lasting and self-sustaining entities, and detailed research has led to the concept of novel ecosystem development and persistence. Hobbs and coworkers [10] revealed that non-analogous plant species play the main role in the vegetation composition of recently created novel ecosystems. As a result of the unusual, frequently extreme habitat conditions, the plants and associated organisms are grouped following new rules and anonymous pathways of ecosystem development, from pioneer vegetation communities to woodland ecosystems.

The functional traits (morphological, physiological, and phenological) of plants affect their survival, propagation, and growth [16], and provide a way to assess their functional diversity (FDiv) in a variety of habitats. Different plant species colonise different habitats based on their traits [17]. Among all functional indices, functional richness (FRic) and functional evenness (FEve) best explain the resilience and resistance of an ecosystem to environmental changes [18]. FDiv measures the degree to which the abundance of a community is distributed towards the extremities of occupied functional trait space, and compares the abundance-weighted Euclidean distances of species to the maximum possible value [19]. To calculate the dispersion in the community, Rao's quadratic entropy (RaoQ) index can be used, which combines functional richness and functional divergence [20].

The species type and functional diversity of the dominant plants drive some short-term soil functions such as nutrient and carbon cycles [21,22]. Autotrophs, such as plants, employ large energy fluxes, synthesis and decomposition processes to produce biomass [23,24]. In

forests, carbon sequestration occurs through the products of photosynthesis and is stored in soil pools, above- and below-ground biomass, fallen leaves, and dead wood. In fact, C sequestration and storage can vary due to differences in photosynthesis, respiration, wood production intensity, and the decomposition of soil organic matter (SOM). It has been suggested that there is no relationship between biomass production and species richness [25], but many studies have linked species richness and functional traits as the main drivers of carbon storage in all pools [26–28]. On forest sites with a single tree species, less carbon is stored due to the reduction in litter production and the depletion of soil biodiversity [29–31]. Increasing the soil temperature by 10 degrees centigrade may increase the soil respiration by two-fold, as this is described as an exponential relationship [32]. Additionally, aerobic respiration decreases as the soil dries out and increases with increasing soil water content (before there is a change to anaerobic respiration when soil becomes water-logged).

The aim of this research was to compare the species and functional diversities of spontaneously developed forests on post-coal mine heaps with managed coniferous and deciduous mixed forests. We hypothesised that diversity indices would have lower values in forests developed in the novel ecosystems of post-coal mine spoil heaps, as the black rock waste mineral substrate of heap forests is inert, has high thermal conductivity, is low in nutrition, and retains less water. We also hypothesised that plant species diversity will influence soil respiration which we have taken as a proxy for ecosystem functioning.

2. Materials and Methods

2.1. Study Area

The Upper Silesia region in Poland is well known for its long history of hard coal excavation, which covered and disturbed more than 2000 hectares of land [33]. The disposed rock waste created large numbers of coal mine spoil heaps consisting of sandstone, carboniferous residuals and coals [34]. Coal mine spoil heaps create harsh abiotic conditions with daily and seasonal temperature and humidity fluctuations, long-lasting periods of water stress, substrate instability, lack of soil, susceptibility to erosion, settling dust, and thermal and chemical activities. Along with the abiotic stressors, coal mine spoil heaps are low in nutrients and lack soil organic matter (SOM) and a seed bank [35]. These oligotrophic coal mine spoil heaps [36] are among the *de novo* ecosystem mosaics where diaspores are still able to germinate and grow despite the harsh abiotic and poor biotic conditions [6,37].

2.2. Study Design and Plant Composition

For this study, 22 plots (140 m²) represented forests which had developed on post-coal mine heaps (HF), based on the preliminary identification of vegetation type. Reclaimed coal mine heaps were excluded to avoid human interference in their spontaneous successional development. Another 10 and 12 plots were evaluated in mixed deciduous forests (DECI) and coniferous secondary forests (CON), respectively (Figure 1).

Within each randomly selected area, we established five subplots in a cross design: one central subplot (circular in shape, with a 3 m radius, and 28 m² in area) and four subplots of the same size at distances of 50 m to the north, south, east, and west directions; thus there were 44 cross designs, with a total of 220 subplots.

The Londo scale [38] was used to record the abundance of rooted vascular species from all vegetation layers, and their presence was registered in three spatial layers (tree, shrub, and herbaceous) in all cross designs and within each forest type.

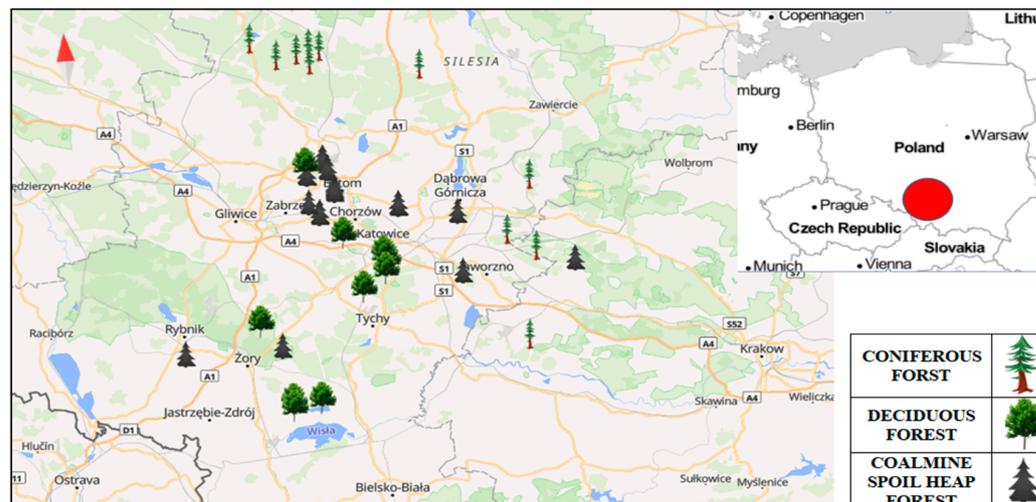


Figure 1. Coal mine study area in Upper Silesia and the locations of the plots in coniferous forest, deciduous forest, and coal mine spoil heap forest.

2.3. Soil/Substrate Sampling, Fieldwork, and Laboratory Analysis

Soil and substrate samples were collected from all of the studied plots from a depth of 0–20 cm for physical and chemical analyses. In each plot, soil and substrate samples were collected randomly from five points. Then, they were mixed together to provide a pooled sample for a given plot and used for estimating both water-holding capacity (WHC %), and soil/substrate fine particles ($PM < 2.0$). The rest were kept in a cold storage room at minus 20 °C for further physical and chemical analyses.

Samples were weighed and dried in an oven at 105 °C for 24 h before submerging them in water overnight. Samples were allowed to drain, then weighed again and the WHC percentage was calculated as:

$$WHC\% = (\text{Saturated weight} - \text{dried weight}) \div \text{saturated weight} \times 100$$

To estimate the soils granulometric composition, the substrate from the post-coal mine heap forests and soil samples from CON and DECI forests were sieved through a 2 mm sieve. The fine particles of the soil or substrate particles smaller than 2 mm were recorded as percentages.

The volumetric water content of the soil (SWC) and substrate temperature (St) were measured along with the soil respiration (Sr). The Delta-T HH2 moisture metre (Delta-T Devices, Cambridge, UK) was used to estimate the soil water content from the 0–20-cm layer. The temperature of the soil was taken using a DT1 Z thermometer from a depth of 0–20 centimetres.

The pH of the soil was measured after 24 h of equilibration in a 1:2.5 substrate/distilled water ratio using a glass electrode. Electrical conductivity (EC) was measured in a 1:5 substrate/distilled water ratio. Total carbon (TC) content was determined by the Turin method modified by Simakov [39] and total N (TN) by the Kjeldahl method [40]. Available forms of P, K, Ca and Mg were extracted with Mehlich-3 solution (1:10 soil/solution ratio) [41], followed by the spectrophotometric method for P determination, flame photometry method for K and Ca, and atomic absorption spectrometry (AAS) method for Mg. Na was extracted with 1 M ammonium acetate at pH 7.0 and determined using AAS [42].

2.4. Measurement of the Soil/Substrate Respiration (Sr)

The CO₂ efflux was recorded in situ using a SRC-2 cylinder chamber linked to the portable photosynthesis (PP) TARGAS-1 system (Amesbury, MA, USA). The PP system uses Auto-Zero to adapt to the surrounding conditions and to sustain the impulse of the CO₂, enabling an accurate, precise, and robust measurement from 78 cm² of the substrate

surface which was attached to the chamber. The TARGAS-1 records the efflux of carbon dioxide in milligrams of CO₂ released from each square metre within one hour (mg/h/m²).

2.5. Plant Functional Traits

A number of plant traits with significant ecological associations were collected for the calculation of functional indices to investigate the dispersal, competition, and colonisation ability of species on post-coal mine spoil heaps. These traits include the broad categories of plant life history, leaf morphology, and reproductive characteristics (Table 1). The data on traits were acquired from LEDA [43], BIEN [44], Pladias [45], BioFlor [46], and the TRY Global Plant Traits Database [47], and were stored in a new database [48].

Table 1. Functional traits and life-history characteristics of plant species recorded within the study plots.

Plant Traits	Code	Data Type	Unit	Mean Value	(Min.–Max.)
Specific Leaf Area	SLA	Numerical	mm ² mg ⁻¹	3.09	2.28–4.08
Leaf Mass	LeafMass	Numerical	mg	4.48	2.67–5.61
Leaf Area	LeafArea	Numerical	mm ²	7.42	5.63–8.54
Seed Mass	SeedMass	Numerical	mg	2.60	0.18–6.44
Canopy Height	CanopyHeight	Numerical	m	1.36	0.33–3.42
Lateral Spread	LateralSpread	Numerical	m/y	0.03	0.00–0.12
Functional Group	FG	Categorical	Four categories: Trees, Legumes, Graminoids, Herbs		
Life Span	Life_span	Categorical	Three categories: Perennial, Biennial, Annual		
Origin of Species	Alien_stat	Categorical	Two categories: Native, Alien		
Life Form	Life_form	Categorical	Six categories: Megaphanerophytes, Nanophanerophytes, Hemicryptophyte, Chamaephytes, Geophytes, Therophytes		
Dispersal Mode	Dispersal_Mode	Categorical	Seven categories: Allium, Cornus, Bidens, Lycopodium, Phragmites, Epilobium, Sparganium		

The content of dry matter in leaves (LDMC) and specific leaf area (SLA) can be used to check the status of the species economic leaf spectrum [49]. Plants produce leaves lower in SLA to tolerate the harsh abiotic stress of the rock waste material on the post-coal mine spoil heaps [49]. Canopy height (CanopyHeight) is related to plant competition ability [50]. The seed mass (SeedMass) explains the ability of a plant species to colonise and survive; species have a lower seed mass when found on post-coal mine spoil heaps which are younger in age and a higher seed mass when associated with older forests [51]. As some species colonising coal mine heaps can be clonal plants, we included lateral spreading distance, which was estimated in categories (<0.01 m, 0.01–0.25 m, >0.25 m) according to Klimeš and Klimešová [52,53].

For plants occurring in the sample plots, we used the dispersal strategies suggested by Sádlo and coworkers [54]. To estimate the contribution of native versus alien species in the floristic composition of the vegetation in managed versus spontaneously developed forests on post-coal mine heaps we divided species into neophytes (kenophytes), and archaeophytes as well as native species [55,56]. To present the persistence of species during spontaneous succession, we used life form types (M—Megaphanerophytes; N—Nanophanerophytes; H—Hemicryptophytes; C—Chamaephytes; G—Geophytes; T—Terophytes).

To study the functional traits, only species from the herbaceous understory layer with a significant presence were included, and we excluded from the analysis those that were present in less than 5 of the total 44 forest plots.

2.6. Data Analysis

The classification of forest sample plots was performed using hierarchical cluster Dendrograms in the vegan package in R software (R Core Team, 2022, ver. 4.2.2) based on the overall plant community composition, and following the dissimilarity among all

plots and all forest types. Plots were treated separately as single clusters, and the Euclidean distance of each pair was computed to merge the most similar clusters. To compute the agglomerative hierarchical clustering of the dataset, the R function *agnes* in the cluster package (version 2.1.6) was used. The Ward.D Method, with 85% strength and the complete linkage method with 55% strength were compared using the *entanglement function*.

To ordinate all samples, a detrended correspondence analysis (DCA) biplot [57] was constructed. The *vegan::envfit* function in R software was used to indicate the direction of diversity indices, functional indices, and the community-weighted means (CWMs) along the gradient. The *vegan* package [58] was also used to obtain taxonomic alpha diversity indices (H'—Shannon–Wiener index, S—Species richness, E—Evenness), while the dominance ($0 < D \leq 1$) Simpson index was calculated using the function *dominance* in the *{abdiv}* package (version 0.2.0).

Traits with a wide range were log-transferred, then we computed the CWM [59] for functional traits (Table 1) and calculated the functional diversity indices (FD) [60] for species that occurred in more than 5 plots of the total plots across all analysed vegetation patches.

The FD package [61] was used to quantify and calculate functional diversity based on the species functional traits: FRic, FDis, FDiv, FEve, and RaoQ entropy. We quantified the functional diversity components: functional richness (FRic), which expressed the quantity of plant functional types present in a community; functional dispersion (FDis), which expressed the size of community species trait hyper-volumes within the functional trait space; functional divergence (FDiv), which expresses the level of trait convergence/divergence; and functional evenness (FEve), which expresses the distribution of trait values within a community [60,62].

Canonical correspondence analysis (CCA) was used to show relationships between the floristic composition of the vegetation and the environmental variables. The normality of the sample distribution within each group was tested using the Shapiro–Wilk multivariate normality test [63], while the comparison of independent variables was conducted by linear models with permutation tests in the *{lmPerm}* package [64], and the Kruskal–Wallis test was used to check significant differences among all habitats for variables that failed to meet the ANOVA assumption of normality.

The Pearson correlation coefficient was used to characterise relationships among variables [65]. Significance was assessed via a permutation test with 999 iterations.

3. Results

3.1. Classification of the Forest Vegetation Patches

Results of hierarchical cluster analysis, based on the floristic criteria, distinguished three types of forests: coniferous managed (CON) forests, deciduous mixed (DECI) forests, and forests which have spontaneously developed on post-coal mine spoil heaps (HF). The average silhouette method suggested that three groups were the optimal number of clusters (Figure 2b). All four clustering methods were used; the Ward.D Method with 85% strength and Complete Linkage with 55% strength were compared using the entanglement function. Unique nodes with plots not matching the other tree (dashed lines) were only found within the same forest type (Figure 2a), and both methods separated the three forests. The entanglement coefficients for both methods were low (0.06), indicating a very good alignment.

The cluster CON was mostly dominated by *Pinus sylvestris* (63%) > *Vaccinium myrtillus* (26%) > *V. vitis-idaea* (11%). The mixed forest DECI cluster was dominated by *Quercus robur* (31%) > *Carex brizoides* (21%) > *Fagus sylvatica* (18%). The heap forests (HF) were more mixed with some significant coverage representatives: *Betula pendula* (19%) > *Robinia pseudoacacia* (17%) > *Acer pseudoplatanus* (11%) > *Tilia cordata* (10%) > *Populus tremula* (6%) > *Impatiens parviflora* (5%) (Table A1).

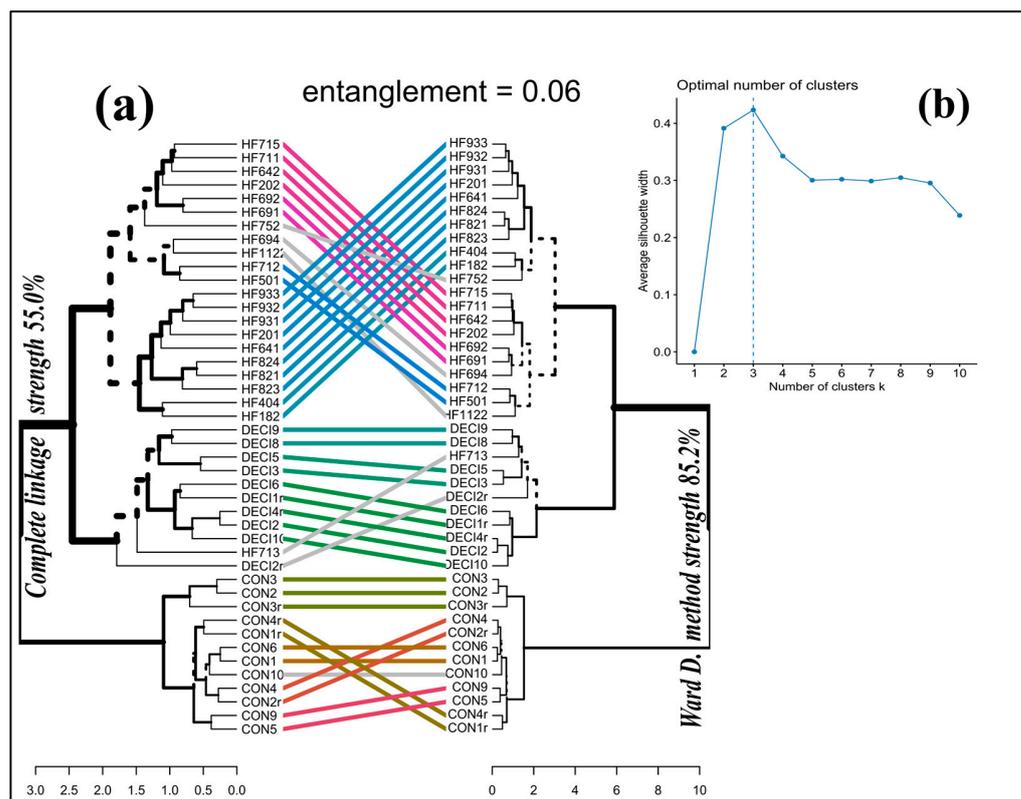


Figure 2. Hierarchical clustering of all forests based on community plant composition. (a) Dendrograms: Complete Linkage Method (left) versus Ward's Method (right). (b) Average silhouette method for optimal number of clusters.

3.2. Alpha Diversity

The dissimilarity analysis divided all the studied forests into three groups: deciduous forest (DECI), coniferous forest (CON) and heap forest (HP). In the mixed deciduous forests (DECI), the most frequent canopy-dominant tree species were *Q. robur* and *F. sylvatica*. The CON forest group was characterised by *P. sylvestris* as the diagnostic species. The heap forests formed a distinct group; the floristic composition of patches included ruderal species (*Erigeron annuus*, *Picris hieracioides*, *Tussilago farfara*, *Urtica dioica*, *Verbascum thapsus*), meadow species (*Daucus carota*, *Poa pratensis*), grassland species (*Coronilla varia*, *Poa compressa*), and forest species (*A. pseudoplatanus*, *Fraxinus excelsior*).

The DCA ordination separated the three types of forests with a qualitative test of all thirteen variables related to plant diversity and functional traits, and emphasised significant differences between the forests, except for the evenness, functional divergence, and functional evenness indices, which are not shown in the DCA biplot (Figure 3).

3.3. Taxonomic and Functional Diversity

The qualitative test to compare the species diversity of the analysed groups, performed by using different diversity measurements, revealed significant differences. A higher species richness (on average 36 species) was detected in the heap forest plots (HF) than in mixed forests (DECI) (22 species) and was double that of coniferous forest (CON) plots (18 species). Significant differences were recorded for species diversity using the Shannon–Wiener (H') and evenness (E) indices. These values were higher in HF (2.7 and 0.76, respectively) compared with both DECI (1.9 and 0.62, respectively) and CON forests (2.0 and 0.71, respectively). The dominance index was the lowest (0.12) in HF, (0.25) in DECI, and (0.21) in CON (Figure 4).

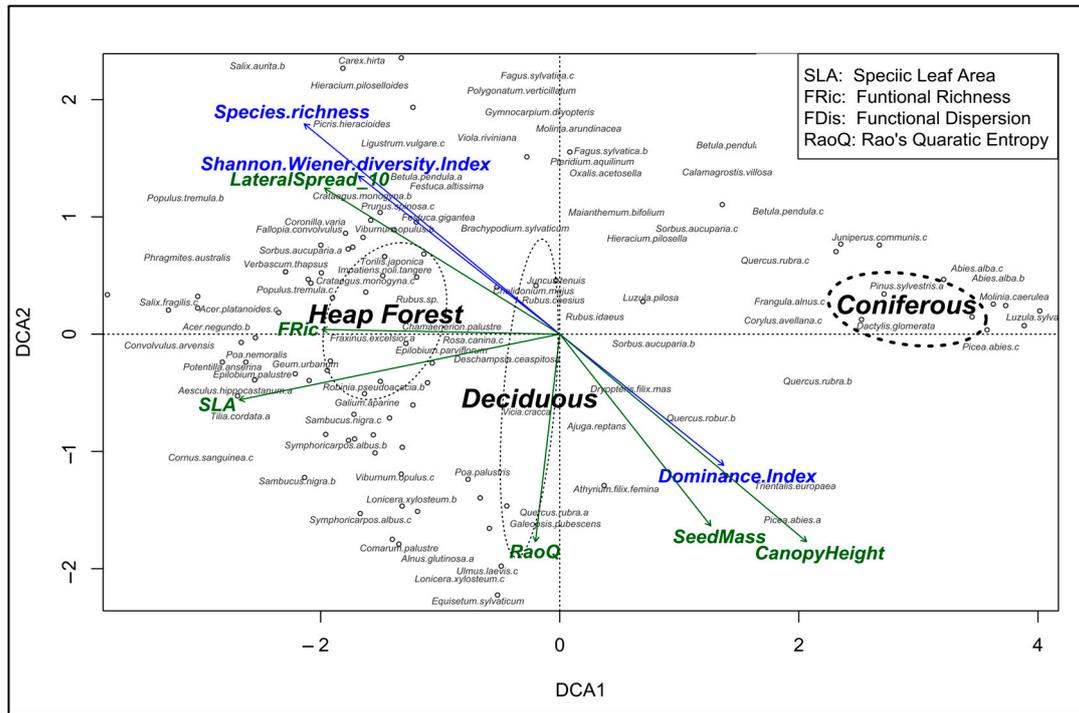


Figure 3. DCA biplot displaying the correspondence between all samples and species in the DCA ordination space.

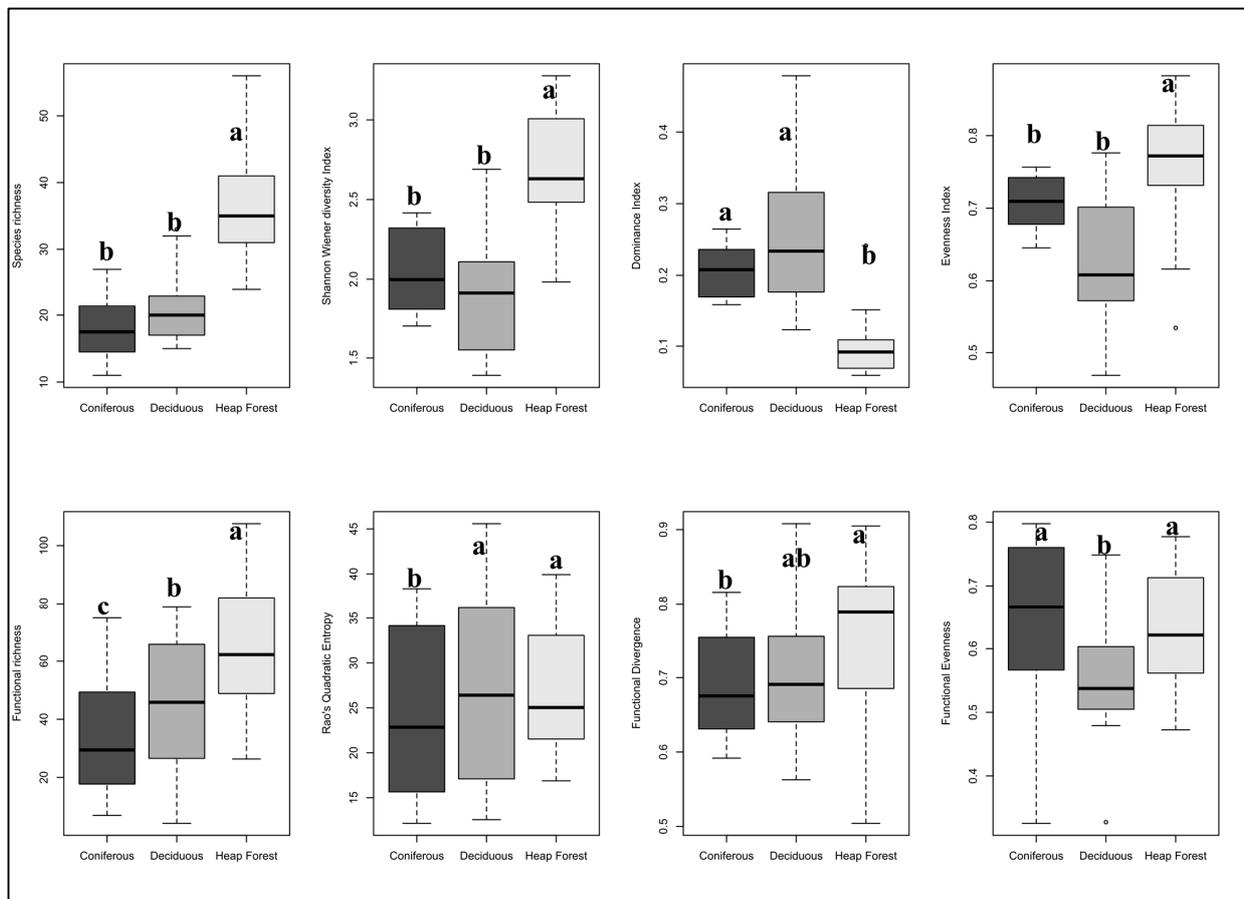


Figure 4. Comparison of the mean values \pm std between different forests; taxonomic diversity indices (1st row) and functional diversity indices (2nd row). Different letters mark significant differences.

The quantitative comparison of environmental factors determined significant differences of most variables between the forests. Heap forests were characterised by a remarkably higher portion of fine particles (PM < 2.0 mm), pH, calcium, potassium, and magnesium (Table 2). Deciduous forests were higher in water-holding capacity, soil water content, total nitrogen, and soil respiration. The coniferous forest plots experienced the highest soil temperature, while factors such as soil organic matter, electrical conductivity, sodium, and phosphorus did not reach significant levels statistically despite differences among the forest types (Table 2).

Table 2. One-way ANOVA results for different environmental parameters in the three different forests; Df is 2. Variables that failed to meet the ANOVA assumption were tested by the Kruskal–Wallis test (with asterisks). Different letters mark significant differences.

		Coniferous Forest	Deciduous Forest	Heap Forest	$p < 0.05$
Soil Parameters	Substrate Water Content	16.9 ^b ± 2.7	33.4 ^a ± 7.1	21.8 ^b ± 10	1.5 × 10 ⁻⁴ *
	Water-Holding Capacity	0.16 ^c ± 0.06	0.39 ^a ± 0.05	0.33 ^b ± 0.04	2.5 × 10 ⁻¹³
	Fine Particles (PM < 2.0)	0.38 ^a ± 0.09	0.51 ^b ± 0.10	0.58 ^c ± 0.10	3.1 × 10 ⁻⁸
	Substrate Temperature	14.77 ^a ± 1	12.70 ^b ± 1.4	10.64 ^c ± 1.4	0.050 *
	Soil Organic Matter%	9.56 ± 4	10.5 ± 3	12.2 ± 5	0.3069 ns
	pH	5.92 ^c ± 0.1	6.07 ^b ± 0.1	6.26 ^a ± 0.1	2.2 × 10 ⁻¹³
	Electrical Conductivity	5.33 ± 0.5	5.39 ± 0.2	5.52 ± 0.5	0.4666 ns
	Sodium ppm	20.47 ± 4	21.69 ± 4	20.19 ± 4	0.6296 ns
	Calcium ppm	324 ^b ± 173	357 ^b ± 250	1974 ^a ± 961	1.1 × 10 ⁻⁸
	Potassium ppm	85 ^c ± 25	149 ^b ± 43	215 ^a ± 55	5.9 × 10 ⁻⁹
	Phosphorus ppm	36.1 ± 9	32.5 ± 5	30.6 ± 5	0.2125464 ns
	Magnesium ppm	30 ^c ± 10	50 ^b ± 20	172 ^a ± 48	2.4 × 10 ⁻¹⁴
	Total Nitrogen%	0.37 ^b ± 0.1	0.60 ^a ± 0.2	0.50 ^a ± 0.2	0.01463
Soil Respiration (mg CO ₂ /h/m ²)	0.90 ^b ± 0.11	0.96 ^a ± 0.27	0.76 ^c ± 0.30	0.0272	

p values with ns are not significant.

As a proxy of the ecosystem function, the substrate respiration (Sr) rate was the lowest (0.76 mg-CO₂ per hour per square metre) in HF forests, followed by CON and DECI forests (0.90 and 0.96 mg-CO₂ per hour per square metre, respectively) (Table 2).

Functional diversity indices calculated for plant traits (plant life history, leaf morphology, and reproductive characteristics) showed some interesting outcomes, such as higher functional richness (FRic) and functional divergence (FDiv) in HF forests. FRic (65.8) of HF plots was much higher than in DECI (44.3) and two folds higher than in CON (35.0), in addition to a higher FDiv (0.76) than in DECI (0.71) and CON forests (0.69), respectively. Much higher specific leaf area (3.35) and lateral spread (0.055) occurred in heap forests, compared to CON (2.68 and 0.007, respectively) and DECI (2.99 and 0.017, respectively) plots (Table 3).

Rao's quadratic entropy (RaoQ) and functional dispersion (FD) showed the same trend of being higher in HF (26.9 and 4.6, respectively) and in DECI (27.3 and 4.5, respectively) forests compared to those in CON forests (24.5 and 4.4, respectively), without reaching statistically significant levels (Table 3).

The CCA ordination revealed the relationship between the distributions of the species in the ordination hyperspace, as affected by the habitat factors. All substrate parameters explained 20.10% of the total variance. Significant environmental factors at alpha level ($p \leq 0.001$) were PM < 2.0, WHC, SWC, St, Mg, K, Ca, and pH, while the nitrogen content was significant at alpha level ($p \leq 0.01$). Differences in soil organic matter, electrical conductivity, sodium, and phosphorus within the habitats were not significant statistically and not shown in Figure 5. Higher concentrations of soil elements such as potassium, magnesium, and calcium with higher pH values, were recorded from heap forests, although higher soil organic matter in heap forests did not reach significant levels. Much higher

fine particle fraction and higher soil temperature were related to the coniferous forests (Figure 5).

Table 3. One-way ANOVA results for different taxonomic diversity, functional diversity indices, and community-weighted mean (CWM) plant traits in the three different forest types; Df is 2. Variables that failed to meet the ANOVA assumptions were tested by the Kruskal–Wallis test (with asterisks). Different letters mark significant differences.

		Coniferous Forest	Deciduous Forest	Heap Forest	<i>p</i> < 0.05
Taxonomic and Functional Indices	Species Richness	18.3 ^b ± 5	21.6 ^b ± 6	36.0 ^a ± 8	9.9 × 10 ⁻⁹
	Shannon–Wiener Index	2.03 ^b ± 0.3	1.90 ^b ± 0.4	2.71 ^a ± 0.3	4.5 × 10 ⁻⁸
	Dominance Index	0.21 ^a ± 0.04	0.25 ^a ± 0.10	0.12 ^b ± 0.05	2.3 × 10 ⁻⁶ *
	Evenness Index	0.71 ^b ± 0.04	0.62 ^b ± 0.09	0.76 ^a ± 0.07	0.0001209
	Functional Evenness	0.65 ^a ± 0.13	0.55 ^b ± 0.11	0.63 ^a ± 0.08	0.059 ns
	Functional Divergence	0.69 ^b ± 0.07	0.71 ^{ab} ± 0.10	0.76 ^a ± 0.09	0.058 ns
	Functional Dispersion	4.4 ^a ± 0.02	4.5 ^a ± 0.05	4.6 ^a ± 0.02	0.67 ns
	Functional Richness	35.0 ^b ± 21	44.3 ^b ± 25	65.8 ^a ± 21	0.026 *
Rao’s Quadratic Entropy	24.5 ^a ± 9	27.3 ^a ± 11	26.9 ^a ± 7	0.62 ns	
CWM Traits	Specific Leaf Area	2.68 ^c ± 0.2	2.99 ^b ± 0.2	3.35 ^a ± 0.3	1.5 × 10 ⁻⁶ *
	Seed Mass	3.6 ^a ± 2	4.4 ^a ± 2	1.2 ^b ± 1	9.6 × 10 ⁻⁵ *
	Canopy Height	2.4 ^a ± 1	2.3 ^a ± 0	0.4 ^b ± 0	7.4 × 10 ⁻⁷ *
	Lateral Spread 0_10	0.007 ^b ± 0.01	0.017 ^b ± 0.01	0.055 ^a ± 0.03	9.1 × 10 ⁻⁶ *
	Leaf Area	6.8 ^c ± 0.6	7.9 ^a ± 0.4	7.5 ^b ± 0.5	1.0 × 10 ⁻⁵ *
	Leaf Mass	4.30 ^b ± 0.4	4.93 ^a ± 0.3	4.37 ^b ± 0.6	4.2 × 10 ⁻³ *

p values with ns are not significant.

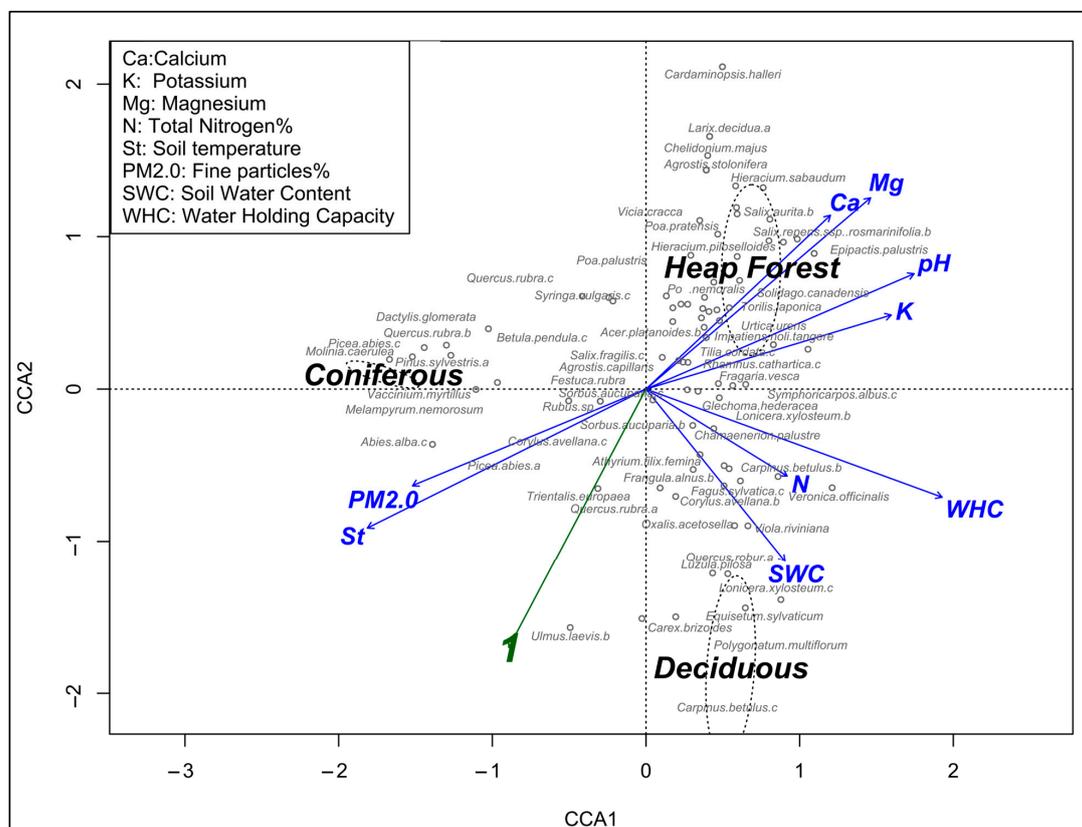


Figure 5. The CCA ordination biplot of forest samples illustrates the significant impact of substrate parameters on species composition. Only significant elements are shown. Soil respiration is not constrained (green arrow).

3.4. Correlation between Variables

Soil respiration was positively correlated with substrate temperature (St; $r = 0.39^{**}$) and negatively correlated with species richness (S; $r = -0.35^*$), with no effect of soil water content on soil respiration (SWC; $r = -0.02$ ns). The positive relationship ($r = 0.41^{**}$) between WHC and SWC was expected; the higher the capacity of the substrate to hold water, the higher the substrate water content. The positive correlation between the soil respiration and the fine particle rate (PM < 2.0; $r = 0.27$ ns) did not reach significant levels statistically (Figure 6).

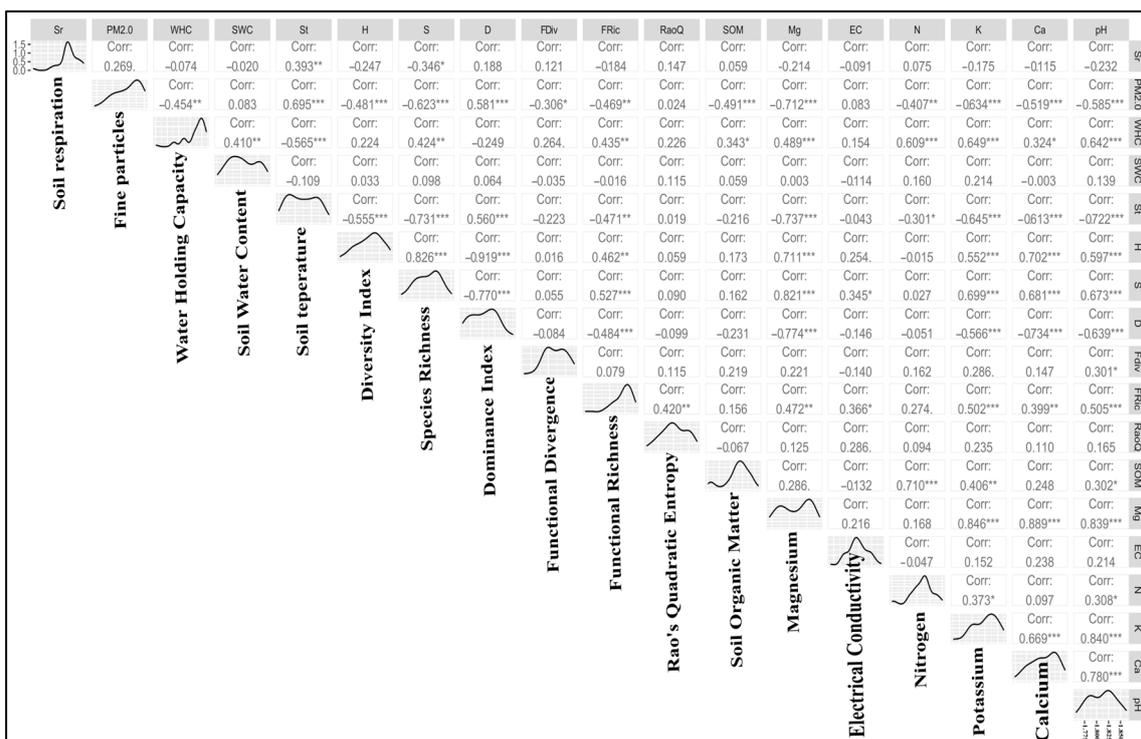


Figure 6. Correlation matrix for environmental variables and diversity measures. Asterisks indicate the significance levels (* = $p < 0.05$, ** = $p < 0.001$, *** = $p < 0.0001$). Minus indicates a negative direction of the relationship between each pair of variables.

Functional richness (FRic) was found to be the functional diversity index that most strongly and positively correlated with species richness (S; $r = 0.53^{***}$), the Shannon–Wiener index (H'; $r = 0.46^{**}$), and water-holding capacity (WHC; $r = 0.44^{**}$), and negatively (St; $r = -0.47^{**}$) correlated with soil temperature, as well as with fine particles (PM < 2.0; $r = -0.47^{**}$) (Figure 6).

The negative correlation between the substrate temperature (St; $r = -0.73^{***}$) and the species richness does not imply causation; the temperature of the rock mineral substrate changes faster due to its high thermal conductivity compared to forest soil, which can lower the temperature with no great difference in depth (Figure 6).

The first two axes of the PCA explained 36.9% and 12.2% of the total variance, respectively (Figure 7). The first axis was correlated with Shannon–Wiener diversity index (H), species richness (S), functional richness (FRic), LateralSpread_10, and specific leaf area (SLA) as the greatest constraints on the system, and to a lesser extent it was also constrained by the life form “Herb” and the dispersal strategy “Allium”. These features of heap forests were opposite to those of coniferous forests, which were characterised by higher canopy and mass, more dominant species, tree life forms, and the Cornus seed dispersal strategy, which correlated positively along the first axis. Rao’s quadratic entropy, functional dispersion (FDis) and functional evenness (FEve) were correlated with the second axis and were higher in both heap forests and deciduous mixed forests (Figure 7).

Sokolov (Czech Republic) and *B. pendula* dominated the recent unreclaimed habitats [73]. On opencast brown coal heaps in Bełchatów (Poland) the tree stands established as a result of the reclamation activity on the heaps and were composed of a mixture of tree species: *B. pendula*, *A. glutinosa*, *P. sylvestris*, and *R. pseudoacacia* [74,75].

Spontaneously generated young forests, with short histories, are characterised by vegetation patches that are species-poor, usually with low herb-layer abundance, few woodland species, and a higher contribution of woodland *anemochorous* species, while the woodland *endozoochory* species have a smaller contribution [76,77]. In young forests, the participation of slow coloniser species, including geophytes, *endozoochores*, and *myrmecochores*, was found to be negatively correlated with distance from the ancient forest [78,79]. In addition to the distance from old forests, the area of the coal mine spoil heap seems to play an important role in its species diversity and species richness [80].

4.2. Functional Diversity in the Studied Forests

With regard to functional diversity, it has been reported that high taxonomic diversity yields high functional diversity [81,82]. In our results, forests developed on post-coal mine heaps were higher in species number, species diversity, evenness index, functional richness, and functional divergence. Buzzard et al. [83] studied revegetation models in tropical dry forests and assumed that the observed directional shift in CWM trait values was in line with the “productivity filtering” hypothesis, where a directional shift in water and light availability shifts physiological strategies from “slow” to “fast”. This was explained by the fact that the trade-off changes are caused by forces responsible for growth vs. survival, consequently reflecting the resource acquisition and resource conservation trade-off [84,85].

The trait-based approach should reveal which of the traits from the “fast–slow” life-history strategy continuum will follow each other in time [83,86,87]. Some studies have stated that variation in traits shows the shifts between individuals with the “slow” strategy to traits useful for persisting under low-nutrient conditions and competitive “fast” growing strategies by acquiring available resources [88–90]. The characteristics of water deficiency, lack of or poorly developed substrate/soil, and high microhabitat variation in forests developed on coal mine spoil heaps have shaped the species composition by filtering species to a subset with physiological abilities to tolerate low nutrient availability and water stress. Theoretically, these habitat constraints might cause reduction of functional trait dispersion. Differences in values of community-weighted mean traits would support Grime’s “productivity filtering” hypothesis. The species trait composition characterised by higher leaf dry matter concentration, lower SLA, higher C:N ratio and leaf phosphorus concentration values can imply drought tolerant “slow” growth strategies and low decomposability [91–96].

In our study, the SLA values were higher in forests developed on coal mine heaps compared with deciduous forests, which, in turn, had higher SLA than in coniferous forests; the only explanation could be the abundance of *B. pendula* [97] and the alien *R. pseudoacacia*. Fast-growing and highly productive plants are mostly characterised by higher specific leaf area, higher phosphorus concentration, and a lower dry matter and carbon/nitrogen ratio in leaves [98]. There are studies that have reported that the availability of resources such as nutrients, water and light, affects the composition of species traits [99,100]. One study reported the over dispersion of traits due to biotic stressors [101].

4.3. Environmental Relevance of Plant Traits in Novel and Managed Forests

The post-coal mine heap forests can be considered as newly established forests, and the process of their development is similar to the forest succession developed in post-agricultural areas, so that the patterns of development could be similar. The recent forests in Europe are characterised by higher light availability, higher pH and nutrient levels [102–104]. The species that constitute the group of post-coal mine heap forests are mostly ruderal species and had higher lateral spread and dispersal via *autochory* (self-driven seed dispersal species), as was confirmed by the results of a previous study [66] carried

out in the same region. Similar results have also been obtained in studies which made a comparison between ancient and recent forests [77,105]. In addition to its high spatial variability in living conditions for organisms, the substrate of post-coal mine heaps is characterised by rapidly changing water and nutrient contents [106]. Therefore, the colonisation of the new diaspores on coal mine spoil heaps is mostly affected by the rock waste mineral substrate [73]. Under harsh environmental conditions of heap substrates, the biomass of young Scots pine stands significantly differed from non-stressed stands in the Bełchatów Forest District, Poland [107].

4.4. Invasive Plants and the Novel Forests of Post-Coal Mine Heaps

In forests developed on post-coal mine spoil heaps, indigenous plant species were the most frequent and abundant in the plant community species composition, with higher alien species abundance than in other forests, supporting results were obtained by Kowarik [108] and Tischew and Lorenz [109]. In post-industrial habitats, these authors reported an important role of exotic plant species in the forest succession process. Alien species that were found in the heap forests in our study were mostly ruderal species with a self-dispersal mode (*Allium* strategy), in comparison to the CON and DECI mixed forests (Figure 7). This was in line with the results of Woźniak et al. [66], who found that forests developed on post-coal mine heaps had a lower contribution of ancient forest indicator species and more wind-dispersed and ruderal species; such patterns were also described by Dzwonko and Gawroński [77], and Bossuyt et al. [105]. The spread of the alien *Buddleja davidii* in the early successional forests in the Ruhr industrial region of Germany has been recorded as forests dominated by *B. pendula* [110]. This work also stated that invasive alien species are frequent in post-coal mine heap forests in the Ruhr area. *Q. rubra*, *Padus serotina*, and *R. pseudoacacia* can change the shrub-layer diversity and the ecosystem services of the forest. In Upper Silesia, *R. pseudoacacia*, *P. sylvestris*, and some mixtures of trees (*P. tremula*, *Alnus glutinosa*, *B. pendula*) are the most frequent in the tree/shrub layer of forests developed on post-coal mine heaps.

The frequent presence of alien species can pose a serious threat to the composition of the herb layer [111,112] or can alter some properties of the habitat, such as soil chemistry and the activity of soil bacteria [113]. Higher seed introduction effort and higher seedling survival were crucial factors in the invasion process in permanent field trials [56,111]. In such de novo created novel forests, the local expansive species (*Calamagrostis epigejos*, *C. brizoides*) are more persistent. In the species composition of the herb layer of young forests, a single plant species might become a competitive dominant that suppresses other species and consequently reduces species diversity; examples that have been recorded doing this include *C. brizoides* [77,114], and *C. epigejos* [73,115]. The further risk of spread of such expansive individuals will be greater when they colonise disturbed sites in urban industrial areas.

4.5. Soil Respiration in the Heap Forests versus Managed and Mixed Deciduous Forest Types

Moisture fluctuation, high thermal conductivity, and low nutrient levels are the main characteristics of the waste rock substrate of forests developed on post-coal mine heaps [116]. Occasionally, higher levels of nutrients are possible in the substrate of a heap forest, but the poorly developed or lack of a soil profile disturbs the balance of the organic matter deposited under the canopy of tree stands and affects the process of mineralisation [106,117,118]. Higher calcium and potassium contents, and to a lesser extent high nitrogen in heap forests were mainly due to the release of such elements from the organic matter decomposition, and this resulted in higher pH; in particular, calcium had the greatest effect on the pH of the substrate. Low levels of salts were observed in all forest types; this was expected in coniferous and deciduous forests; in the heap forests, when the rock waste is first disposed of, the salt concentration is high, but over time the salt is washed out, consequently decreasing the electrical conductivity in heap forests too.

The steep increase in soil respiration in summer in irrigated lands is due to temperature increase [32], accompanied by an increase in soil humidity within the field capacity range. Thus, diurnal changes in soil respiration are lower compared with seasonal shifts. Although the bulk of soil respiration in forests with different species and climatic regions shows a poor correlation with temperature, it seems that both soil respiration rates and Q_{10} values of mixed forests exceed those of coniferous managed forests. We recorded higher soil respiration in deciduous mixed forests compared with coniferous forests, supporting the findings of the aforementioned study. Less soil respiration despite higher organic matter is due to the lower substrate temperature in coal mine spoil heap forests, and this trend is clearly evidenced by the negative relationship between soil respiration and soil temperature. This observation follows the more pronounced effects of temperature on deciduous forests' growth found in the study by Ryan [119] but not by Way and Oren [120].

Despite the fact that the waste rock of the coal mine spoil heaps is an inert substrate and different from the soil in natural and semi-natural forests, both WHC and SWC were positively correlated with the particle size of the substrate and the soil. Despite the spatial and temporal variation in terrestrial habitats, both anaerobic and aerobic pathways contribute to the total respiration in soil, with more steady rates from soil organic carbon (SOC) mineralisation [121].

5. Conclusions

Unexpectedly, forests developed on post-coal mine spoil heaps were higher in species and functional diversity. This study revealed a higher functional richness and functional divergence in forests developed on post-coal mine heaps, indicating their higher resilience to environmental changes and increasing ecosystem function due to more efficient resource use by the species present. The well-known relationship between species diversity and ecosystem function was assessed in our study by respiration intensity measurements. Lower carbon release from the forests developed on post-coal mine spoil heaps was due to low levels of substrate organic matter and less water content. Investigating the earlier stages of spontaneous vegetation succession, from initial colonisation to fully developed forests, by taking into account the age and area of the spoil heaps, will better aid our understanding of the complex successional processes in these newly established novel forest ecosystems.

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Appendix A

Table A1. List of the most characteristic species found in each habitat and their respective abundances within the different vegetation layers and different growth types.

		A Layer%	B Layer%	C Layer%	Total%
Coniferous	<i>Pinus sylvestris</i>	58	2.75	1.8	63
	<i>Vaccinium myrtillus</i>				26
	<i>V. vitis-idaea</i>				11.5
Deciduous	<i>Quercus robur</i>	27.8	04	3	31
	<i>Carex brizoides</i>				21.3
	<i>Fagus sylvatica</i>	14	3	1	18
Heap Forest	<i>Betula pendula</i>	17.8	1.5	0.33	19
	<i>Robinia pseudoacacia</i>	14.6	2.32	0.25	17
	<i>Acer pseudoplatanus</i>	6.68	3.4	1.2	11
	<i>Tilia cordata</i>	6.68	2.6	0.91	10
	<i>Populus tremula</i>	5.56		0.26	5.82
	<i>Impatiens parviflora</i>				5.37

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