### Institute of Dendrology, Polish Academy of Sciences



### MSc Quadri Agbolade Anibaba

### Ecosystem diversity along a successional gradient of post-mining spoil heaps

Zróżnicowanie ekosystemów w gradiencie sukcesyjnym zwałowisk pogórniczych

Doctoral dissertation in the field of natural sciences in the discipline of biological sciences

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> > Supervisor: prof. dr hab. inż. Andrzej M. Jagodziński Auxiliary supervisor: dr hab. inż. Marcin K. Dyderski

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### List of publications constituting the doctoral dissertation

The research results have been published in the following scientific articles:

- Anibaba, Q. A., Dyderski, M. K., Woźniak, G., & Jagodziński, A. M. (2023). Native plant community characteristics explain alien species success in post-industrial vegetation. *NeoBiota*, 85, 1-22. <u>https://doi.org/10.3897/neobiota.85.97269</u>
- 2. Anibaba, Q. A., Dyderski, M. K., Woźniak, G., & Jagodziński, A. M. (2024). The inhibitory tendency of *Calamagrostis epigejos* and *Solidago spp.* depends on the successional stage in post-industrial vegetation. *Land Degradation and Development*. https://doi.org/10.1002/ldr.5348
- **3.** Anibaba, Q. A., Dyderski, M. K., Woźniak, G., & Jagodziński, A. M. (2024). Remote sensing for site selection in vegetation survey along a successional gradient. *Ecology and Evolution*, 14, e70200. <u>https://doi.org/10.1002/ece3.70200</u>

### **Abstract (in English)**

The advantages of spontaneous vegetation as an approach for the restoration of post-coalmining spoil heaps are enormous due to its economic, and conservation importance. However, spontaneously revegetated spoil heaps are faced with the problem of alien species, successional inhibitors, and the need for a robust measure in the assessment of restoration success. The dissertation aimed to investigate the vegetation diversity in post-mining areas and to assess the role of alien species and successional inhibitors in spontaneously vegetated spoil heaps. To achieve this aim, the following hypotheses were tested: H1: Native community characteristics will explain alien species invasion level (alien richness) and ecological success (alien cover) on spontaneously vegetated post-coal mine heaps (Publication 1); H2: The inhibitory effect of invasive alien and expansive native species on diversity will depend on the successional stage (Publication 2); H3: Diversity, functional and phylogenetic distinctiveness of ecosystems will increase along successional gradients (Publication 3). The main results showed that native community characteristics drive alien species invasion level and ecological success. Alien species cover decreased with native species cover. In contrast, alien species richness and cover increased with native functional richness. While community-weighted mean (CWM) of native species seed mass and plant height significantly predict alien species cover, native CWM of specific leaf area (SLA) marginally predicts alien species richness (Publication 1). The impact of *Calamagrostis epigejos* and *Solidago* spp. cover on diversity indices was strong in the midsuccessional stage. In the mid-successional stage, species richness and functional richness decreased significantly with the cover of Calamagrostis and Solidago. Shannon diversity marginally decreased while phylogenetic diversity marginally increased with the cover of *Calamagrostis*. Shannon diversity was negatively while phylogenetic diversity was positively correlated with the cover of Solidago (Publication 2). While species richness and Shannon diversity were significantly higher in the early- and mid-successional stages than in the latesuccessional stage, these response variables reached their maximum in the mid-successional stage, revealing an arch-shaped pattern. Late-successional vegetation had the lowest functional richness and highest functional dispersion, and phylogenetic diversity differed between successional stages (Publication 3). The study concluded that while the mid-successional stage hosts the largest species pool and diversity, it is also threatened by successional inhibitors. The dissertation highlights the significance of biotic interactions, especially competition in postcoal-mining areas; therefore increasing our understanding of ecological dynamics and context dependency, which are vital for the effective conservation and management of post-industrial areas.

### Streszczenie (in Polish)

Wykorzystanie spontanicznej sukcesji roślinności w rekultywacji hałd po wydobyciu węgla wiąże się z wieloma zaletami o charakterze ekonomicznym oraz ekologicznym. Z drugiej jednak strony hałdy pozostawione do spontanicznej sukcesji borykają się z problemem obecności gatunków nierodzimych oraz inhibitorów sukcesji. Co więcej, zastosowanie tej metody wymaga również opracowania ilościowych mierników oceny sukcesu rekultywacji. Celem dysertacji było określenie różnorodności biologicznej roślinności na terenach pokopalnianych oraz ocena wpływu gatunków obcych i rodzimych inhibitorów sukcesji na przebieg procesu sukcesji. Aby osiągnąć ten cel, przetestowano następujące hipotezy: H1: cechy funkcjonalne rodzimych komponentów zbiorowisk roślinnych wyjaśnią poziom inwazji gatunków obcych (liczba taksonów) i ich sukces ekologiczny (pokrycie; Publikacja 1); H2: Inhibicyjny wpływ inwazyjnych gatunków obcych oraz ekspansywnych rodzimych gatunków na różnorodność będzie zależał od wieku hałdy (Publikacja 2); H3: Różnorodność funkcjonalna i filogenetyczna badanych ekosystemów będą się różnicować wzdłuż gradientu sukcesji (Publikacja 3). Wykazano, że cechy rodzimych komponentów zbiorowisk roślinnych wpływają na poziom inwazji gatunków obcych i ich sukces ekologiczny. Pokrycie gatunków obcych malało wraz ze wzrostem pokrycia gatunków rodzimych, natomiast bogactwo i pokrycie gatunków obcych rosły wraz z bogactwem funkcjonalnym rodzimych gatunków. Podczas gdy masa nasion i wysokość roślin określone dla rodzimych komponentów roślinności były dobrymi predyktorami pokrycia gatunków obcych, specyficzna powierzchnia liści miała niewielki wpływ (Publikacja 1). Negatywny wpływ inhibitorów sukcesji na wskaźniki różnorodności był silnie zależny od etapu sukcesji na hałdach pokopalnianych. Wpływ pokrycia Calamagrostis epigejos i Solidago spp. na wskaźniki różnorodności był silny na pośrednim etapie sukcesji: liczba gatunków i bogactwo funkcjonalne znacząco malały wraz z pokryciem badanych gatunków. Różnorodność Shannona marginalnie malała, podczas gdy różnorodność filogenetyczna marginalnie rosła wraz z pokryciem Calamagrostis. Różnorodność Shannona była negatywnie, natomiast różnorodność filogenetyczna pozytywnie skorelowana z pokryciem Solidago (Publikacja 2). Bogactwo gatunkowe, różnorodność Shannona, bogactwo funkcjonalne, dyseprsja funkcjonalna oraz różnorodność filogenetyczna różniły się między stadiami sukcesji. Bogactwo gatunkowe i różnorodność Shannona były znacząco wyższe we wczesnych i średnich etapach sukcesji niż w późnym stadium, a średnie stadium sukcesji cechowało się maksymalnymi wartościami badanych wskaźników, wskazując na nieliniową zależność w czasie. Roślinność w późnym stadium sukcesji charakteryzowała się najniższym bogactwem funkcjonalnym i najwyższą dyspersją funkcjonalną, a różnorodność filogenetyczna różniła się między stadiami sukcesji (Publikacja 3). Z pracy wynika, że choć pośrednie stadium sukcesji cechuje najwyższe bogactwo i różnorodność gatunkowa, jest ono także najbardziej zagrożone przez inhibitory sukcesji. Praca podkreśla znaczenie interakcji biotycznych, zwłaszcza konkurencji, na terenach pokopalnianych, zwiększając tym samym nasze rozumienie dynamiki ekologicznej i zależności od kontekstu środowiskowego, które są kluczowe dla skutecznej ochrony i zarządzania terenami poprzemysłowymi.

### 1. Introduction

Globally, most ecosystems are confronted with unprecedented anthropogenic impacts (Chapin III *et al.* 2000; Steffen *et al.* 2015; Vitousek *et al.* 1997) with human activities at the forefront in modifying the types and rates of ecosystem change. The impacts have resulted in changes to species distributions and abiotic life conditions (Dyderski *et al.* 2018; Hanewinkel *et al.* 2013; Thuiller *et al.* 2011), and the emergence of novel ecosystems which are in contrast to natural ecosystems (Hobbs *et al.* 2006; Kowarik 2011; Prach 2003). These novel ecosystems have species compositions that have not occurred previously within a given biome due to varied anthropogenic local and global changes.

Aside from climate change, urbanization, and agricultural intensification, an important factor modifying ecosystem diversity is the industrial economy (Tropek *et al.* 2010), specifically mining. Mining activities have been identified as a key driver of ecosystem transformation (Hobbs *et al.* 2009; Walker 1999). Mining modifies the landscape and accounts for approximately 1% of the global land area (Maus *et al.* 2022). Across the world, the Russian Federation, China, Australia, the United States of America, and Indonesia are responsible for 11.6%, 10.2%, 8.4%, 8.1%, and 7.9% of global mining land use, respectively (Maus *et al.* 2022). Due to the impacts of mining land use on ecosystem diversity, there is a need to understand species interaction and how it can help restore post-mining areas to their natural functioning.

A significant proportion of post-mining areas consist of substrates of overburden materials deposited on spoil heaps. If allowed to undergo spontaneous succession, these spoil heaps are excellent experimental sites for research on the patterns of diversity including taxonomic, functional, and phylogenetic diversity of plant communities, roles of alien species in delaying the rate of succession, and species colonization processes. Furthermore, spoil heaps may provide refuges for ecologically important, rare, endangered, and sentinel species, thus, valuable sites for conservation (Prach *et al.* 2011; Tropek *et al.* 2010, 2012) and where primary succession occurs, a unique circumstance in present-day European landscapes.

Post-coal mining heaps are composed of mineral substrate low in nutrients, extreme pH, high salinity, adverse texture, and structure presenting extreme challenges for plant species colonization and the formation of stable ecosystems (Woźniak *et al.* 2021). Nevertheless, the few species that are tolerant to these conditions may form sparse vegetation cover, commencing the processes of primary succession (Prach 2013). Spontaneous primary succession on heaps formed from post-coal underground mining may begin from bare substrate materials with few

and scattered annual, biennial, and ruderal plant species usually lasting up to 10 years (Prach *et al.* 1993). Then the ruderals start to decline and species typical of grasslands start to spread, although ruderals may persist further, however decreasing their cover over time (Frouz *et al.* 2008). At the late phase of this replacement of ruderal by non-ruderal species, which coincides with significant changes in soil structure and soil biota, there is an expansion of shrubland which facilitates the encroachment of broadleaved forest (Badraghi *et al.* 2023; Prach & Pyšek 2001; Wiegleb & Felinks 2001) (**Figure 1**).

Alien species invasion is one of the major challenges in the restoration of post-industrial sites (Ekka & Behera 2011; Hapsari et al. 2020; Nsa et al. 2021; Simonová & Lososová 2008; Tomlinson et al. 2008). Most post-coal-mining areas are under active technical reclamation with only a few left to spontaneous vegetation processes (Bradshaw 2000; Chaturvedi & Singh 2017; Šebelíková et al. 2019). There is limited evidence that shows whether alien plant species on spontaneously-vegetated heaps follow known patterns (Ballesteros et al. 2021). In addition, we have limited understanding of how alien invasion level and ecological success are related to native community and functional diversity metrics in the context of spontaneous vegetation development on post-coal mine heaps (Ballesteros et al. 2021; Renault et al. 2022). Several authors have studied the effect of invasive Solidago species (i.e., S. canadensis and S. gigantea) on taxonomic diversity (Bartha et al. 2014; Rebele 2013), and the impacts of the expansive native species – Calamagrostis epigejos – on nutrient availability (Kompała-Bąba et al. 2020; Stefanowicz et al. 2015) and as a strong competitor in post-industrial sites (Mudrák et al. 2010; Rebele & Lehmann 2002; Somodi et al. 2008). There is limited understanding on the roles of these herbaceous species as successional inhibitors, specifically how they affect functional and phylogenetic diversity at the community level between successional stages (Kompała-Bąba et al. 2020; Woźniak et al. 2021). The debate on the pattern of diversity along successional gradients is still unresolved. There is a need to use a contemporary novel approach – functional traits and phylogenetic diversity - to advance our knowledge of ecological succession in a changing world (Chang & Turner 2019). My dissertation fills these knowledge gaps by determining the drivers of alien species invasion level and ecological success on post-coal mine heaps, assessing the inhibitory role of alien and native species with known behaviour from the literature, using the chronosequence of spontaneously developed vegetation in post-mining sites to understand the vegetation dynamics and pattern of diversity along the successional gradients.



### Figure 1

Vegetation pattern across various stages of succession on post-coal mine spoil heaps; early-successional stage with black and coaly spoil materials majorly colonized by synanthropic species (A-B); mid-successional stage with species characteristic of dense low vegetations (meadows) (C-E); late-successional stage with dense woody vegetation dominated by tree, shrub, and forest herbaceous species (F-G). Photo: Quadri A. Anibaba

### 2. Research objectives and hypotheses

The main aim of my dissertation was to investigate vegetation diversity in post-mining areas and to assess the role of alien species and successional inhibitors on spontaneously vegetated spoil heaps.

The following research hypotheses were evaluated:

# H1: Native community characteristics will explain alien species invasion level (alien richness) and ecological success (alien cover) on spontaneously vegetated post-coal mine heaps (Publication 1).

**Premises:** The biotic acceptance theory predicts that highly native plant communities support the establishment of diverse alien species (Fridley *et al.* 2007; Stohlgren *et al.* 2006). On spontaneously-vegetated heaps, alien species can benefit from the unoccupied niches; therefore, filling them makes the functional space more saturated (Loiola *et al.* 2018). In contrast, functionally diverse communities are less susceptible to alien species invasion (Hooper & Dukes 2010). Therefore, the ability of native communities to limit or support alien species invasion could be mediated by functional diversity (Feng *et al.* 2019).

## H2: The inhibitory effect of invasive alien and expansive native species on diversity will depend on the successional stage (Publication 2).

**Premises:** The competitive inhibition model is one of the main drivers of ecological succession in natural communities (Connell & Slatyer 1977). Herbaceous perennials can dominate this successional stage, often by monopolising light, water, and nutrients through dense vegetation development (Kompała-Bąba *et al.* 2020; Rebele 2013).

### H3: Diversity, functional and phylogenetic distinctiveness of ecosystems will increase along successional gradients (Publication 3).

**Premises:** Connell (1978) proposed the arch-shaped pattern of diversity along a successional gradient – diversity gradually increases during early succession when pioneers dominate, and reaches its maximum in mid-stages when there are still pioneers but the mid- and late-successional species are already beginning to establish, and diversity gradually falls into the late stages of succession when the pioneers are eliminated.

These hypotheses are important because they address critical gaps in our understanding of ecological processes and species interactions. By investigating these relationships, we can enhance our knowledge of ecosystem dynamics, which is vital for effective conservation and management strategies. This knowledge not only informs ecological theory but also has practical implications for biodiversity preservation and ecosystem restoration efforts in a rapidly changing environment. Ultimately, the significance of this research lies in its potential to contribute to sustainable practices and policies that protect natural ecosystems.

### 3. Material and methods

### 3.1. Study area

The study was conducted in Upper Silesia – a region with a rich history of coal mining (since the  $18^{th}$  century). The long-lasting coal mining activities have resulted in large areas of post-coal mine sites, occupying > 2000 ha (Szczepańska 1987). These mineral sites built of carboniferous sediments on pre-Cambrian crystalline rocks have shaped the anthropogenic landscape. The carboniferous mudstone and sandstone complexes are mixed with numerous coal elements. These stone complexes are also overlain by Triassic carbonate formations (Cabała *et al.* 2004).

Plant species establishment and the development of vegetation communities on coal mine heaps is difficult due to the mineral material habitats having extreme abiotic conditions, for example, large variations in daily temperatures (often reaching 50 °C) and humidity, substrate instability, lack of soil, susceptibility to erosion, dusting, thermal and chemical activities. In addition to abiotic parameters, the post-coal mine heap is characterised by extreme biotic conditions, such as soil organic matter deficiency in the substrate and lack of seed bank (Woźniak *et al.* 2021). These habitat characteristics impact the ability of seeds to germinate and colonize post-industrial ecosystems (Bradshaw 2000; Prach *et al.* 2013).

#### 3.2. Study design and data collection

Sixty spontaneously regenerated spoil heaps of uniform origin, diverse ages, and sizes were selected at random. After the selection of spoil heaps, Landsat satellite imagery (Sentinel-2A) was acquired to obtain multispectral bands and spectral products (mainly vegetation indices) of the spoils using the sen2r package (Ranghetti *et al.* 2020). Using the k-nearest neighbours algorithm (k-NN), each map pixel was subjected to unsupervised classification. The result of the classification produced five vegetation clusters. A random selection of 80 vegetation patches that were at least 150 m long and wide was established using the results of the vegetation clusters. Within each randomly selected patch, five plots in a cross design were established (i.e. one central plot and four subplots at distances of 50 m in the north, south, east,

and west directions) (**Figure 2**). Within the plots, plant abundance was collected using the Londo scale at  $28.3 \text{ m}^2$  (Londo 1976). A total of 400 plots were sampled on the spoil heaps.



#### Figure 2

Distribution of study plots (n = 400) in Upper Silesia. The study design shows plots in the north (N), south (S), east (E), and west (W) directions at 50 m from the central plot (C). Source: (Anibaba *et al.* 2024).

### 3.3. Statistical analyses

All analyses were conducted using R (R Core Team 2023). The following packages from the tidyverse were used for data exploration, processing, and visualization: dplyr (Wickham *et al.* 2023), reshape2 (Wickham 2020) and ggplot2 (Wickham *et al.* 2024). Community-weighted mean values (CWMs) were calculated for functional traits that best describe plant life strategies – plant height (PH), specific leaf area (SLA), seed mass (SM), and leaf dry matter content (LDMC) (Westoby 1998) and Ellenberg's indicator values describing the habitat requirements of plant species (Ellenberg & Leuschner 2010). Functional traits data were acquired from BEIN (Maitner *et al.* 2018), LEDA (Kleyer *et al.* 2008), BioFlor (Klotz *et al.* 2002), and Pladias (Chytrý *et al.* 2021) databases. The phylogenetic tree of vascular plant species present in study plots was derived from a mega tree in the V.phylo.maker package (Jin & Qian 2019). In

addition, functional diversity components were calculated – dispersion (FDis), divergence (FDiv), and richness (FRich) (Laliberté *et al.* 2014; Laliberté & Legendre 2010). The taxonomic richness and Shannon diversity indices were calculated using the vegan package (Oksanen *et al.* 2022). Faith's phylogenetic diversity (PD) and mean pairwise phylogenetic distance (MPD) were calculated using the PhyloMeasures package (Tsirogiannis & Sandel 2016). A null model approach was used to test whether the phylogenetic diversities differed from the randomly generated assemblage of species. To gain insights into the species composition of all study plots across successional stages, a presence-absence transformed data matrix was used in nonmetric multidimensional scaling (NMDS) implemented in the vegan package (Oksanen *et al.* 2022).

To test hypothesis 1, two models were developed: the generalised linear mixed effects model (GLMM) and the linear mixed effects model (LMM), the former assumes a Poisson distribution with a log link function of alien species richness while the latter assumes a Gaussian distribution of alien species cover. In these models, heap age and native community characteristics (i.e. native species richness, native species cover, native CWMs SLA, native CWMs SM, native CWM PH, native FDis, and native FRich) were predictors. Blocks of plots nested within the heap were random variables to account for the spatial dependence of the study design. The lme4 package was used to develop GLMM and LMM (Bates *et al.* 2015), and the lmerTest package (Kuznetsova *et al.* 2017) was used for the p-values of GLMMs. The ggeffects package was used to extract marginal responses of models (i.e., predicted responses assuming a constant (mean) value of all other predictors and excluding random effects) (Lüdecke 2018).

To test hypothesis 2, linear mixed-effects models were used, except for species richness and functional richness, for which generalized linear mixed-effect models assuming Poisson distributions and zero-inflated Beta distributions of the dependent variables were used, respectively. These models were developed using the 'lme4' and 'glmmTMB' packages (Bates *et al.* 2015; Brooks *et al.* 2017). The percentage cover of invasive *Solidago* and expansive native *Calamagrostis*, successional class, and their interactions were used as predictors. To obtain distributions that were close to normal, the square root transformed cover of *Solidago* and *Calamagrostis* was employed. Square root transformation decreases the relatively large differences between midpoints of cover classes and allows for better handling of species that occur with lower coverage. In addition, we included blocks of plots nested within the heap identifiers as random intercepts in the models, to account for the spatial dependence of the study design. The ggeffects package (Lüdecke 2018) was used to obtain marginal responses from models (i.e., predicted responses excluding random effects and assuming a constant (mean) value for all other predictors). To test hypothesis 3, the differences in alpha diversity indices and CWMs were determined using linear mixed-effects models (LMMs), accounting for dependencies among plots within blocks and heaps by the random intercepts. A generalised linear mixed-effects model (GLMM), which assumes a Poisson distribution, was used to determine species richness. The lme4 (Bates *et al.* 2015) and lmerTest (Kuznetsova *et al.* 2017) packages were used to develop LMMs and GLMM.

### 4. Main results

## 4.1. Publication 1: Native plant community characteristics explain alien species success in post-industrial vegetation

Alien species accounted for 20.4% of all recorded vascular plant species (i.e., 64 out of 318 taxa) on spoil heaps: with 55% being neophytes and 45% archaeophytes. Post-coal-mining areas left to spontaneous succession have been characterized by low frequencies of alien species (Prach *et al.* 2013; Prach & Pyšek 1999; Tischew *et al.* 2014). Nevertheless, this study found a high frequency of alien species – *Erigeron canadensis, Solidago gigantea, Solidago canadensis, Erigeron annuus* and *Impatiens parviflora* (the five most common alien species) across the studied plots. The most important alien species were *S. gigantea* and *I. parviflora* with a mean cover of 14.25% and 14.7%, respectively. While *S. gigantea* was prevalent in open habitats characterized by high light intensity, *I. parviflora* was common in the understory layer of forests.

For **H1**, native community characteristics drive alien species invasion level and ecological success. Alien species cover decreased with native species cover. In contrast, alien species richness and cover increased with native functional richness. Although native CWM seed mass and plant height significantly predicted alien species cover, native CWM SLA marginally predicted alien species richness. Our findings are important because they underscore the significance of exploring native community characteristics toward understanding the invasibility and management of post-industrial vegetation.

To achieve the restoration of post-coal-mining sites using spontaneous vegetation, our findings demonstrate that management actions aimed at reducing invasibility at the early- and mid-successional stages are important and should be encouraged. Most important is the prevention of invasive species with ruderal traits and the promotion of competitive native species while practicing limited ecological disturbance on post coal-mining areas. To achieve robust alien species management actions in the ecosystems, regular monitoring is needed both within spoil heaps and around the surrounding landscapes. Recent findings suggest that surrounding landscapes – roads, railways and arable land – support alien species (Ballesteros *et al.* 2021), thus affirming that areas of urban sprawl around spoil heap sites are an important pathway for alien species dispersal and should be prioritised for management.

## 4.2. Publication 2: The inhibitory tendency of *Calamagrostis epigejos* and *Solidago* spp. depends on the successional stage in post-industrial vegetation

The cover of *Calamagrostis epigejos* and *Solidago* spp. differed between successional stages. Vegetation pattern across stages revealed that succession proceeds from an early stage with black coaly materials, mainly colonized by synanthropic species (e.g., *Tussilago farfara*, *Erigeron canadensis*, *Taraxacum officinale*, *Echium vulgare*, *Daucus carota*, or *Cirsium arvense*). The mid-successional stages showed species adapted to low dense vegetation (i.e., meadows and grasslands, e.g., *C. epigejos*, *Poa compressa*, *P. pratensis*, *Polygonum aviculare*, *S. canadensis*, *S. gigantea*, *Artemisia vulgaris*, or *Hypericum perforatum*). Finally, the late-successional stage revealed species characteristic of dense high vegetation (trees and shrubs). The most frequent species in the late-successional stage were herbaceous species adapted to shade or moderate shade conditions – Urtica dioica, *Impatiens parviflora*, *Geum urbanum*, and *Deschampsia cespitosa*.

For **H2**, the inhibitory effects of herbaceous species on diversity indices strongly depended on the successional stage on post-coal-mining spoil heaps. The impact of *Calamagrostis* and *Solidago* cover on diversity indices was strong in the mid-successional stage. In the mid-successional stage, species richness and functional richness decreased significantly with the cover of *Calamagrostis* and *Solidago*. Shannon diversity marginally decreased while phylogenetic diversity marginally increased with the cover of *Calamagrostis*. Shannon diversity was negative while phylogenetic diversity was positive with the cover of *Solidago*.

Species that are expansive and perennial can dominate a particular successional stage, thereby inhibiting the successional pathway and affecting vegetation diversity. Both *Calamagrostis* and *Solidago* can reduce species richness, specifically, in the mid-successional stage, which is characterized by high biomass and large species pool, and where biotic interactions, especially competition, shape the structure of plant communities (Bartha *et al.* 2014; Rehounková & Prach 2006). The study provides evidence of the significance of environmental context for the assessment of the ecological impacts of invasive alien species and expansive native herbaceous species. It demonstrates the importance of the mid-successional stage as integral ecosystems for achieving restoration goals of spontaneous vegetation development on post-coal-mining spoil heaps.

### **4.3.** Publication 3: Remote sensing for site selection in vegetation survey along a successional gradient in post-industrial vegetation

An assessment of indicator species (i.e., a species that is more frequent/associated with a particular successional stage) on post-coal-mining spoil heaps revealed 15, 12, and 10 indicative species in the early-, mid-, and late-successional stages, respectively. The indicative lawn grass species *Lolium perenne* and ruderals: *Oxybasis* spp., *Chenopodium album*, and *Echinochloa crus-galli* had higher frequency in the early-successional stage. In contrast, the mid-successional stage revealed a high frequency of indicative species typical of meadows and grasslands: *Achillea millefolium*, *Dactylis glomerata*, *Festuca rubra*, *Galium mollugo*, *Silene latifolia*, and *Vicia cracca*. The late-successional stage showed a high frequency of ancient forest indicator species (Hermy *et al.* 1999): *Lolium giganteum*, *Circaea lutetiana*, *Millium effusum*, and *Poa nemoralis*, as well as forest-edge species: *Rubus idaeus*, *Geum urbanum*, and *Impatiens parviflora*.

For **H3**, species richness and Shannon diversity differed between successional stages. While species richness and Shannon diversity were significantly higher in the early- and midsuccessional stages than in the late-successional stage, these response variables were at their maximums in the mid-successional stage, revealing an arch-shaped pattern of successional dynamics. Community-weighted means for ecological indicator values (light, soil fertility) and functional traits (plant height and SLA) differed significantly between successional stages, indicating the increasing importance of competition as succession proceeds. The significant CWM light EIV in the late-successional stage suggests the influence of abiotic filtering – plant species in the late stage show less demand for light during the seedling stage; thus the elimination of species that perform best at optimum light and in open habitats. The difference in CWM soil fertility EIV in the late-successional stage indicates an increasing demand for soil nutrients with the advancement of succession. Similarly, plant height was significantly higher in the late-successional stage which infers that the species have strong competitive capacity. The CWM SLA was significantly higher in the late-successional stage. Late-successional vegetation had the lowest functional richness and highest functional dispersion, and phylogenetic diversity expressed as Faith's PD and MPD was significantly higher in the latesuccessional stage.

The study provides evidence on the conservation value of late-successional vegetation by hosting ancient forest indicator species. It also supports the importance of spontaneously developed areas to host diverse vegetation communities while conserving rare species.

### 5. Main conclusions

The findings from the doctoral thesis add to a critical gap in our understanding of the diversity of alien species and their predictors, the role of successional inhibitors in limiting the progress of succession, and the pattern of vegetation diversity in post-coal-mining areas. The results will increase the knowledge of better management approaches in post-coal-mining areas undergoing the spontaneous vegetation restoration process. As a result of the conducted research, it was found that:

- the most frequent alien species on post-coal-mining spoil heaps are *Erigeron canadensis*, *Solidago gigantea*, *Solidago canadensis*, *Erigeron annuus*, and *Impatiens parviflora*;
- native functional richness and native CWM SLA are determinants of alien species invasion level while native species cover, native functional richness, native CWM plant height, and native CWM seed mass are predictors of alien species ecological success;
- the pattern of vegetation development along successional stages revealed a transition from black and coaly spoil materials with synanthropic species in the early stage, to species peculiar to meadows and grasslands in the mid-stage, and the dense high vegetation (forest and shrub) in the late stage;
- the inhibitory effects of herbaceous species *Calamagrostis epigejos* and *Solidago* spp. strongly depended on the successional stage, and the impact of both species was the most evident in the mid-successional stage;
- the early-successional stages hosted species indicative of ruderal sites, the mid-successional stages had a high proportion of species indicative of meadows and grasslands, while the late-successional stages were characterized by the frequent occurrences of forest and forest edge species;
- species richness and Shannon diversity followed an arch-shaped pattern: they were highest in the mid-successional stage and lowest in the early- and late-successional stages, supporting the intermediate disturbance theory;
- functional composition differed significantly in the late-successional stage; low for light EIV, and high for soil fertility EIV and CWMs plant height and SLA;
- the late-successional stage had significantly higher phylogenetic diversity (Faith's Phylogenetic diversity and mean pairwise distance) than other stages.

The findings of this dissertation will increase our understanding of vegetation dynamics in post-industrial landscapes, especially the role of biotic interactions. It demonstrates the significance of context dependence in the restoration and management of post-coal-mining sites. Management actions aimed at limiting the spread of successional inhibitors, specifically in the mid-successional stage, should be prioritized.

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**Co-authors statements** 

dr hab. inż. Marcin K. Dyderski, prof. ID PAN Institute of Dendrology, Polish Academy of Sciences Department of Ecology

### **AUTHORSHIP STATEMENT**

I declare that I am a co-author of the following original articles, which are the part of MSc. Quadri Agbolade Anibaba doctoral dissertation and my contributions are as follows:

**Publication 1**: Anibaba, Q. A., Dyderski, M. K., Woźniak, G., & Jagodziński, A. M. (2023). Native plant community characteristics explain alien species success in post-industrial vegetation. *NeoBiota*, 85, 1-22. <u>https://doi.org/10.3897/neobiota.85.97269</u>

### Author's contributions:

Conceptualization, Methodology, Investigation, Writing – review & editing. I estimate my percentage contribution at 10%.

**Publication 2**: Anibaba, Q. A., Dyderski, M. K., Woźniak, G., & Jagodziński, A. M. (2024). The inhibitory tendency of *Calamagrostis epigejos* and *Solidago* spp. depends on the successional stage in post-industrial vegetation. *Land Degradation and Development*. https://doi.org/10.1002/ldr.5348

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### Author's contributions:

Conceptualization, Methodology, Writing – review and editing. I estimate my percentage contribution at 10%.

M.Dyour

signature of the co-author

dr hab. Gabriela Woźniak, prof. UŚ University of Silesia in Katowice Faculty of Natural Sciences Institute of Biology, Biotechnology and Environmental Protection

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### Author's contributions:

Conceptualization, Methodology, Writing – review and editing. I estimate my percentage contribution at 10%.

Cabriela Kormiale

signature of the co-author

prof. dr hab. inż. Andrzej M. Jagodziński Institute of Dendrology, Polish Academy of Sciences Department of Ecology

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signature of the co-author

### Attachments

### **PUBLICATION 1**

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RESEARCH ARTICLE



### Native plant community characteristics explain alien species success in post-industrial vegetation

Quadri A. Anibaba<sup>1</sup>, Marcin K. Dyderski<sup>1</sup>, Gabriela Woźniak<sup>2</sup>, Andrzej M. Jagodziński<sup>1</sup>

I Institute of Dendrology, Polish Academy of Sciences, Parkowa 5, 62-035 Kórnik, Poland **2** University of Silesia, Jagiellońska 28, PL-40-007, Katowice, Poland

Corresponding author: Quadri A. Anibaba (qanibaba@man.poznan.pl)

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#### Abstract

Biological invasions are one of the major challenges to the restoration of post-mining sites. Most postmining sites are under technical reclamation with only a few left to spontaneous vegetation processes. Therefore, we know little about alien plant species on spontaneously-vegetated post-coal mine heaps and how native community characteristics predict their establishment. To fill the knowledge gap, we aimed to determine the drivers of alien species colonisation on post-coal mine heaps. Specifically, we asked: (i) Which alien species are the most successful on post-coal mine heaps and why? (ii) What are the drivers of alien species richness and cover, and how are they affected by the native community? (iii) What does it mean for predicting threats from alien species and management? We recorded vascular plant species and their abundance across 400 plots on post-coal mine heaps in Upper Silesia, Poland. We calculated plant community taxonomic and functional characteristics and, using mixed-effects models, we estimated predictors of alien species richness and cover. We found 65 alien species on post-coal mine heaps, comprising 20.4% of all recorded species, including 36 neophytes and 29 archaeophytes. Amongst them - Erigeron canadensis, Solidago gigantea, Solidago canadensis, Erigeron annuus and Impatiens parviflora - were the most frequent on the studied heaps. We showed that native functional richness significantly predicts alien species richness and cover. Similarly, native community-weighted mean (CWM) seed mass and plant height predict alien species cover. However, CWM of specific leaf area for native species marginally predicts alien species richness. We showed that alien species cover decreases with native species cover. Our findings revealed the ecological significance of niche-filling and the biotic acceptance hypotheses on post-coal mine heaps. We demonstrated how exploring native community characteristics can help in understanding the invasibility and management of post-industrial vegetation.

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#### **Keywords**

Biological invasions, coal mines, community-weighted means, functional diversity, native species, oligotrophic mineral material, post-coal mine heaps

## Introduction

Invasion by alien species severely threatens the biodiversity and function of transformed ecosystems and may interfere with ecosystem restoration and establishment efforts after disturbance, for example, due to high competitiveness. In natural and semi-natural ecosystems invaded by alien plants, several attempts have been made to explain the relationships between the alien species richness and cover and the increase in native species functional richness. The niche-filling hypothesis states that niches are available for alien species in a community of functionally-rich native species. In contrast, in a functionally-poor community, the niches are fewer and already occupied by native species (Thuiller et al. 2010; Loiola et al. 2018). Alien species can benefit from the unoccupied niches; therefore, filling them makes the functional space more saturated (Loiola et al. 2018). The biotic resistance theory posits that species-rich communities are more resistant to alien species invasion than species-poor ones (Jeschke 2014; Beaury et al. 2020). The biotic resistance theory contradicts the biotic acceptance hypothesis (Stohlgren et al. 2006; Fridley et al. 2007), which predicts that higher diversity of native species supports diverse alien species establishment.

Alien species invasion represents one of the major challenges in restoration ecology (Weidlich et al. 2020). Numerous studies have recorded the spontaneous establishment of alien plant species on different types of heaps, for example, in India (open cast coal field) (Ekka and Behera 2011), Indonesia (Hapsari et al. 2020) and Nigeria (Nsa et al. 2021). In temperate ecosystems, there are similar examples. Tomlinson et al. (2008) showed that alien plant species constituted approximately 40% of the flora on abandoned quarry sites in southern Ontario, Canada. In the Czech Republic, the mean proportion of alien plant species between 1945 and 2005 was 39.3% in different types of anthropogenic vegetation including post-coal mine heaps (Simonová and Lososová 2008). Together, some of these studies identified noxious alien plant species that hinder the restoration of heaps.

In habitats that have been established due to human activity, such as post-excavation mineral sites, the relationship between alien species occurrence and native plant community functional richness is unknown. Understanding the relationship between the alien and native species and communities has become increasingly important as ecosystems transformed by mining occupy approximately 1% of the global land area (Maus et al. 2022). Mining modifies the landscape, thereby creating novel ecosystems with profound implications for biodiversity conservation, ecosystem functioning and restoration (Hobbs et al. 2009). Part of mining, specifically coal mine sites, are heaps where overburdened materials are dumped (Prach 2013). The post-coal mining heaps contain sedimentary rock extracted together with coal and are characterised by extreme abiotic conditions, thus creating challenges for land management and restoration. In these challenging habitat conditions, plant communities with non-analogous species composition are assembled as a result of spontaneous colonisation. Nevertheless, for a long time, restoration ecologists and land managers have aimed to restore species composition on mineral material of post-coal mine heaps towards that of undisturbed vegetation (Bradshaw 2000).

Possible mechanisms for alien species establishment in man-made habitats have been proposed by Prach and Walker (2011). Specifically, the use of functional diversity indices can help elucidate ecosystem processes and biotic interactions that drive alien species colonisation (Dyderski and Jagodziński 2019a). The ability of native communities to limit alien species invasion could be mediated by functional diversity (Feng et al. 2019). Furthermore, functionally diverse communities are less susceptible to alien species invasion (Hooper and Dukes 2010). When multiple species traits are considered, functional diversity can help predict the invasibility of native communities, as well as being the main mechanism directing the rate of invasibility (Catford et al. 2019; Feng et al. 2019). Although most studies conclude that functional diversity increases the resistance of communities to invasion (Fargione et al. 2003; Fargione and Tilman 2005; Larson et al. 2013; Wei et al. 2015), in contrast, a few have shown that a highly functionally diverse native community can increase alien species invasion success (Renault et al. 2022). The increased number of alien species could be linked to high resources produced by native plant species in the resident community (Renault et al. 2022).

Most post-industrial sites are under active technical reclamation with only a few left to spontaneous vegetation processes (Bradshaw 2000; Chaturvedi and Singh 2017; Šebelíková et al. 2019). Therefore, only limited evidence allows us to test whether alien plant species on spontaneously-vegetated heaps follow known patterns (Ballesteros et al. 2021). Similarly, the use of functional diversity metrics to determine alien species invasion success is very recent (Renault et al. 2022); to our knowledge, there is a lack of empirical study in the context of spontaneous vegetation development on post-industrial sites, including the mineral post-coal mine habitats. Thus, our study aims to determine the drivers of alien species colonisation on post-coal mine heaps, therefore, providing a theoretical understanding of the structure and function of plant communities in these novel ecosystems. Specifically, we addressed the following questions: (1) Which alien species are the most successful on post-coal mine heaps and why? (2) What are the factors affecting alien species richness and cover, and how are they affected by the native community? (3) What does it mean for predicting threats from alien species and management?

# Methods

## Description of the study site

The study was conducted in Upper Silesia – the region has a long tradition of coal mining (since the 18<sup>th</sup> century). The long-lasting black coal mining activities have resulted in large areas of post-coal mine sites, occupying > 2000 ha (Szczepańska 1987).

These mineral material sites built of carboniferous sediments on Pre-Cambrian crystalline rocks have shaped the anthropogenic landscape. The carboniferous mudstone and sandstone complexes are mixed with numerous coal elements. These stone complexes are also overlain by Triassic carbonate formations (Cabała et al. 2004). Plant species colonisation and the development of vegetation communities on coal mine heaps is difficult because the mineral material habitats have extreme abiotic conditions, for example, large variations in daily temperatures (often reaching 50 °C) and humidity, substrate instability, lack of soil, susceptibility to erosion, dusting, thermal and chemical activities. In addition to abiotic parameters, the post-coal mine heap is characterised by extreme biotic conditions, such as soil organic matter deficiency in the substrate and lack of seed bank (Woźniak et al. 2021). These habitat characteristics impact the ability of diaspores to establish and the development of vegetation communities and mosaic of ecosystems on post-industrial sites (Bradshaw 2000; Prach et al. 2013), particularly on mineral oligotrophic coal mine heap sites (Woźniak 2010).

## Study design and vegetation sampling

From the list of 112 post-mining sites with available information about age, size, vegetation and reclamation method (Woźniak 2010), we excluded 31 sites differing in size, land-use patterns in the neighbourhood, thermal activity or were artificially shaped. As these factors could significantly alter observed patterns of vegetation assembly, we decided to exclude them, focusing on the most frequent cases. Although this decreased the total variance of abiotic conditions, it allowed us to make conclusions about trends not affected by noise connected with the abovementioned treatments. From the remaining 81 sites, we randomly selected 60 sites proportionally to post-coal mine heap size, age and surrounding land cover. Amongst them, we distinguished five types of land cover and randomly selected plots proportionally to cover class (Jagodziński et al., in prep.). Using the results of this investigation, we randomly selected 80 vegetation patches, proportionally to the cover of each land-use class which forms an area of at least  $150 \times 150$  m. Within each randomly selected patch, we established five plots in a cross design (i.e. one central plot and four subplots at distances of 50 m in the north, south, east and west directions; 400 plots in total; Fig. 1). Each plot was circular with a 3 m radius (28.3 m<sup>2</sup>). In all plots, we registered vascular plant species and their abundances using the Londo scale (Londo 1976). Alien species status (i.e. casual, naturalised and invasive) and historical-ecological groups (i.e. archaeophytes and neophytes) were determined using the database of alien plants in Poland (Tokarska-Guzik et al. 2012).

## Functional traits

These traits include a broad category of plant life history, leaf morphology and reproductive characteristics (Table 1). Traits data were acquired from LEDA (Kleyer et al. 2008), BIEN (Maitner et al. 2018), Pladias (Chytrý et al. 2021) and BioFlor (Klotz et al. 2002).

The functional approach was based on a set of traits known to have significant ecological implications for plant species competitive ability, dispersal, establishment and



**Figure 1.** Scheme of study design – distribution of study plots within land use types. Additional plots are in north, south, east and west directions at 50 m from the central plot.

Plant traits	Code	Data type	Unit	Value (Min., Max.)	Missing data (%)
Leaf dry matter content	LDMC	Numeric	mg g <sup>-1</sup>	0.3, 509.5	18.9
Seed mass	SM	Numeric	mg g <sup>-1</sup>	0.001, 13737.6	5.5
Specific leaf area	SLA	Numeric	mm <sup>2</sup> mg <sup>-1</sup>	51.8, 899.1	12.1
Plant height	PH	Numeric	m	0.033, 60.0	1.1
Light EIV	EIV-L	Ordinal	Ordinal	1, 9	1.9
Moisture EIV	EIV-M	Ordinal	Ordinal	2, 11	13.2
Temperature EIV	EIV-T	Ordinal	Ordinal	2, 8	27.1
Nitrogen EIV	EIV-N	Ordinal	Ordinal	1, 9	12.3
Soil reaction EIV	EIV-SR	Ordinal	Ordinal	1, 9	30.9
Start of flowering	Flow_start	Ordinal	Month	1,9	1.1
Duration of flowering	Flow_dur	Ordinal	Month	1, 12	1.1
Insect pollinated	Poll-ins	Binary			4.1
Wind pollinated	Poll-wind	Binary			4.1
Self-pollinated	Poll-self	Binary			4.1
Alien status	Alien_stat	Categorical	2 categories		0.0
Life form	Life_form	Categorical	8 categories		0.0

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

stress tolerance on post-coal mine heaps. Specific leaf area (SLA) and leaf dry-matter content (LDMC) serve as proxies of species status on the leaf economic spectrum (Perez-Harguindeguy et al. 2016). High LDMC and low SLA unveil a conservative approach with resistance to the harsh abiotic stress in the mineral material of post-coal mine heaps, while low LDMC and high SLA infer the increased importance of an acquisitive strategy by plant species (Perez-Harguindeguy et al. 2016). Plant height (PH)

was used as an approximation of plant competitive competence (Westoby et al. 2002). The seed mass (SM) helps to explain the colonisation and establishment ability of plant species – with low seed mass for species found on post-coal mine heaps of younger age and vice versa (Piekarska-Stachowiak et al. 2014).

# Trait imputation

We used a random forest algorithm in combination with phylogenetic trait imputation to fill gaps in the trait data and not omit missing data (Penone et al. 2014). To strengthen the predictive power of the model, we used the *missForest::misForest()* function (Stekhoven 2022) and phylogenetic eigenvectors (Diniz-Filho et al. 1998) derived from the *PVR::PVPdecomp()* function (Santos 2018). The variation explained by the first 15 phylogenetic eigenvectors was 59.3% of phylogenetic distances. The Normalised Root Mean Square Error (NRMSE) of imputed traits was 1.011 for continuous predictors and the proportion of falsely classified categorical variables was 0.079. In general, trait imputation has been shown to decrease bias when compared to removing species with missing trait data (Penone et al. 2014).

# Community-Weighted Means (CWMs) and Functional Diversity (FD) indices

To understand important aspects of the functional community structure, we combined plant trait data with species cover to calculate the community-weighted means (CWMs) and the functional diversity indices. We calculated the CWMs of seed mass, plant height and specific leaf area using the FD::FunctComp() function (Laliberté et al. 2014). These traits influence plant germination and dispersal ability, life form and growth rate. We log-transformed numeric trait data to attain normality before the calculation of CWMs. Using the *FD::dbFD()* function (Laliberté et al. 2014), we quantified functional diversity indices: functional richness and functional dispersion. These indices show the distribution of plant species traits within the community hyperspace (Laliberté and Legendre 2010). Functional richness (FRich) quantifies the trait space of plant functional types present in a community. Communities with a low functional richness of native plants are expected to be more invasible by competitive alien species (Renault et al. 2022). This implies that niche differentiation within the native community will be low, thereby resulting in trait convergence and competition (Czortek et al. 2021). Functional dispersion (FDis) measures distances between functional traits carried by plant species to the centroid (centre point) in the community hypervolume (Villéger et al. 2008). High functional dispersion delineates strong functional differences between native species in a community – thus suggesting co-occurrence rather than competition (Carroll et al. 2011).

# Data analyses

All analyses were performed in R software (version 4.2.1) (R Core Team 2022). Using the *base::scale()* function, we standardised and scaled explanatory variables before

analyses. Such an approach helps to reduce biases linked with uneven ranges amongst these variables and it ensures that the estimated coefficients are all on the same scale, making it easier to compare the effect sizes.

To assess the drivers of alien species richness and cover in post-coal mine heaps, we built a generalised linear mixed effect model (GLMM) and linear mixed effect model (LMM), assuming a Poisson distribution with a log linking function and Gaussian distribution, respectively. In these models, heap age and native community characteristics (i.e. native species richness, native species cover, native CWM SLA, native CWM SM, native CWM PH, native FDis and native FRich) were predictors. In our models, blocks of plots nested within the heap are random variables to account for the spatial dependence of the study design. We used the 'Ime4' package (Bates et al. 2015) to develop GLMM and LMM, and the 'ImerTest' package (Kuznetsova et al. 2017) for the p-values of GLMMs. To extract marginal responses of models, i.e. predicted response excluding random effects and assuming a constant (mean) value of all other predictors, we use the *ggeffects::ggpredict()* function (Lüdecke 2018).

Prior to model development, we assessed correlations between variables using variance inflation factors (VIF). Hypothesised predictors with high collinearity (VIF > 5) were not included in the global model. The final model for alien species richness and abundance on post-coal mine heaps was: glmer(formula = alien.rich ~ native.rich + native.FRich + native.CWM.SLA + (1 |heap/block)); lmer(formula = alien.abundance ~ native.abundance + native.FRich + native.CWM.H + native.CWM.SM + (1|heap/block)), where alien.rich = alien species richness, native.rich = native species richness, alien.abundance = alien species cover, native.abundance = native species cover, native.FRich = Functional richness of native species, native.CWM.SLA = native community-weighted means of specific leaf area, native.CWM.H = native community-weighted means of plant height, native.CWM.SM = native community-weighted means.

To identify models with variables that best predict alien species richness and cover on post-coal mine heaps, we used a model selection in the *MuMIn::dredge()* function (Bartoń 2022) ranked, based on corrected Akaike Information Criterion, corrected for small sample size (AICc). For each model, we reported the AICc of the global model (i.e. all hypothesised predictors), final model and null (intercept and random effect only) model, to show how the final model differs from them. We ensured that the Poisson GLMM was not biased by overdispersion using the *performance::check\_overdispersion()* function (Lüdecke et al. 2021).

# Results

Amongst the 318 plant species recorded in our dataset, we found 253 (79.6%) native species, 36 (11.3%) neophytes (four casual, 15 naturalised and 17 invasive) and 29 (9.1%) archaeophytes (two casual, 24 naturalised and three invasive). Amongst the 65 recorded alien species, 15 occurred in more than 11 plots and 17 had a percentage mean > 9.0% (Table 2; Suppl. material 1).

Species	Native region	Life form	Status	Frequency	Mean	Pollination	Dispersal
-				(number of plots)	cover (%)	agent	agent
Erigeron canadensis	N America	Therophyte	Invasive (Neo)	108	2.5	Self	Anemochory & Autochory
Solidago gigantea	N America	Hemicryptophyte	Invasive (Neo)	87	14.25	Insect	Anemochory & Autochory
Solidago canadensis	N America	Hemicryptophyte	Invasive (Neo)	77	7.29	Insect	Anemochory & Autochory
Erigeron annuus	N America	Therophyte	Invasive (Neo)	67	5.24	Insect	Anemochory & Autochory
Impatiens parviflora	Asia	Therophyte	Invasive (Neo)	40	14.7	Insect, Self	Autochory
Tripleurospermum inodorum	Anecophytes	Therophyte	Naturalized (Ar)	38	2.21	Insect	Autochory
Echinochloa crus-galli	Anecophytes	Therophyte	Invasive (Ar)	30	1.97	Wind, Self	Autochory
Silene latifolia	S Europe, Mediterranean, Asia	Hemicryptophyte	Naturalized (Ar)	27	1.74	Insect	Autochory
Hordeum jubatum	N America	Hemicryptophyte	Naturalized (Neo)	18	3.06	Self	Autochory
Kali turgidum	Europe, Mediterranean	Therophyte	Casual (Neo)	16	1.75	Wind, Insect, Self	Autochory
Lepidium ruderale	Mediterranean	Therophyte	Naturalized (Ar)	15	1.53	Self	Autochory
Pastinaca sativa	Mediterranean	Hemicryptophyte	Naturalized (Ar)	14	2.29	Insect	Autochory
Setaria viridis	Mediterranean	Therophyte	Invasive (Ar)	13	9.62	Wind	Autochory & Epizoochory
Diplotaxis muralis	Mediterranean	Therophyte	Invasive (Neo)	12	2.33	Insect, Self	Autochory
Prunus serotina	N America	Phanerophyte	Invasive (Neo)	12	16.33	Wind, Insect	Autochory & Endozoochory

**Table 2.** Frequency and cover of the 15 most common alien species occurring on post-coal mine heaps. Status and historical-ecological group – Neo (Neophyte), Ar (Archaeophytes) source: Tokarska-Guzik et al. (2012). For the full list, see Suppl. material 1.

Amongst all tested predictors for alien species richness in post-coal mine heaps, the best-fit model was explained by the native functional richness and SLA CWM (AICc global model = 618.08; AICc null model = 663.40; AICc best model = 599.66). Predicted alien species richness increased by 0.47 per unit change in native functional richness (P < 0.001) (Table 3; Fig. 2A). A marginal increase of 0.06 predicted alien species richness was recorded with native CWM SLA (P = 0.052) (Table 3; Fig. 2B). We found a non-significant decrease of 0.03 predicted alien species richness with native species richness (P = 0.26) (Table 3).

For alien species cover, the most parsimonious model contained native species cover, functional richness, CWM plant height and CWM seed mass as predictors (AICc global model = 1641.71; AICc null model = 1660.71; AICc best model = 1641.18). Predicted alien species cover decreased by 7.01 with native cover (LMM,  $\chi^2$  = 16.56, P < 0.001) (Table 3; Fig. 3A). Conversely, an increase of 4.54 predicted alien species cover was found with native functional richness (LMM,  $\chi^2$  = 9.91, P < 0.01) (Table 3; Fig. 3B). A similar trend occurred in a predicted increase in alien species cover by 6.98 and 5.87 with native CWM seed mass and native CWM plant height, respectively (CWM seed mass LMM,  $\chi^2$  = 5.22, P < 0.05; CWM plant height LMM,  $\chi^2$  = 4.63, P < 0.05) (Table 3; Fig. 3C, D).

**Table 3.** Estimates of the most parsimonious GLMM and LMM predicting native cover, native richness, functional richness, community-weighted means (CWMs) of specific leaf area (SLA), plant height and seed mass on the alien richness and cover, respectively.

Predictor	Estimate	SE	Z/t value <sup>*</sup>	Р
	Alien	species richness		
Intercept	0.57	0.08	6.74	< 0.001
Native species richness	-0.08	0.08	-1.12	0.26
Native functional richness	0.51	0.07	7.79	< 0.001
Native CWM of SLA	0.15	0.08	1.94	0.052
	Alier	1 species cover		
Intercept	9.71	4.44	2.19	0.083
Native functional richness	4.54	1.44	3.15	< 0.01
Native species cover	-7.02	1.72	-4.07	< 0.001
Native CWM of plant height	2.94	1.37	2.15	0.033
Native CWM of seed mass	3.49	1.53	2.28	0.023

\*Z value = GLMM; t value = LMM.



**Figure 2.** Alien species richness, estimated using GLMM, assuming the Poisson distribution of the dependent variable (Table 3) as a function of **A** native functional richness (Native FRich) **B** native community weighted means of specific leaf area (Native CWM SLA). Dots represent observed values, line – marginal prediction and grey area – 95% confidence interval of prediction.

# Discussion

Which alien species are the most successful on post-coal mine heaps and why?

We found that alien plant species accounted for 20.4% of all recorded vascular plants (65 out of 318 taxa) on heaps, with 55% of those being neophytes and the rest being archaeophytes. A higher proportion of native species is well-known from other post-industrial sites (e.g. old Solvay process heaps (Cohn et al. 2001); mining sites in the Czech Republic in central Europe (Prach et al. 2013); and the central German lignite mining district (Tischew et al. 2014)). The moderately high establishment of neophytes in our study is an indication that heaps are still at an early age and have relatively stable plant cover. Post-industrial sites left to spontaneous succession are usually characterised



**Figure 3.** Alien species cover, estimated using LMM assuming a Gaussian distribution of the response variable (Table 3) as a function of **A** native cover **B** native functional richness (Native FRich) **C** native community weighted means seed mass (Native CWM SM) **D** native community weighted means plant height (Native CWM PH). Dots represent measured values, lines – marginal prediction and grey area – 95% confidence interval of prediction.

by low frequencies of alien species (Prach and Pyšek 1999; Prach et al. 2013; Tischew et al. 2014). However, in our study site, we found a high frequency of important alien species – *Erigeron canadensis, Solidago gigantea* and *Solidago canadensis.* In the Czech Republic, Ballesteros et al. (2021) recorded 129 archaeophytes and 67 neophytes in spontaneously established vegetation and the most invaded successional series were the deforested landscapes. Similarly, Simonová and Lososová (2008) found a high proportion of archaeophytes in a large variety of man-made habitats in the Czech Republic.

The high proportion of archaeophytes in their study was due to the inclusion of less urbanised areas that were characterised by the presence of archaeophytes.

Erigeron canadensis, Solidago gigantea, Solidago canadensis, Erigeron annuus and Impatiens parviflora were the most frequent alien plant species in the studied plots on heap sites. Most important were S. gigantea and I. parviflora which had a high mean percentage cover. Solidago gigantea was found mainly in open habitats characterised by high light intensity and heap sites with early-successional communities. The species germinates by seed and rhizomes (Weber and Jakobs 2005). Clonal growth allows S. gigantea to form dense stands, promoting its abundance (Jakobs et al. 2004). Szymura et al. (2018) demonstrated the high competitiveness of S. gigantea in a replacement series experiment and found that S. gigantea outcompetes native grasses. Solidago gigantea in post-agricultural lands reaches the highest cover in sites with low functional richness (Czortek et al. 2020). Our study revealed the opposite pattern, as we focused on the cover of all alien species and we studied ecosystems with a lower level of interspecific competition. Two Erigeron species (E. canadensis and E. annuus) were frequent; however, they reached a low cover in the study plots. Both species are widespread in many ecosystem types on the mineral material of post-coal mine heap sites. This is because both E. canadensis and E. annuus plants produce 10 000-50 000 seeds annually that are wind-dispersed over long distances (Stratton 1989; Dauer et al. 2007; Pacanoski 2017). However, as ruderal species, they are more frequent in the initial phases of heap succession.

We found *Impatiens parviflora* in forest habitats within gaps in the herbaceous layer and heap sites at the late-successional stage. *I. parviflora* colonises sites with high native species richness (Chmura and Sierka 2006). Forest management practices, for example, canopy openings (gaps), propagule pressure from *I. parviflora* in plant communities around forests, increasing light availability and partial understorey disturbance promote invasion of *I. parviflora* in forests (Eliáš 1999). In general, the invasive ability of *S. gigantea* and *I. parviflora* is promoted through their physiological adaptation to water stress (Nolf et al. 2014; Quinet et al. 2015) and, for *I. parviflora*, through a high level of SLA intraspecific variability (Paź-Dyderska et al. 2020).

*Prunus serotina* was relatively less frequent on heap sites; however, in plots where it occurred, it had a high cover, thus, giving the species a high mean percent cover. *Prunus serotina* is a woody plant that encroaches on intermediate stages of succession due to its persistence in the shade and quick growth after disturbance (Closset-Kopp et al. 2007; Vanhellemont et al. 2009; Dyderski and Jagodziński 2019b; Jagodziński et al. 2019; Esch and Kobe 2021). *Prunus serotina* produces large numbers of seeds per year (Van den Tweel and Eijsackers 1986) with a major quantity of seeds present within 5 m of the parent tree and further dispersal of the seeds is done by frugivorous birds (Pairon et al. 2006; Deckers et al. 2008). As birds perch in a mature tree stand, the regurgitated *P. serotina* seeds are defecated and emptied as faeces, which then germinate (Jagodziński et al. 2019), thereby creating an efficient establishment of *P. serotina* seedlings within plots. This mechanism could explain *P. serotina* dispersal and spread. The most frequent alien species in the studied spoil heaps were mainly herbaceous plants, self or insect-pollinated and self or wind-and-self dispersed. These are traits associated with the invasiveness of alien plants (Pyšek and Richardson 2007). In the analysis of the invasion success of the Czech alien flora, Pyšek et al. (1995) found that alien species in man-made habitats were mainly pollinated by either self or insects. However, Pyšek et al. (1995) found that animal or wind modes of dispersal of alien species were the most frequent in made-made habitats. In our studied system, most alien species are in the Asteraceae and Poaceae families with ruderal characteristics. This is expected because many of the traits contributing to the evolutionary success of Asteraceae and Poaceae have also encouraged some of the species within these families to be successful invaders (Lenzner et al. 2021).

# What are the drivers of alien species richness and cover and how are they affected by the native community?

We found that alien species richness and cover increased with native functional richness in the studied heap sites. Our finding is consistent with the niche-filling hypothesis (Thuiller et al. 2010; Loiola et al. 2018). The theory states that there are available niches left for alien species establishment in a functionally-rich community, while in a functionally-poor community, the niches are fewer and already occupied by native species. Alien species likely benefit from the presence of unoccupied ecological niches; therefore, filling them makes the functional space more saturated (Loiola et al. 2018). Therefore, our results do not support the biotic resistance theory – species-rich communities are more resistant to alien invasion than species-poor ones (e.g. Elton (1958), Bezeng et al. (2015)).

Our findings revealed that alien species cover decreased with native species cover on heap sites. Early native colonisers may control the establishment of later-arriving species by occupying niches and ensuring their persistence by creating abundant shade (Perry and Galatowitsch 2006). In our studied system, native species, such as *Tussilago farfara*, *Chamaenerion dodonaei* and *Calamagrostis epigejos*, are perennial early colonisers; therefore they persist for some years on heap sites (Stefanowicz et al. 2015; Kompała-Bąba et al. 2020). These native perennials could reduce the chances of the establishment of alien species with the same ecological requirements (Connell and Slatyer 1977). Therefore, ecologically-similar native species and early colonisers would be expected to capture more resources required by alien species due to niche overlap; thus, further suppressing alien species cover via limiting similarity (Abrams 1983). It has been hypothesised that niche takeover would occur when early- and later-arriving species are ecologically similar (Vannette and Fukami 2014). Our finding is in contrast to Lanta et al. (2022), who recorded an increase in alien species cover with native species cover in temperate lowland forests.

Our results showed that native CWM seed mass and plant height significantly predict alien species cover. Studies on the relationship between vegetation cover and the participation of species with different seed masses have shown that low cover (i.e. more open habitats) favoured the occurrence of species with small seed masses, while species with heavy seeds are successful in shaded habitats (Reader 1993; Kidson and Westoby 2000). A comparison of seedling survival of three temperate forest species differing in seed mass (*Prunus serotina*, *Quercus rubra* and *Robinia pseudoacacia*) confirmed that claim (Dyderski and Jagodziński 2019b). In our study, the native species pool had a low seed mass. Usually, alien species tend to avoid habitats where competitive natives with heavy seed masses were successful (Rees 1995; Turnbull et al. 1999). However, within early-successional communities, we found that alien plant cover increased with native plant seed mass. This suggests that pioneer alien species with low cover were frequent on newly-formed heaps (less than a year), while more competitive aliens with high cover (e.g. *Solidago* spp., *Impatiens parviflora*) invade sites where abiotic filtering does not limit the native species seedling establishment (early and mid-successional stages does not lead to strong competitive advantage over alien species during seedling establishment.

Plant height is an important ecological parameter in spontaneously-vegetated heap sites (Woźniak et al. 2011). Similarly, height controls the competitive ability of plant species (Weiher et al. 1999). In our study, the native species pool is characterised by low plant height. However, we found a positive relationship between alien cover and native plant height. This is because pioneer alien species usually have low cover and more competitive ones have a higher cover. Since our study is in successional communities, it only shows part of the whole gradient, revealing methodological differences in context dependence (Catford et al. 2022). Nevertheless, disturbance in closed habitats where natives have tall heights will continue to promote alien establishment through the creation of gaps. A similar result of increased alien species cover with native CWM plant height was obtained in temperate low-land forests (Lanta et al. 2022).

# What does it mean for predicting threats from alien species and management?

Our findings showed that alien species establishment was prominent in the early stage of post-coal mine vegetation development, but not on newly-formed heaps. Heap sites at the early developmental stage were characterised by alien species showing ruderal features that benefit from disturbance, for example, *Solidago gigantea*, *Solidago canadensis*, *Erigeron canadensis* and *Erigeron annuus*. These species reached a high level of ecological success. Therefore, to reduce invasibility, we recommend that the management objectives should be directed to the early stage of spontaneous vegetation formation on heap sites. Similarly, reduced ecological disturbance should be encouraged on heap sites to prevent ruderal colonising species and promote competitive native species.

Monitoring alien species invasion level and establishment on heaps and the surrounding landscape has high importance. Recent findings have shown that landscapes surrounding roads, railways and arable land harbour neophytes (Ballesteros et al. 2021). This affirms that the degree of urbanisation around colonised sites is an important invasion pathway and should be prioritised in alien species management strategies.

To prevent secondary invasion – an increase in the colonisation of non-target alien species after the removal of targeted invasive plants (Pearson et al. 2016), native species addition should be encouraged, specifically at the early successional stage. Our findings

showed that plant communities at the early stage of spontaneous vegetation development on heaps are most threatened by alien species; thus, the addition of competitive natives would prevent non-target alien species from exploiting the space created by the removed targeted invader (Hess et al. 2019). Similarly, species addition will not only help restore native species lost from the ecosystem due to mining activities, but can also increase the number of competitors which may act to reduce alien species recruitment, invasion level and ecological success (Bakker and Wilson 2004). A more detailed study on the abundance shifts between the alien and native plant species in the vegetation patches during the developmental stages might give additional insight into the relationship between the role of alien and native plant species in the establishment and functioning mechanisms of the novel ecosystems on post-coal mine heaps mineral habitats.

# Conclusions

Our study identified successful alien species and developed models on how native community characteristics explain alien species invasion level (alien richness) and ecological success (alien cover) on spontaneously-vegetated post-coal mine heaps. Amongst studied plant communities, those at the early stage of spontaneous vegetation development are the most threatened by alien species, thus requiring active management and conservation. *Erigeron canadensis, Solidago gigantea, Solidago canadensis, Erigeron annuus* and *Impatiens parviflora* should be designated as priority aliens for management action on post-industrial vegetation. Introducing native species at early stages of vegetation development can decrease the level of threat from invasive species.

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# Supplementary material I

#### Frequency and cover of alien species occurring on post-coal mine spoil heaps

Authors: Quadri A. Anibaba, Marcin K. Dyderski, Gabriela Woźniak, Andrzej M. Jagodziński

Data type: table (word document)

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Appendix 1: Frequency and cover of alien species occurring on post-coal mine spoil heaps.

Species	Frequency (number of plots)	Mean cover (%)
Erigeron canadensis	108	2.50
Solidago gigantea	87	14.25
Solidago canadensis	77	7.29
Erigeron annuus	67	5.24
Impatiens parviflora	40	14.70
Tripleurospermum inodorum	38	2.21
Echinochloa crus-galli	30	1.97
Silene latifolia	27	1.74
Hordeum jubatum	18	3.06
Kali turgidum	16	1.75
Lepidium ruderale	15	1.53
Pastinaca sativa	14	2.29
Setaria viridis	13	9.62
Diplotaxis muralis	12	2.33
Prunus serotina	12	16.33
Clematis vitalba	11	14.09
Reynoutria japonica	9	31.67
Sonchus asper	9	1.44
Avena sativa	8	9.75
Digitaria ischaemum	7	11.00
Medicago sativa	7	5.71
Symphyotrichum salignum	7	5.14
Fallopia convolvulus	6	2.33
Typha minima	6	4.67
Cichorium intybus	5	1.80
Amaranthus retroflexus	4	1.00
Sisymbrium officinale	4	3.25
Bromus sterilis	3	2.33
Caragana arborescens	3	30.00
Iuncus tenuis	3	1.00
Lathyrus tuberosus	3	2.33
Lepidium campestre	3	1.00
Setaria helvola	3	1.00
Sinapis arvensis	3	1.00
Solanum nigrum	3	1.00
Apera spica-venti	2	5.00
Eragrostis minor	2	3.00
Helianthus tuberosus	2	10.50
Lactuca serriola	2	1.00
Matricaria discoidea	2	1.00
Robinia pseudoacacia	$\frac{1}{2}$	50.50
Senecio vulgaris	$\frac{1}{2}$	1.00
Aesculus hippocastanum	- 1	10.00
Atriplex sagittata	1	1.00

Bidens frondosa	1	5.00
Brassica napus	1	1.00
Bunias orientalis	1	5.00
Centaurea cyanus	1	1.00
Cornus alba	1	15.00
Datura stramonium	1	1.00
Elaeagnus angustifolia	1	5.00
Erechtites hieraciifolia	1	10.00
Helianthemum nummularium	1	1.00
Hippophae rhamnoides	1	20.00
Leonurus cardiaca	1	1.00
Myosotis arvensis	1	1.00
Prunus domestica	1	1.00
Solanum tuberosum	1	1.00
Spiraea media	1	5.00
Symphoricarpos albus	1	21.00
Typha laxmannii	1	1.00
Urtica urens	1	1.00
Vicia sativa	1	1.00
Vicia tetrasperma	1	1.00
Vitis vinifera	1	20.00

# **PUBLICATION 2**

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# The Inhibitory Tendency of *Calamagrostis epigejos* and *Solidago* spp. Depends on the Successional Stage in Postindustrial Vegetation

Quadri A. Anibaba<sup>1</sup> 💿 | Marcin K. Dyderski<sup>1</sup> 💿 | Gabriela Woźniak<sup>2</sup> 💿 | Andrzej M. Jagodziński<sup>1</sup> 💿

<sup>1</sup>Instytut Dendrologii Polskiej Akademii Nauk, Kórnik, Poland | <sup>2</sup>Institute of Biology, Biotechnology and Environmental Protection, Faculty of Natural Sciences, University of Silesia, Katowice, Poland

Correspondence: Quadri A. Anibaba (qanibaba@man.poznan.pl)

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#### ABSTRACT

In spontaneously vegetated postindustrial areas, we have limited knowledge of whether the known inhibitory tendencies of herbaceous species—*Calamagrostis epigejos* and *Solidago* spp.—vary across successional stages. Our study fills this knowledge gap to assess the inhibitory role of the invasive alien and expansive native species with known behavior from the literature. Specifically, we hypothesized: (i) there will be an inhibitory effect of these species on diversity across successional classes; (ii) the effect of a species will depend on the successional class due to abiotic requirements of plant communities in each successional class. We recorded vascular plant species and their abundance across 400 plots on post-coal mine heaps in Upper Silesia, Poland. We classified spoil heaps into three successional classes (early-stage; mid-stage; late-stage). We calculated plant community taxonomic, functional, and phylogenetic diversity and, using generalized linear mixed-effects models, we estimated predictors of diversity indices across successional classes. While we found no limiting effects of these species on diversity indices across successional classes (be found no limiting effects of claamagrostis and *Solidago* cover on diversity indices in the mid-successional stage. This implies that the early-successional stage is controlled by the lottery (random) model of community assembly. However, in the mid-successional stage, the competitive exploitation mechanism is evident, resulting in declines in diversity indices. Thus, the impacts of *Calamagrostis* and *Solidago* on diversity indices are evident in the mid-successional stage.

#### 1 | Introduction

Globally, the need for the restoration of postindustrial sites, for example, post-coal-mining spoil heaps, stone quarries, or sand pits is of urgent significance. Mining areas occupy about 1% of the global land area (Maus et al. 2022), and specifically, coal mining and related disturbances impact biodiversity, leading to the creation of novel ecosystems (Conradi, Henriksen, and Svenning 2021; Erskine and Fletcher 2013; Hobbs et al. 2006;

van Andel 2013). These emerging ecosystems result from novel combinations of species in response to rapidly changing land use and direct human impacts (Hobbs, Higgs, and Harris 2009; Lindenmayer et al. 2008). Thus, novel ecosystems can be hypothesized to occupy a midpoint between a gradient of "natural" ecosystems and intensively managed systems (Hobbs et al. 2006).

In recent times, spontaneous succession has received great attention for the restoration of post-mining sites (Hodačová and

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Prach 2003; Mudrák, Frouz, and Velichová 2010; Šebelíková et al. 2019; Vaverková et al. 2018). This is due to the enormous potential of spontaneous vegetation development for nature conservation, and its high cost-effectiveness. By adopting a chronosequence approach, we were able to depict communities of various successional classes through vegetation patches of different ages (Fu et al. 2023; Li et al. 2022).

In central European post-mining areas, spontaneous primary succession on post-brown coal open-cast heaps begins from bare substrate materials with few and scattered annual and biennial plants, usually lasting up to 10 years. Then, these species are replaced by dominant herbaceous plants. In the subsequent sere, shrublands expand after 15 years, facilitating the encroachment of broadleaved tree species (Badraghi et al. 2023; Prach and Pyšek 2001; Wiegleb and Felinks 2001). While the process of spontaneous succession in post-mine areas may seem straightforward, it has low predictability and is dependent on site characteristics (Mudrák, Doležal, and Frouz 2016; Prach 2003). Besides, the role of biotic interactions, for example, competitive inhibition, becomes significant in the course of succession (Błońska et al. 2019; Kompała-Baba et al. 2020; van Kleunen, Fischer, and Schmid 2001; Wiegleb and Felinks 2001; Woźniak, Chmura et al. 2021).

Competitive inhibition is one of the three models controlling the mechanism of succession in natural communities (Connell and Slatyer 1977). In the inhibition model, early colonists suppress the development of later colonists, and the latter succeed only if they have adequate resources, to provide them with competitive superiority. Therefore, inhibition can delay or even block successional change, provided that the inhibitor can maintain its dominance (Walker and del Moral 2003). In successional communities of post-mine areas, the inhibitory role of invasive species and expansive natives is important but underappreciated (Bartha et al. 2014; Rebele 2013; Somodi, Virágh, and Podani 2008). Perennial native and invasive species can both dominate a successional stage, often by monopolizing light, water, and nutrients through dense vegetation development (Kompała-Bąba et al. 2020; Rebele 2013).

In our recent findings, two invasive Solidago species (i.e., S. canadensis and S. gigantea), and the expansive native species-Calamagrostis epigejos, were among the most frequent plant species in postindustrial vegetation (Anibaba et al. 2023). In post-mine areas, an increasing body of literature concerning the impacts of these invasive alien species on spontaneous vegetation development has focused on their effects on taxonomic diversity (e.g., Bartha et al. 2014), or as succession inhibitors (e.g., Rebele 2013). Other authors have studied the effect of the expansive native—C. epigejos—on nutrient availability (Kompała-Bąba et al. 2020; Stefanowicz et al. 2015), or the species impact as a strong competitor and its ability to halt spontaneous succession (Mudrák, Frouz, and Velichová 2010; Rebele and Lehmann 2002; Somodi, Virágh, and Podani 2008). Only a few studies have focused on how these species can affect the functional and phylogenetic diversity of vegetation developing spontaneously in postindustrial and post-agricultural areas (Czortek et al. 2023; Kompała-Baba et al. 2020; Woźniak, Dyderski et al. 2021). We have a limited understanding of whether the inhibitory tendencies of these species during spontaneous vegetation development in post-mine areas depend on the successional stage or are species-specific. In this context, the results obtained may be applied to other invasive alien species and expansive natives with a similar ecology to *S. canadensis*, *S. gi-gantea*, and *C. epigejos*.

Our study aimed to assess the inhibitory role of alien and native species with known behavior from the literature. We hypothesize: (i) there will be an inhibitory effect of these species on diversity across successional classes (vegetation patches of different ages); (ii) the effects of a species will depend on the successional class due to abiotic requirements of plant communities in each successional class.

#### 2 | Materials and Methods

#### 2.1 | Studied Species

*S. canadensis* and *S. gigantea* are North American plant species from the Asteraceae family. Both species are herbaceous perennials forming above-ground shoots and below-ground rhizomes (Weber and Jakobs 2005; Werner, Gross, and Bradbury 1980). They are non-native to central Europe ecosystems and have been recognized as successional inhibitors. On rich soil types, *S. canadensis* can delay succession toward forest (Rebele 2013). Similarly, *S. gigantea* can dominate the mid-successional stage, negatively impact diversity and temporarily arrest succession (Bartha et al. 2014). Both *S. canadensis* and *S. gigantea* cooccur in wasteland communities in central Europe (Czortek et al. 2023). They can colonize these man-made habitats and dominate in early and mid-successional stages. Both *S. canadensis* and *S. gigantea* are similar in size, dispersal characteristics, and growth form.

C. epigejos is a tall rhizomatous perennial grass native to Eurasia and thrives in a broad range of natural, semi-natural, and manmade habitats (Rebele and Lehmann 2001). The grass is a strong competitor due to its rapid clonal propagation. As an expansive native, C. epigejos is problematic not only in Central Europe but also in Western Europe. C. epigejos can halt the early stages of spontaneous succession (Mudrák, Frouz, and Velichová 2010; Rebele and Lehmann 2001; Somodi, Virágh, and Podani 2008). It suppresses other plant species and causes considerable problems in the restoration of post-mine sites (Rebele and Lehmann 2002; Somodi, Virágh, and Podani 2008), as a successional inhibitor (Hegedüšová and Senko 2011; Jańczyk-Węglarska 1996; Marozas, Racinskas, and Bartkevicius 2007). Overall, S. canadensis, S. gigantea, and C. epigejos can delay woody species colonization and succession by closure of the bare ground which inhibits germination, then by competition for light, water, and nutrients with woody seedlings.

# 2.2 | Description of the Study Site

The study was conducted in Upper Silesia, an area with a long history of coal mining (since the 18th century). The long-term mining activity has resulted in enormous regions of post-coal mine sites covering more than 8 km<sup>2</sup> (Szczepańska 1987). The anthropogenic landscape has been altered by these

mineral material sites formed by Carboniferous deposits on pre-Cambrian crystalline rocks. The Carboniferous mudstone and sandstone complexes are combined with various coal components (Cabała, Cmiel, and Idziak 2004).

Plant development on coal mine heaps is difficult due to the harsh abiotic conditions of the mineral material habitats, such as wide differences in daily temperatures (often reaching 50°C) and moisture, substrate instability, absence of soil, vulnerability to erosion, dusting, thermal, and chemical actions. Aside from abiotic factors, the post-coal mine waste is distinguished by extreme biotic characteristics such as substrate nutrient deficit and lack of a seed bank (Woźniak, Dyderski et al. 2021). These habitat characteristics influence the ability of vegetation to colonize postindustrial areas (Bradshaw 2000; Prach et al. 2013).

# 2.3 | Study Design and Vegetation Sampling

From a record of 112 post-mining sites with accessible data on age, size, vegetation, and reclamation techniques (Woźniak 2010), we removed 31 varying in size, land-use patterns in the surrounding area, thermal activity, or were technically formed (i.e., covering the sites with fertile topsoil and intentional planting of herb mixtures and trees). We opted to remove these factors because they may significantly influence observed patterns of vegetation assembly (Anibaba et al. 2023). While this reduced the overall variation of abiotic conditions, it allowed us to conclude that trends in the data were not impacted by noise associated with the treatments outlined above. From the remaining 81 sites, we selected 60 sites at random based on post-coal mine heap size, age, and adjacent land cover. Among the selected sites, we classified three spoil heap classes representing successional stage (i.e., early-stage [1-8 years] - Class 0; mid-stage [6-14 years] - Class 1; late-stage [25–56 years] – Class 2) (Figure S1) and randomly chose plots corresponding to these classes (Anibaba et al. 2024). Using the findings of this study and that of Anibaba et al. (2023), we randomly selected 80 vegetation patches within the 60 sites. The 80 vegetation patches proportionally represent the spoil heap classes on the study sites, and each patch encompasses an area of at least 150×150m. The vegetation patch forms the basis of plot selection. We created five plots in a cross pattern inside each randomly selected vegetation patch (i.e., one central plot and four subplots at distances of 50 m in the north, south, east, and west directions; 400 plots in total; Figure 1). Each plot had a 3m radius (28.3 m<sup>2</sup>). Within each plot, we recorded all vascular plant species and their abundance using a Londo scale (Londo 1976). For Calamagrostis and Solidago cover, we did not preferentially sample these species, but we used a natural gradient of their abundance resulting from our field survey data based on random establishment of sample plots.





Using the "V.PhyloMaker" package (Jin and Qian 2022), we acquired a phylogenetic tree comprising all plant species recorded in the study plots, derived from a mega-tree provided in the package. We also obtained plant species functional traits (Table 1) from the LEDA (Klever et al. 2008), BIEN (Maitner et al. 2018), Pladias (Chytrý et al. 2021), and BioFlor (Klotz et al. 2002) databases that comprise a wide variety of plant reproductive characteristics, life-history traits, and measures of leaf morphology. We also acquired Ellenberg's ecological indicator values (EIVs) characterizing species environmental requirements (Ellenberg and Leuschner 2010). In order not to omit missing data, we used the random forest-based trait imputation to fill gaps in the trait and EIV data (Penone et al. 2014) implemented in the missForest::misForest() function (Stekhoven 2022) and the phylogenetic eigenvectors (Diniz-Filho, de Sant'Ana, and Bini 1998) obtained from the PVR package (Santos 2018). The first 15 phylogenetic eigenvectors explained 59.3% of the variation in phylogenetic distances among plant species.

In this study, we analyzed the three facets of species diversity measures: taxonomic, phylogenetic, and functional at the alpha (within site) level. Using the "vegan" package (Oksanen et al. 2022), we estimated taxonomic alpha diversity by species richness and Shannon's diversity index. We estimated the standardized effect size of Faith's phylogenetic diversity (SES.PD) using the "picante" package (Kembel et al. 2020). Standardized effect sizes account for the influence of species richness (Pavoine et al. 2013; Swenson 2014), and were calculated as (observed value - expected value)/standard deviation of the expected value. The expected values were computed using a null distribution of 999 random species assemblages chosen without replacement from the species pool. Species identities within communities were randomized, but the number of species remained fixed-the "Independentswap" null model (Gotelli 2000). Positive SES.PD values imply phylogenetic overdispersion (i.e., species more distantly related to each other than expected by chance), while negative values indicate clustering (i.e., species more closely related to each other than expected by chance). Using the dbFD() function from the "FD" package (Laliberté, Legendre, and Shipley 2022), we calculated Functional richness (FRic) a metric that estimates the trait space of plant functional types present in a community (Laliberté and Legendre 2010). We calculated correlations between taxonomic, phylogenetic, and functional measures (Figure S3). We removed our focal species—S. canadensis, S. gigantea, and C. epigejos from the calculations of taxonomic, phylogenetic, and functional diversity measures to avoid circular reasoning (Czortek, Orczewska, and Dyderski 2021; Dyderski and Jagodziński 2018; Thomsen et al. 2016).

# 2.5 | Data Analyses

All analyses were conducted using R software, version 4.3.0 (R Core Team 2023). To gain insights into the species composition of all study plots across the three classes of successional stages, we used presence-absence transformed data in the nonmetric

Numeric traits		min	max	Mean	CV (%)	Completeness (%)
Light EIV		1	9	6.8	21.9	98.1
Moisture EIV		2	11	5.3	31.7	86.8
Temperature EIV		2	8	5.6	15.2	72.9
Nitrogen EIV		1	9	5.0	40.5	87.7
Soil reaction EIV		1	9	6.3	24.0	69.1
Start of flowering (months)		1	9	5.6	20.9	98.9
Duration of flowering (months)		1	12	3.4	40.6	98.9
Seed mass (SM) (mg)		0.001	13,737.6	108.1	902.9	94.5
Specific leaf area (SLA) (cm <sup>2</sup> g <sup>-1</sup> )	)	51.8	899.1	250.7	43.3	87.9
Maximum plant height $(H)$ (m)		0.033	60.0	4.1	242.4	98.9
Leaf dry matter content (LDMC	$(mgg^{-1})$	300	509.5	229.4	30.9	81.1
Categorical traits	Number of	classes	Classes a	and their frequ	iency	Completeness (%)
Insect pollinated	2		Yes (7	/3.7%), no (26.39	%)	95.9
Wind pollinated	2		Yes (2	28.9%), no (71.19	%)	95.9
Self-pollinated	2		Yes (5	3.5%), no (46.59	%)	95.9
Life form	8		Chamaephytes Hemicryptoph (0.9%), Lianas Phanerophytes (	s (4.6%), Geoph ytes (53.2%), H s (2.9%), Parasi 15.0%), Therop	ytes (7.2%), ydrophytes tes (0.6%), hytes (15.6%)	100.0

TABLE 1 | Ellenberg's ecological indicator values (EIVs) and traits used in the study, their ranges, variation coefficient (CV), and completeness.

multidimensional scaling (NMDS) implemented in the vegan package (Oksanen et al. 2022). Before NMDS, we excluded 28 plots without vegetation and 14 plots with only one species, that produced artifacts and did not allow NMDS to reach convergence (resulting in n = 358 for NMDS).

To assess the limiting effects of Solidago and Calamagrostis cover on diversity indices across the successional classes. we developed linear mixed-effect models, except for species richness and functional richness, for which we used generalized linear mixed-effect models assuming Poisson distributions and zero-inflated beta distributions of the dependent variables, respectively. We developed these models using the "lme4" and "glmmTMB" packages (Bates et al. 2015; Brooks et al. 2017). We used the percentage cover of Solidago and Calamagrostis, successional class, and their interaction as predictors. We square root transformed cover of Solidago and Calamagrostis to obtain distributions closer to normal. Square root transformation decreases the relatively higher differences between midpoints of cover classes and allows for better handling of species that occur with lower coverage. In addition, we used blocks of plots nested with the heap identifiers as random intercepts to account for the spatial dependence of the study design. We used the ggeffects::ggpredict() function in the "ggeffects" package (Lüdecke 2018) to obtain marginal responses from models, that is, predicted responses excluding random effects and assuming a constant (mean) value for all other predictors.

To identify models with variables that best predict diversity indices across successional classes on post-coal mine heaps, we used a model selection—*dredge()* function in the "MuMIn" package (Bartoń 2022), where all combinations of variables in the model were ranked based on the corrected Akaike Information Criterion, corrected for small sample size (AICc). For each model, we reported the AICc of the global model (i.e., all hypothesized predictors), final model, and null (intercept and random effect only) model, to show how the final model differs from them. We ensured that the Poisson GLMM was not biased by overdispersion using the *check\_overdispersion()* function in the "performance" package (Lüdecke et al. 2021).

## 3 | Results

Solidago and Calamagrostis cover differed across successional classes (Tables S1 and S2; Figure S2). The general pattern of vegetation development across successional stages on postcoal mine spoil heaps revealed that vegetation succession generally proceeds from an early-successional stage with black and coaly spoil materials majorly colonized by synanthropic species. These species establish on open sites and spoils at the early stage of successional development (e.g., Tussilago farfara, Erigeron canadensis, Taraxacum officinale, Echium vulgare, Daucus carota, or Cirsium arvense). The mid-successional stage was dominated by species that are characteristic of dense low vegetation (i.e., meadows and grasslands, e.g., C. epigejos, Poa compressa, P. pratensis, Polygonum aviculare, S. canadensis, S. gigantea, Artemisia vulgaris, or Hypericum perforatum). Only four herbaceous species were most frequent in the latesuccessional stage, covered by dense high vegetation, and dominated by trees and shrubs. These species were Urtica dioica, Impatiens parviflora, Geum urbanum, and Deschampsia cespitosa, and all of them adapted to shade or moderate shade conditions (Figure 2).

# 3.1 | The Impact of *Calamagrostis* Cover on Diversity Indices Across Successional Stages

Among all tested predictors of species richness in post-coal mine spoil heaps, the best-fit model was explained by the interaction of percentage cover of *Calamagrostis* and spoil heap successional class (AICc global model=1990.09, AICc null



**FIGURE2** | Results of nonmetric multidimensional scaling (NMDS) analysis for all study plots showing species having a frequency (number of plots recorded) ≥40. Spoil heap class: 0, early-successional; 1, mid-successional; 2, late-successional. [Colour figure can be viewed at wileyonlinelibrary. com]

model = 2014.91, AICc best model = 1982.63). Species richness had a nonsignificant relationship with the percentage cover of *Calamagrostis* under the early- and late-successional stages. However, under the mid-successional class, predicted species richness decreased significantly with the percentage cover of *Calamagrostis* (Table 2; Figure 3a).

For predicted Shannon diversity, the best model was explained by the interaction of percentage cover of *Calamagrostis* and spoil heap successional class (AICc global model = 551.63, AICc null model = 588.19, AICc best model = 548.92). While the percentage cover of *Calamagrostis* marginally predicted Shannon diversity under the mid-successional class, we found a nonsignificant relationship between Shannon diversity and percentage cover of *Calamagrostis* under the early- and late-successional stages, respectively (Table 2; Figure 3b).

The best model for predicted functional richness was explained by the interaction of percentage cover of *Calamagrostis* and spoil heap successional class (AICc global model = -1219.12, AICc null model = -1211.51, AICc best model = -1227.98). The relationship between predicted functional richness and percentage cover of *Calamagrostis* was negative under the midsuccessional class, however under early- and late-successional

TABLE 2 | Estimates of the final model predicting percentage cover of *Calamagrostis* on diversity indices.

Predictor	Estimate	SE	t/Z value <sup>a</sup>	р
Species richness				
Intercept	2.07	0.11	18.75	< 0.0001
Calamagrostis cover (square root)	0.06	0.02	3.20	0.0014
Class 1	0.58	0.16	3.69	0.0002
Class 2	-0.30	0.15	-1.99	0.0465
Calamagrostis cover (square root) × Class 1	-0.06	0.02	-2.85	0.0043
Calamagrostis cover (square root)×Class 2	0.07	0.06	1.07	0.2853
Shannon diversity				
Intercept	1.43	0.12	11.84	< 0.0001
Calamagrostis cover (square root)	0.11	0.02	4.43	< 0.0001
Class 1	0.40	0.18	2.16	0.0337
Class 2	-0.16	0.16	-1.03	0.3071
Calamagrostis cover (square root) × Class 1	-0.06	0.03	-1.88	0.0610
Calamagrostis cover (square root) × Class 2	< 0.01	0.08	0.03	0.9773
Functional richness				
Intercept	-2.79	0.14	-19.31	< 0.0001
Calamagrostis cover (square root)	0.09	0.03	3.02	0.0025
Class 1	0.61	0.22	2.80	0.0051
Class 2	-0.20	0.19	-1.06	0.2894
Calamagrostis cover (square root) × Class 1	-0.10	0.03	-3.05	0.0023
Calamagrostis cover (square root) × Class 2	0.10	0.09	1.13	0.2573
(zero-inflated)				
Intercept	-22.43	4010.00	-0.006	0.9960
SES.PD				
Intercept	-1.36	0.19	-7.14	< 0.0001
Calamagrostis cover (square root)	-0.11	0.04	-2.44	0.0156
Class 1	-0.42	0.30	-1.39	0.1679
Class 2	1.47	0.26	5.60	< 0.0001
Calamagrostis cover (square root)×Class 1	0.10	0.06	1.70	0.0895
Calamagrostis cover (square root)×Class 2	-0.39	0.16	-2.42	0.0162

<sup>a</sup>Z value for Poisson and beta GLMMs (species richness and functional richness); t value for Gaussian GLMMs.





Predicted functional richness Predicted SES PD 0.0 0.10 0.05 0.0 50  $\dot{7}5$ 10.0 50 5 10.0 5.0 7.5 Percentage cover (Square root) Spoil heap class - Class 0 - Class 1- Class 2 FIGURE 3 | Partial regression models with covers of Calamagrostis, Solidago, and spoil heap successional class as predictors influencing the

b

Predicted Shannon diversity

d

2

0.0

2.5

10.0

75

Calamagrostis

5.0

Calamagrostis

75

Solidago

50

Solidago

species richness (a), Shannon diversity (b), functional richness (c), and predicted standardized effect size phylogenetic diversity (SES PD) (d). Interactions between Calamagrostis, Solidago cover, and spoil heap successional class were visualized by blue, orange, and green lines, which are marginal predictions for three levels of spoil heap class: 0, 1, and 2 (0, early-successional; 1, mid-successional; 2, late-successional). Dashed lines represent a 95% confidence interval of prediction. [Colour figure can be viewed at wileyonlinelibrary.com]

classes, we found a nonsignificant relationship between functional richness and percentage cover of Calamagrostis (Table 2; Figure 3c).

10.0

0.0

а

Predicted species richness

С

0.20

20

0.0

Calamagrostis

Calamagrostis

For predicted standard effect size phylogenetic diversity (SES PD), the best model was explained by the interaction of percentage cover of Calamagrostis and spoil heap successional class (AICc global model=995.34, AICc null model=1038.84, AICc best model=988.40). Predicted SES PD increased marginally with Calamagrostis cover under the mid-successional class. However, under the late-successional class, SES PD decreased with Calamagrostis cover. We found a nonsignificant relationship between SES PD and Calamagrostis cover under the earlysuccessional class (Table 2; Figure 3d).

# 3.2 | The Impact of Solidago Cover on Diversity **Indices Across Successional Stages**

The most parsimonious model for predicted species richness was the interaction of Solidago cover and spoil heap successional class (AICc global model = 2018.64, AICc null model = 2043.16, AICc best model=2004.10). Predicted species richness decreased with Solidago cover under the mid-successional class. Conversely, a nonsignificant relationship was found between species richness and Solidago cover under the early- and latesuccessional classes (Table 3; Figure 3a).

The best model for predicted Shannon diversity was explained by the interaction of Solidago cover and spoil heap successional class (AICc global model=508.38, AICc null model = 519.21, AICc best model = 504.15). The relationship between predicted Shannon diversity and Solidago cover was negative under the mid-successional stage, however in early- and late-successional classes, we found a nonsignificant relationship between Shannon diversity and Solidago cover (Table 3; Figure 3b).

For predicted functional richness, the best model was explained by the interaction of Solidago cover and spoil heap successional class (AICc global model = -1222.33, AICc null model = -1207.89, AICc best model = -1228). While predicted functional richness significantly decreased with Solidago cover under the mid-successional class, we found a nonsignificant relationship between functional richness and Solidago cover under the early- and late-successional classes (Table 3; Figure 3c).

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**TABLE 3** Estimates of the final model predicting percentage cover of *Solidago* on diversity indices.

Predictor	Estimate	SE	t/Z value <sup>a</sup>	р
Species richness				
Intercept	2.14	0.10	21.10	< 0.0001
Solidago cover (square root)	0.09	0.03	2.84	0.0045
Class 1	0.57	0.14	4.02	< 0.0001
Class 2	-0.45	0.15	-3.00	0.0027
Solidago cover (square root) × Class 1	-0.11	0.03	-3.26	0.0011
Solidago cover (square root) × Class 2	-0.01	0.04	-0.25	0.8009
Shannon diversity				
Intercept	1.41	0.12	11.81	< 0.0001
Solidago cover (square root)	0.11	0.045	2.55	0.0110
Class 1	0.47	0.17	2.76	0.0078
Class 2	-0.19	0.17	-1.14	0.2600
Solidago cover (square root)×Class 1	-0.11	0.049	-2.15	0.0330
Solidago cover (square root) × Class 2	-0.02	0.056	-0.27	0.7840
Functional richness				
Intercept	-2.56	0.12	-20.48	< 0.0001
Solidago cover (square root)	0.12	0.05	2.23	0.0256
Class 1	0.49	0.18	2.78	0.0054
Class 2	-0.54	0.19	-2.84	0.0045
Solidago cover (square root)×Class 1	-0.15	0.06	-2.59	0.0097
Solidago cover (square root) × Class 2	-0.04	0.07	-0.61	0.5443
(zero-inflated)				
Intercept	-22.32	3765.75	-0.006	0.9950
SES.PD				
Intercept	-1.44	0.15	-9.70	< 0.0001
Solidago cover (square root)	-0.19	0.09	-2.11	0.0359
Class 1	-0.42	0.22	-1.91	0.0635
Class 2	1.62	0.23	6.95	< 0.0001
Solidago cover (square root)×Class 1	0.20	0.10	2.00	0.0460
Solidago cover (square root) × Class 2	0.04	0.11	0.34	0.7348

<sup>a</sup>Z value for Poisson and beta GLMMs (species richness and functional richness); t value for Gaussian GLMMs.

# 4 | Discussion

In spontaneously vegetated postindustrial areas, it was unclear whether the known inhibitory tendencies of *Calamagrostis* and *Solidago* vary across successional stages. In this study, we addressed this knowledge gap using data from post-coal mining spoil heaps in Upper Silesia, Poland (Anibaba et al. 2023) to assess the inhibitory role of alien species and expansive native species across successional gradients. We found the inhibitory effects of these herbaceous species on diversity indices strongly depended on the successional stage. The impact of *Calamagrostis*  and *Solidago* cover on diversity indices were strong in the midsuccessional stage. Even with a low effect size, the effect in the mid-successional stage was significant due to more representation and high dispersion in the early- and late-successional stages. Besides, such a limiting effect is not straightforward because the cover of *Calamagrostis* and *Solidago* were square root transformed.

In the early stage of succession, we found a nonsignificant relationship between diversity indices and the cover of *Calamagrostis* and *Solidago*. As revealed in the model of

succession, diversity in newly disturbed areas is not limited by competition for limited resources, instead, it delineates the capability of species to colonize, grow rapidly, and tolerate environmental conditions (Connell and Slatyer 1977; Huston and Smith 1987). Therefore, colonization and fast growth rate are regarded as important traits for a plant species to occupy available space in early succession. Environmental conditions following post-coal mine heaps formation such as light, high temperature, drought, high salinity, and low levels of soil development (Woźniak, Dyderski et al. 2021) are particularly suitable for colonization by both native and alien species that possess stress-tolerant and ruderal characteristics (Fazlioglu et al. 2021; Kompała-Bąba et al. 2019). In our study sites, we recorded a high frequency of species that show stress tolerance and ruderal characteristics such as T. farfara, E. canadensis, T. officinale, E. vulgare, D. carota, and C. arvense. Therefore, to fill the available niche created due to spoil heap formation, early stages of succession are most susceptible to colonization by both native and alien species and this is consistent with successional theory (Huston and Smith 1987). Similarly, species composition of early successional plant communities is determined by colonization probabilities (Foster et al. 2004), and interspecific interactions are weak as assumed in lottery models of community assembly-plant species compete for colonization of available space made vacant by disturbance (in our case spoil heap formation) (Pacala and Tilman 1994). As such, exploitative competition resulting in a decline in diversity indices is less important in the early stages of successional development.

In the mid-successional stage, species richness and functional richness decreased significantly with the cover of Calamagrostis and Solidago. Shannon diversity was negative while phylogenetic diversity was positive with the cover of Solidago. Shannon diversity marginally decreased while phylogenetic diversity marginally increased with the cover of Calamagrostis. We argue that native and alien species colonize and establish in the early stages of succession which also supports our previous findings (Anibaba et al. 2023). However, some of these species that are perennial and expansive can persist into the mid-stage of succession, thereby inhibiting the successional pathway and affecting species diversity. Calamagrostis and Solidago can reduce species richness at the community scale, especially in the mid-successional stage, which is characterized by high biomass and species richness, where competitive interactions shape the structure of plant communities (Bartha et al. 2014; Rehounková and Prach 2006).

From our previous findings in the same study site, the midsuccessional stage possesses plant communities with a greater number of co-occurring alien plant species (Anibaba et al. 2023). These species, when they are abundant, could have an adverse impact on diversity indices, and this could result from several mechanisms. Firstly, different invasive alien species that are frequent in the mid-successional stage could have varied extents of impacts (Hejda, Pyšek, and Jarošík 2009; Pearson et al. 2016), therefore a large alien species pool (richness) could increase the probability that *Solidago* has a strong negative impact. Secondly, the occurrence of multiple alien species in the mid-successional stage could be a signal that one species is altering the abiotic environment, thus creating a niche for subsequent invasion by more impactful invaders such as *Solidago*—a case of the invasional meltdown hypothesis (Ricciardi et al. 2013; Simberloff and Von Holle 1999).

Our study is in line with some previous studies, while others differ. In a study of abandoned agricultural old-fields with species composition shaped by long-term anthropogenic influence and disturbance in Hungary, Bartha et al. (2014) reported that dominant species of Calamagrostis and Solidago led to a decline in diversity in the mid-successional stage. Similarly, Rehounková and Prach (2006) found that perennial grasses and forbs were dominant in the mid-successional stage of spontaneous vegetation succession in disused gravel-sand pits in the Czech Republic. They found that typical species in dry sites were C. epigejos, Festuca ovina, Avenella flexuosa, Achillea millefolium, and Agrostis capillaris, while Carex brizoides, Poa palustris ssp. palustris, and D. cespitosa were typical of wet sites. Kompała-Bąba et al. (2020) studied the impacts of four dominant species (C. epigejos, D. carota, P. compressa, and T. farfara) on species and functional diversity in post-coal mining spoil heaps and reported that T. farfara resulted in declines in species and functional diversity, whereas C. epigejos did not cause a decline in species or functional diversity. It should be noted that the Kompała-Baba et al. (2020) study focused on the earlysuccessional stage, and did not include later stages of succession. Besides, Frouz et al. (2008) found that the cover of T. farfara peaked in early succession and steadily declined in later stages of succession, whereas that of C. epigejos gradually increased in early succession, and became optimum in mid-succession in non-reclaimed post-mining sites of Sokolov, Czech Republic. Therefore, the claim by Kompała-Bąba et al. (2020) that C. epigejos did not have an impact on species richness and functional diversity agrees with our findings for the early stage of succession in post-coal mining sites.

In general, *Calamagrostis* and *Solidago* exhibited an exploitative competition mechanism which was visible in the midsuccessional stage of post-coal mining sites—where resources become limiting, disturbance is reduced and diversity is high. Thus, if an invasive alien species or expansive native species is more competitive, it can utilize more of the available resources leading to a decline in diversity indices (White, Wilson, and Clarke 2006). It has been shown that disturbances such as mowing can reduce the inhibitory tendency of *Calamagrostis* and *Solidago* in the restoration of landfill sites in Berlin, Germany (Rebele and Lehmann 2002).

In the late-successional stage, we found a nonsignificant prediction of species richness, Shannon diversity, and functional richness with the cover of *Calamagrostis* and *Solidago*. Phylogenetic diversity significantly increased with the cover of *Calamagrostis*, and nonsignificant with *Solidago* cover. It is expected that because *Calamagrostis* and *Solidago* are intolerant of full or moderate shade (see Rebele and Lehmann 2001; Weber and Jakobs 2005; Werner, Gross, and Bradbury 1980), they will not affect diversity indices in the late-successional stage, because species present in that stage are dominated by trees, shrubs, and shade-tolerant forest herbs. We recorded a high frequency of these species adapted to full or moderate shade—*U. dioica, I. parviflora, G. urbanum*, and *D. cespitosa*. Most importantly *I. parviflora* was recorded in sites not disturbed by flooding, with

dense tree canopies. This agrees with the fact that *I. parviflora* is a shade-tolerant species with an effective dispersal strategy and is present in late-successional ecosystems (Dyderski and Jagodziński 2016; Florianová and Münzbergová 2017; Lanta et al. 2022).

#### 5 | Conclusions

We studied the inhibitory tendencies of *Calamagrostis* and *Solidago* across successional gradients. We found that the inhibitory effects of these herbaceous species on diversity indices strongly depended on the successional stage. The impacts of *Calamagrostis* and *Solidago* on diversity indices were evident in the mid-successional stage. This highlights the importance of environmental context and successional dynamics for the assessment of ecological impacts of invasive non-native and expansive native herbaceous species. Our approach can be applied to other invasive alien species and expansive natives with similar ecology niches to *Solidago canadensis*, *S. gigantea*, and *Calamagrostis*.

#### Author Contributions

Quadri A. Anibaba: conceptualization, data curation, methodology, formal analysis, visualization, writing – original draft, writing – review & editing. Marcin K. Dyderski: conceptualization, methodology, writing — review & editing. Gabriela Woźniak: conceptualization, methodology, investigation, writing — review & editing. Andrzej M. Jagodziński: conceptualization, funding acquisition, writing — review & editing.

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#### **Conflicts of Interest**

The authors declare no conflicts of interest.

#### Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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#### **Supporting Information**

Additional supporting information can be found online in the Supporting Information section.


Figure S1: Distribution of age across spoil heap class. Spoil heap class: 0 - early-successional, 1 - mid-successional, 2 - late-successional.

Predictor	Estimate	SE	z value	Р
Calamagrostis cover				
Intercept	-1.6204	0.2404	-6.7390	< 0.0001
class1	0.9036	0.3175	2.8460	0.0044
class2	-1.0133	0.5151	-1.9670	0.0491
(Zero-inflated)				
Intercept	-0.4568	0.1108	-4.1220	< 0.0001

Table S1: Estimates of *Calamagrostis* cover between spoil heap class.

Table S2: Estimates of *Solidago* cover between spoil heap class.

Estimate	SE	z value	Р
-2.8037	0.2835	-9.8900	< 0.0001
0.7371	0.3544	2.0800	0.0375
0.8672	0.3860	2.2470	0.0247
0.3553	0.1091	3.2570	0.0011
	Estimate -2.8037 0.7371 0.8672 0.3553	Estimate         SE           -2.8037         0.2835           0.7371         0.3544           0.8672         0.3860           0.3553         0.1091	Estimate         SE         z value           -2.8037         0.2835         -9.8900           0.7371         0.3544         2.0800           0.8672         0.3860         2.2470           0.3553         0.1091         3.2570



Figure S2: Predicted cover of Solidago and Calamagrostis between soil heap class.



Figure S3: Correlation matrix between taxonomic, phylogenetic, and functional measures for *Solidago* and *Calamagrostis* data. FDis – Functional dispersion, FDiv – Functional divergence, FEve – Functional evenness, FRich – Functional richness, Faith.PD – Faith's Phylogenetic diversity, SES.MPD – Standardized effect size of mean pairwise distances, SES.PD – Standardized effect size of phylogenetic diversity, SES.MNTD – Standardized effect size of mean nearest taxon distances, NRI – Net relatedness index, SM – Seed mass, SLA – Specific leaf area, H – Plant height, LDMC – Leaf dry matter content, EIV.T – Ellenberg indicator values temperature, EIV.L – Ellenberg indicator values light, EIV.M – Ellenberg indicator values moisture, EIV.N – Ellenberg indicator values nitrogen, EIV.SR – Ellenberg indicator values soil reaction, diversity – Shannon diversity, richness – species richness.

# **PUBLICATION 3**

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#### **RESEARCH ARTICLE**



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# Remote sensing for site selection in vegetation survey along a successional gradient in post-industrial vegetation

Andrzej M. Jagodziński<sup>1</sup> 💿

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Quadri A. Anibaba<sup>1</sup> | Marcin K. Dyderski<sup>1</sup> | Gabriela Woźniak<sup>2</sup> |

<sup>1</sup>Institute of Dendrology, Polish Academy of Sciences, Kórnik, Poland

<sup>2</sup>Institute of Biology, Biotechnology and Environmental Protection, Faculty of Natural Sciences, University of Silesia, Katowice, Poland

#### Correspondence

Quadri A. Anibaba, Institute of Dendrology, Polish Academy of Sciences, Parkowa 5, 62-035 Kórnik, Poland. Email: qanibaba@man.poznan.pl

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#### Abstract

Vegetation characteristics are an important proxy to measure the outcome of ecological restoration and monitor vegetation changes. Similarly, the classification of remotely sensed images is a prerequisite for many field ecological studies. We have a limited understanding of how the remote sensing approach can be utilized to classify spontaneous vegetation in post-industrial spoil heaps that dominate urban areas. We aimed to assess whether an objective a priori classification of vegetation using remotely sensed data allows for ecologically interpretable division. We hypothesized that remote sensing-based vegetation clusters will differ in alpha diversity, species, and functional composition; thereby providing ecologically interpretable division of study sites for further analyses. We acquired remote-sensing data from Sentinel 2A for each studied heap from July to September 2020. We recorded vascular plant species and their abundance across 400 plots on a post-coal mine in Upper Silesia, Poland. We assessed differences in alpha diversity indices and community-weighted means (CWMs) among remote sensing-based vegetation units. Analysis of remotely sensed characteristics revealed five clusters that reflected transition in vegetation across successional gradients. Analysis of species composition showed that the 1st (early-succession), 3rd (late-succession), and 5th (mid-succession) clusters had 13, 10, and 12 exclusive indicator species, respectively, however, the 2nd and 4th clusters had only one species. While the 1st, 2nd, and 4th can be combined into a single cluster (early-succession), we found the lowest species richness in the 3rd cluster (latesuccession) and the highest in the 5th cluster (mid-succession). Shannon's diversity index revealed a similar trend. In contrast, the 3rd cluster (late-succession) had significantly higher phylogenetic diversity. The 3rd cluster (late-succession) had the lowest functional richness and the highest functional dispersion. Our approach underscored the significance of a priori classification of vegetation using remote sensing for vegetation surveys. It also highlighted differences between vegetation types along a successional gradient in post-mining spoil heaps.

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# KEYWORDS

functional diversity, indicator species, phylogenetic diversity, post-mining sites, species composition

TAXONOMY CLASSIFICATION

Biodiversity ecology, Community ecology, Ecoinformatics, Ecological engineering, Ecosystem ecology, Functional ecology, Restoration ecology, Spatial ecology

# 1 | INTRODUCTION

Ecological succession, a sequence of changes in communities over time, is a widely studied process of community ecology (Connell & Slatyer, 1977; Li et al., 2023; Meiners et al., 2015; Prach & Walker, 2020; Pulsford et al., 2016). Across ecosystems, there is evidence of changes in community composition and traits over succession (Fu et al., 2023; Hobbs et al., 2007; Nowak et al., 2022; Pickett et al., 1987; Rejmanek & Katwyk, 2005). Yet there is doubt about the mechanisms responsible for this change (Backhaus et al., 2021). Theory predicts that the colonization probability as assumed by the lottery model and environmental filtering is responsible for community assembly in the early stage of succession, while at the late successional stage, interspecific competition is assumed to be the major driving force (Foster et al., 2004; Pacala & Tilman, 1994; Purschke et al., 2013).

Earlier studies of plant community composition along successional gradients in post-mining areas have majorly focused on temporal changes in species (taxonomic) composition (Alday et al., 2011a; Frouz et al., 2008; Prach et al., 2001; Rehounková & Prach, 2006; Wiegleb & Felinks, 2001b), less frequently on changes in single traits or functional groups (Prach et al., 1997; Rehounková & Prach, 2006; Woźniak et al., 2011). However, approaches based solely on species composition do not account for the species ecological differences. Exploring functional groups cannot permit the possibility that species within functional groups may be functionally distinct from one another (Anibaba et al., 2023; Marguard et al., 2009). Moreover, these studies use a phytosociological approach for vegetation classification and plot locality selection, which is a disadvantage since vegetation patterns in novel ecosystems such as post-mining areas are distributed in a complex mosaic and most vegetation is heterogenous (Woźniak et al., 2021). Therefore, there is a need to explore the potential of remote sensing for vegetation classification of postmining areas.

Remote sensing is a good tool for the detection of land-use changes (e.g., Akiwumi & Butler, 2008), vegetation health (e.g., Erener, 2011), and vegetation type, as well as for assessing topographic features and vegetation height (Wężyk et al., 2015). The latter may be simply used for tree biomass estimations (Badreldin & Sanchez-Azofeifa, 2015; Jagodziński et al., 2018). In recent years numerous studies used remote sensing for the detailed characterization of ecosystem species composition and diversity, as well as their transformation under global environmental changes (e.g., Cârlan et al., 2020; Martin-Gallego et al., 2020; Tymińska-Czabańska et al., 2022; Unberath et al., 2019). Especially, advancement in highresolution satellites and sensors has enabled increases in the scope and accuracy of estimations (e.g., Große-Stoltenberg et al., 2018; Hawryło et al., 2020; Silva et al., 2021).

In contrast to natural ecosystems, fewer studies used remote sensing to investigate post-mining vegetation. For example, Game et al. (1982) used remotely sensed data to analyze changes in space and time among patches of vegetation on a surface coal mine undergoing natural succession in Missouri, U.S.A. They classified vegetation development on spoil heaps into three stages representing vegetation cover categories. Schmidt and Glaesser (1998) used remote sensing data to monitor the environmental impact of open-cast lignite mining in Eastern Germany. They classified the vegetation into two clusters: bare open-cast areas and areas of less dense vegetation. Other studies have described the applicability of remote sensing for the recognition of land-use types and coarse vegetation categories (e.g., LeClerc & Wiersma, 2017; Maimaitijiang et al., 2015; Small, 2001). Yang et al. (2018) used remote sensing for the assessment of vegetation disturbance and recovery in surface mining sites. However, only a few studies have used remote sensing to detect more detailed vegetation units such as those that can be described based on species composition and functional traits (Woźniak et al., 2021). Most studies identified a priori-defined vegetation clusters, assessing the accuracy of supervised classification. However, none of them assessed whether using only remotely sensed data can result in vegetation classification into ecologically interpretable units. Here we filled this gap by using a remote sensing approach to inform both the classification and ground data collection of vegetation for the assessment of taxonomic, functional, and phylogenetic diversity. Our study can help provide a method for detailed ecological research.

The vegetation classification of novel ecosystems is important for the ecological restoration of degraded land (Hobbs et al., 2006; Kowarik, 2011). It is necessary to assess large areas of land both before, and after reclamation. For the effective management of post-industrial land to fulfill the required social functions and other ecosystem services, there is a need to make a simple and relatively cheap inventory of its basic features. The novelty of our study is an analysis of the chronosequence of spontaneously developed vegetation, where we might assume either confirmation or rejection of remote sensing applicability for mapping vegetation. We expect that similarly to other types of ecosystems successfully recognized

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using airborne methods (e.g., Akiwumi & Butler, 2008; Hoffmann et al., 2019; Wężyk et al., 2015), post-industrial spontaneous vegetation can also be remotely sensed. Due to the high convergence of vegetation types and habitat filtering (e.g., Prach et al., 2017), we may also expect weak relationships between plant species composition and remotely sensed features. Therefore we aimed to assess whether objective a priori classification of vegetation using remotely sensed data allows for ecologically interpretable division. We hypothesized that remote sensing-based vegetation clusters will differ in alpha diversity, species, and functional composition, providing an ecologically interpretable division of study sites for further analyses.

### 2 | METHODS

#### 2.1 | Study area

We conducted our study in Upper Silesia, a region with a long tradition of coal mining (since the 18th century). Long-lasting mining activity resulted in large amounts of post-industrial sites, occupying more than 2000ha (Szczepańska, 1987). These objects shape the anthropogenic landscape, built of Carboniferous sediments on pre-Cambrian crystalline rocks. The Carboniferous mudstone and sandstone complexes are mixed with numerous coal elements. They are also overlain by Triassic carbonate formations (Cabała et al., 2004). Coal mine spoil heaps are habitats that are difficult for plant development. They are characterized by extreme abiotic conditions, for example, large variations in humidity and daily temperatures (often reaching 50°C), high salinity, lack of soil, susceptibility to erosion, substrate instability, dusting, chemical, and thermal activity, and also biotic parameters such as lack of a seed bank and a deficiency of nutrients in the substrate (Woźniak et al., 2021). These habitat features impact vegetation able to colonize these post-industrial sites (Bradshaw, 2000; Prach et al., 2013; Woźniak, 2010).

From the list of 112 post-mining objects with available information about age, size, vegetation, and reclamation method (Woźniak, 2010) we excluded 31 sites that have been underrepresented, for example, thermally active, regularly formed, or spoil heaps outlying in terms of size or age. Within the remaining 81 post-mining objects, we randomly selected 60 objects (75% of postmining objects), proportionally to size, age, and characteristics of the surrounding landscapes.

### 2.2 | Remote sensing data acquisition

For each spoil heap, we downloaded harmonized Sentinel 2A satellite images using the "sen2r" package (Ranghetti et al., 2020). We used the same package for the selection and correction of images. We selected images with <10% cloud cover and acquired them between June and September 2020. We used images from 1st July,

9th September, and 14th September. All images have a pixel size of 10m (best available spatial resolution). Although we excluded pixels with thick clouds, some thin clouds could affect our calculations of spectral indices. According to timeanddate.com archival weather forecasts, on July 1, 2020 the Katowice sky was moderately cloudy, while on 9th and 14th September it was cloudless. For each date, we obtained raw bands and calculated spectral indices (Table 1). We decided to use raw bands and spectral indices that are correlated with plant chemical composition (Gamon et al., 1997; Hoffmann et al., 2019; Merzlyak et al., 1999) and both vegetation intensity and biomass (Boelman et al., 2003; Butterfield & Malmström, 2009). These variables in the previous study (Woźniak et al., 2021) supported the classification of vegetation on post-mining sites. We also included burn indices (García & Caselles, 1991; Trigg & Flasse, 2001; Vermote et al., 2016) that discriminate areas with black and gray surfaces, typical of early successional stages, where remnants of hard coal and rocks are visible on the surface. We used the "rgugik" package (Dyba & Nowosad, 2021) to obtain a digital elevation model and digital surface model for each site. We used the difference between them as an approximation of vegetation height (Table 1).

#### 2.3 | Remote sensing data processing

We assessed the optimal number of clusters using an elbow method: we ran k-means classification for 2:20 clusters and then we compared decreases in total within-cluster sum of squares. An optimal number of clusters was reached when a further decrease in the sum of squares (when adding another cluster) was not significant. After ensuring that five is the optimal number, we ran a k-means algorithm and assigned each map pixel to one of five classes. Assessed vegetation on remotesensing-based clusters was formed over time and was not spatially consistent (i.e., some clusters are younger than others) (see Figure S1 in Supplementary material for the age distribution of remote-sensingbased clusters). We used Principal components analysis (PCA) to explore differences in remotely sensed parameters of a particular cluster. Before PCA we scaled predictors to overcome differences in their ranges. We developed PCA using the "vegan" package (Oksanen et al., 2018).

# 2.4 | Field site selection and data collection

After assigning each pixel to one of the five clusters, we polygonized the raster layer using the sf package (Pebesma, 2018) in R and selected patches with an area of more than 14,400 m<sup>2</sup>, that is, large enough to host five plots in a block, with distances of 50m from each other (Figure 1). To find potential locations of study sites, we used a regular grid (120 × 120 m) and at the grid intersections, we drew circles (r=60m). For further analyses, we used only homogenous circles (with a minimum variance of class number <0.2). That way we selected 551 potential sites that can host a block of five study plots. Then, we manually inspected their airborne images in Google Earth Pro, to exclude

# TABLE 1 List of remotely sensed variables.

Abbreviation	Name, source	Explanation
AVI	Ashburn Vegetation Index (Ashburn, 1978)	SB850 – SB655; correlated with biomass
EVI	Enhanced Vegetation Index (Huete et al., 2002)	$2.5*\frac{\text{SB850}-\text{SB655}}{(\text{SB850}+6*\text{SB655}-7.5*\text{SB460})-1}\text{, correlated with vegetation cover and biomass}$
MIRBI	Mid-Infrared Burn Index (Trigg & Flasse, 2001)	10*SB2180-9.8*SB1580+2, useful in the detection of burned areas and assessing burn severity; here we used it for the classification of nonvegetated sites
NBR	Normalized Difference NIR/SWIR Normalized Burn Ratio (García & Caselles, 1991)	$\frac{(SB850 - SB1580)}{(SB850 + SB1850)}$ , another index for burn detection, but based on other bands WIR
NBR2	Normalized Burn Ratio 2 (Trigg & Flasse, 2001; Vermote et al., 2016)	(SB1580 – SB2180) (SB1580 + SB2180), burn index based on short-wave infrared
NDVI	Normalized Difference Vegetation Index (Rouse et al., 1974)	$\frac{(58850-58655)}{(58850+58655)}$ , classic index of vegetation, correlated with biomass and cover
SB460	Reflectance of 460 nm band	Blue reflectance. The reflectance of particular bands is useful for the construction of other spectral indices and classifications
SB555	Reflectance of 555 nm band	Green, see above
SB655	Reflectance of 655 nm band	Red, see above
SB850	Reflectance of 850nm band	Visible and near-infrared, see above
SB1580	Reflectance of 1580nm band	Short-wave infrared, see above
SB2180	Reflectance of 2180 nm band	Short-wave infrared, see above
VH	Vegetation height	Difference between the digital elevation model and the digital surface model from LIDAR measurements, expressed in meters

sites with roads, buildings, or water bodies. After exclusion, we obtained 427 potential sites. Within each spoil heap and cluster, we randomly assigned numbers of potential sites, that reflected priority of plot establishment. We then establish 400 study plots (i.e., 80 sites) proportionally to cluster abundance: in cluster 1 - four sites, cluster 2-19 sites, cluster 3-19 sites, cluster 4-14 sites, and cluster 5-24 sites. For site selection, first, we assigned random numbers to each potential site within each heap, within each cluster. Then, we used these numbers in priority order for selecting sites during fieldwork. In the summer of 2021, we visited each heap and firstly we went to the site with the number one in each cluster. If we confirmed in the field that the site is suitable for establishing study plots (homogeneity, lack of major human interventions, not intersected by roads, etc.), then we established five plots there. If it was impossible to establish a study plot we visited the next number. Although we primarily intended to establish one site per cluster per heap, due to dynamic changes in heaps ownership structure and construction work that started before fieldwork, it was impossible and we had to exclude some heaps from the study and establish more sites per cluster in some heaps. In total, we established 80 sites that were planned (i.e., 400 study plots) (Figure 2). Still, due to the inaccessibility of some heaps, we changed the structure of cluster proportions: three in cluster 1, 19 in cluster 2, 17 in cluster 3, 15 in cluster 4, and 26 in cluster 5. Within each plot, we recorded vascular plant species and their cover using the Londo scale (Londo, 1976). The size of the study plot  $(28.3 \text{ m}^2)$  is large enough to describe the species composition of nonforest vegetation and typical of usually used plots in sampling synanthropic, meadow, and grassland vegetation. Chytrý and Otýpková (2003) recommend even smaller study plots (16 m<sup>2</sup>) for such vegetation types.

# 2.5 | Vegetation characteristics

We aimed to check whether the obtained clusters differ in species composition, functional composition, and biodiversity. For that reason, we decided to assess species composition, the functional composition based on trait values, and alpha diversity indices. To obtain that, we prepared a dataset of species abundances, traits, and phylogeny. For the set of vascular plant species present in study plots, we obtained a phylogenetic tree derived from the mega tree included in the "V.phylo.maker" package (Jin & Qian, 2022). We also acquired functional traits (Table 2) from LEDA (Kleyer et al., 2008), BIEN (Maitner et al., 2018), BiolFlor (Klotz et al., 2002), and Pladias (Chytrý et al., 2021) databases, and ecological indicator values from Ellenberg and Leuschner (2010). We imputed missing data using the random forest-based imputation (Penone et al., 2014), implemented in the missForest package (Stekhoven & Bühlmann, 2012). We developed a model based on known trait values and phylogenetic eigenvectors (Diniz-Filho et al., 1998), obtained using the PVR package (Santos, 2018). The first 15 phylogenetic eigenvectors covered 59.3% of the variation in phylogenetic distances among species. The normalized root mean squared error of imputed traits was 1.011 for continuous predictors and the proportion of falsely classified categorical variables was 0.079.

We described alpha diversity for each plot using six indices. For taxonomic diversity, we calculated species richness and Shannon's diversity index. For phylogenetic diversity, we used Faith's phylogenetic diversity (PD; that is, the sum of phylogenetic tree branch lengths, representing all species present in the community) and mean pairwise phylogenetic distance (MPD). For functional diversity, we



**FIGURE 1** Example of site and plot selection using the background of remotely sensed classes and their distribution on chosen post-industrial objects (black numbers).

measured the functional richness (FRic) expressing the quantity of plant functional types present in a community and functional dispersion (FDis), expressing the size of community species traits hypervolume within the functional trait space (Laliberté & Legendre, 2010; Mason et al., 2005).

We used a null model approach to test whether the phylogenetic diversities differed from the randomly generated assemblage of species. We calculated PD and MPD using the "PhyloMeasures" package (Tsirogiannis & Sandel, 2016) while FRic and FDis using the "FD" package (Laliberté et al., 2014).

#### 2.6 | Data analysis

We analyzed data using R software v. 4.0.1 (R Core Team, 2021). We assessed the species composition of study plots (using the presenceabsence transformed data) by nonmetric multidimensional scaling (NMDS), implemented in the "vegan" package (Oksanen et al., 2018). Before NMDS we excluded 28 plots without vegetation and 14 plots with only one species that produced artifacts and did not allow NMDS to reach a convergence (producing n=400-28-14=358 for NMDS). Using the IndVal method (Cáceres & Legendre, 2009) we assessed whether a species is an indicator of a spoil heap cluster (i.e., a particular species is more frequent/associated with a particular cluster than others). For each species, we provided IndVal statistics and *p*-value informing about the strength and significance of the association (Cáceres & Legendre, 2009).

We assessed differences in alpha diversity indices and CWMs using linear mixed-effects models (LMMs), accounting for dependencies among plots within blocks and heaps by the random intercepts. For species richness, we used generalized LMM (GLMM) assuming Poisson distribution. We used the "Ime4" (Bates et al., 2015) and "ImerTest" (Kuznetsova et al., 2017) packages to develop LMMs and GLMM. Before GLMM development we checked potential problems with zero-inflation and overdispersion using tests implemented in the "DHARMa" package (Hartig, 2020). We assessed the impacts of remote sensing-based clusters on response variables by ANOVA. Although models could reveal differences among forest types with p-values <.05, via Tukey's posteriori tests we applied a single-step adjustment of p-values, to account for multiple hypothesis testing. Single-step adjustment decreases the probability of committing Type I error (i.e., rejection of the true null hypothesis), and also accounts for correlations among variables tested (Bretz et al., 2011). We also reported Akaike's Information Criterion (AIC) for full and null (intercept and random effects only, AIC<sub>o</sub>) models, to show how including clusters increases the model performance. We calculated marginal  $(R_m^2)$  and conditional  $(R_c^2)$  coefficients of determination, indicating the proportion of variability explained by fixed effects only and by both random and fixed effects, respectively (Nakagawa & Schielzeth, 2013) using the "MuMIn" package (Bartoń, 2017).

# 3 | RESULTS

# 3.1 | Remotely sensed characteristics of vegetation

Analysis of remotely sensed characteristics of clusters revealed that the PC1 axis explained 62.4% of variability while PC2 explained 25.2% (Figure 3). Axis PC1 divided vegetated sites (i.e., clusters 3 and 5) from sparsely vegetated sites (i.e., clusters 1, 2, and 4). This axis of division reflected both spectral vegetation and burn indices, as well as vegetation height. The latter is divided between cluster 3, covered by woody vegetation and cluster 5, covered by herbaceous vegetation. Axis PC2 differentiated sites with high values of infrared reflectance (SB1580 and SB2180), from sites with lower reflectance of these bands. This axis divided less-vegetated sites into three clusters, according to thermal activity and proportion of reflectance. Cluster 2 had low reflectance of all bands, indicating close to black surface color.



FIGURE 2 Distribution of study plots (n = 400) in Upper Silesia. The study design shows plots in the north (N), south (S), east (E), and west (W) directions at 50m from the central plot (C).

#### 3.2 | Species and functional composition

In total, we observed vascular plants within 372 plots, 15 in the 1st cluster, 62 in the 2nd cluster, 93 in the 3rd cluster, 72 in the 4th cluster, and 130 in the 5th cluster. We found more than one species of vascular plants in 358 plots. Ordination (NMDS) revealed differentiation of remote sensing-based clusters along main axes (Figure 4). Main axis (NMDS1) differentiated 1st, 2nd, and 4th clusters from 3rd and 5th. However, these three left clusters (1st, 2nd, and 4th) representing initial vegetation did not differentiate in ordination space. The most distinct was 3rd cluster, representing woody vegetation, which had almost no overlap with other clusters.

Analysis of species composition revealed that the 1st, 3rd, and 5th clusters had 13, 10, and 12 exclusively indicative species, respectively, while the 2nd and 4th—had only one species (*Epilobium parviflorum* and *Carlina vulgaris*, respectively). The first cluster differed from others by a high frequency of the grassland species *Lolium perenne*, and ruderals: *Oxybasis* spp., *Chenopodium album*, and *Echinochloa crus-galli* (Table 3). The third cluster differed by a high frequency of forest species: *Lolium giganteum*, *Circaea lutetiana*, *Millium effusum*, and *Poa nemoralis*, as well as forest-edge species: Rubus idaeus, Geum urbanum, and Impatiens parviflora. The fifth cluster differed by a high frequency of meadow and grassland species: Achillea millefolium, Dactylis glomerata, Festuca rubra, Galium mollugo, Silene latifolia, and Vicia cracca. The 3rd cluster had the lowest number of indicative species in common with other clusters. Analysis of functional composition revealed that the most distinct 3rd cluster differed significantly from other clusters in light and soil fertility EIVs, and height and SLA CWMs (Table 4; Figure 5). However, cluster 5 (second most distinct in NMDS) did not differ from other clusters in any CWMs.

# 3.3 | Biodiversity

We found the lowest number of species in the 3rd cluster  $(5.9\pm8.4 \text{ species})$  while the highest was in the 5th cluster  $(14.0\pm1.9 \text{ species})$ ; Figure 6; Table 5). Shannon's diversity index revealed a similar trend. In contrast, the 3rd cluster had significantly higher phylogenetic diversity, expressed by both Faith's PD and MPD. All other clusters indicated strong phylogenetic clustering while the 3rd cluster revealed random phylogenetic composition (no difference from the null model). The 3rd cluster had the lowest functional richness, twice as



Completeness [%]

98.1 86.8

69.1

87.7

72.9

98.9

98.9

87.9 81.1

94.5

98.9

100.0

95.9

95.9 95.9

Completeness [%]

ABLE 2 Traits used in the study, their r	anges, variation coeffic	ient (CV), and co	mpleteness.	
Numeric traits	Min	Max	Mean	CV [%]
EIV-Light (EIV-L)	1	9	6.7	22.2
EIV-Moisture (EIV-M)	2	11	5.3	33.7
EIV-Soil reaction (EIV-SR)	1	9	6.2	28.8
EIV-Nutrients (EIV-N)	1	9	5.0	42.7
EIV-Temperature (EIV-T)	2	8	5.6	16.5
Flowering beginning [months]	1	9	5.5	21.6
Flowering duration [months]	1	12	3.4	40.7
Specific leaf area (SLA) [cm <sup>2</sup> g <sup>-1</sup> ]	51.8	899.1	247.7	45.5
Leaf dry mass content (LDMC) $[mgg^{-1}]$	0.3	509.5	230.6	33.7
Seed mass (SM) [mg]	0.001	13737.6	103.6	941.3
Maximum height (H) [m]	0.033	60.0	4.6	230.5
Categorical traits	Number of classes	Classes and	I their frequency	
Life form	8	Chamaephy Hemicrypto (0.82%), Lia Therophyte	vtes (4.4%), Geopl ophytes (51.8%), F nas (3.3%), Phane es (15.3%)	nytes (7.1%), Iydrophytes erophytes (16.7%),
Pollination mode-insect	2	Yes (71.7%)	, no (28.3%)	
Pollination mode—selfing	2	Yes (52.0%)	, no (48.0%)	
Pollination mode—wind	2	Yes (31.1%)	, no (68.9%)	

FIGURE 3 Result of principal components analysis (PCA) of remotely sensed characteristics of pixels (Table 1), colored according to k-means clustering.



low as the 4th, and the 5th cluster had the highest values. However, the 3rd cluster had the highest functional dispersion.

#### 4 DISCUSSION

# 4.1 | Remotely sensed characteristics of vegetation and indicative species

Remote-sensing classification of post-mining areas shows a mosaic of vegetation types due to patchy characteristics of the mineral material of the heaps (Hüttl & Weber, 2001; Kirmer et al., 2008).

Axis PC1 was differentiated into vegetated and sparsely vegetated sites. This differentiation reflects the successional development of the vegetation and the remotely sensed clusters which can be combined as clusters 1, 2, and 4-early-succession, cluster 5-midsuccessional stage, and cluster 3-late-successional stage. Among remotely sensed characteristics, vegetation height (VH) was divided into meadow and forest suggesting a transition from mid- to late-successional stage. Axis PC2 divided the early successional stage according to thermal-related indices and proportion of reflectance. This indicates sites that are close to black surface color (i.e., newly established spoil heaps) and areas with sparse vegetation (i.e., pioneer species). Our results could be affected by temporal

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FIGURE 4 Result of nonmetric multidimensional scaling (NMDS, stress=0.1631) of vegetation in study plots (points), colored according to kmeans clustering (Figure 2).

resolution—we used images acquired in summer when only some of the species flower, which could affect spectral indices based on red, blue, and infrared. However, to minimize that effect we averaged images from the beginning of July with those from September, to capture both flowering and nonflowering dates.

Observed vegetation pattern revealed by ordination (NMDS) showed ecological interpretation of clusters-the development of plant species from the early successional stage (1st. 2nd. and 4th clusters) through mid-succession (5th cluster) to late succession (3rd cluster). We found 15 indicative species (i.e., 13 in the 1st cluster and one each in the 2nd and 4th clusters) in early succession. The indicative grassland species Lolium perenne showed significantly higher frequency in early successional stages. In a 6-year permanent plot study, Alday et al. (2011b), found that cover of Lolium perenne declined over time during early succession on coal wastes in northern Spain. Other indicative species, including Oxybasis spp., Chenopodium album, and Echinochloa crus-galli, with ruderal characteristics (Klotz et al., 2002) were highly frequent in early succession. This is expected considering the openness of spoil heaps during the early stages of vegetation development. In a similar study in Upper Silesia, a high frequency of ruderal species was found on young spoil heaps (Piekarska-Stachowiak et al., 2014).

The mid-successional stage (i.e., 5th cluster) differed by having a high frequency of indicative species characterized by dense low vegetation (i.e., meadow and grassland): Achillea millefolium, Dactylis glomerata, Festuca rubra, Galium mollugo, Silene latifolia, and Vicia cracca. Prach (2013), referred to the mid-succession stage as postruderal—the period where ruderal species are substituted by nonruderals. Frouz et al. (2008) showed that the mid-successional stage corresponds to a period of substantial change in soil structure and biota.

In the late-successional stage (i.e., 3rd cluster), we found a high frequency of ancient forest indicator species (Hermy et al., 1999): Lolium giganteum, Circaea lutetiana, Millium effusum, and Poa nemoralis, as well as forest-edge species: Rubus idaeus, Geum urbanum, and Impatiens parviflora. Jabs-Sobocińska et al. (2022) found Circaea lutetiana among the species significantly occurring more often in recent forests in the Carpathian. Although shade-tolerant Millium effusum is generally considered an ancient woodland indicator (De Frenne et al., 2017), it is also known to colonize secondary, post-agricultural forests in Poland (Brunet et al., 2012) and Sweden (Brunet et al., 2012). Poa nemoralis is a moderately strong indicator of ancient forest. When not hindered by dispersal limitation and elevated nutrient levels, P. nemoralis rapidly colonizes recently established forest areas adjacent to ancient forests (Plue et al., 2020). That way the presence of such forest species indicates the progress of secondary succession, the dynamics of which was reflected in vegetation clusters determined in our study based on remote sensing.

# 4.2 | Change in species richness and diversity along a successional gradient

Species diversity in post-mining areas is controlled by mechanisms of community assembly which represents our remotely sensed cluster classification. There are two main models explaining how species diversity responds to community succession. The first posits that diversity increases throughout succession by migration and decreases over time through competition (Odum, 1969). The second suggests that diversity gradually increases at early succession when pioneers dominate, becomes at maximum in mid stages ANIBABA ET AL.

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TABLE 3 The frequency (%) of plant species within remote sensing-based clusters (1–5; Figure 1) and the strength of association assessed using the IndVal method (we bolded frequency for clusters where species is indicative).

Species	1	2	3	4	5	IndVal statistic	p-Value
Matricaria discoidea	13.3	0.0	0.0	0.0	0.0	0.365	0.002
Bromus sterilis	13.3	0.0	0.0	1.4	0.0	0.359	0.003
Amaranthus retroflexus	13.3	0.0	0.0	2.8	0.0	0.332	0.010
Epilobium roseum	13.3	4.8	0.0	0.0	3.8	0.266	0.034
Setaria helvola	20.0	0.0	0.0	0.0	0.0	0.447	0.001
Sonchus asper	20.0	9.7	0.0	0.0	0.0	0.407	0.002
Plantago major	33.3	4.8	0.0	5.6	6.2	0.485	0.001
Cirsium palustre	33.3	12.9	0.0	13.9	3.1	0.385	0.010
Echinochloa crus-galli	46.7	8.1	0.0	12.5	6.9	0.440	0.003
Chenopodium album	53.3	17.7	0.0	4.2	0.8	0.649	0.001
Oxybasis rubra	60.0	16.1	0.0	2.8	0.0	0.584	0.001
Oxybasis glauca	66.7	8.1	0.0	0.0	5.4	0.750	0.001
Lolium perenne	80.0	0.0	0.0	0.0	3.1	0.877	0.001
Epilobium parviflorum	0.0	17.7	2.2	0.0	0.0	0.404	0.003
Lolium giganteum	0.0	0.0	10.8	0.0	0.0	0.328	0.009
Clematis vitalba	0.0	0.0	11.8	0.0	0.0	0.344	0.005
Prunus serotina	0.0	0.0	12.9	0.0	0.0	0.359	0.008
Rubus idaeus	0.0	0.0	12.9	0.0	0.0	0.359	0.008
Circaea lutetiana	0.0	0.0	19.4	0.0	0.0	0.440	0.002
Poa nemoralis	0.0	0.0	19.4	0.0	0.0	0.440	0.002
Sambucus nigra	0.0	0.0	19.4	0.0	0.0	0.440	0.001
Milium effusum	0.0	0.0	20.4	0.0	0.0	0.452	0.003
Impatiens parviflora	0.0	0.0	43.0	0.0	0.0	0.656	0.001
Geum urbanum	0.0	0.0	57.0	0.0	1.5	0.754	0.001
Carlina vulgaris	0.0	3.2	0.0	12.5	2.3	0.290	0.039
Scabiosa ochroleuca	0.0	0.0	0.0	0.0	11.5	0.340	0.013
Thymus pulegioides	0.0	0.0	0.0	0.0	12.3	0.351	0.011
Arrhenatherum elatius	0.0	1.6	0.0	0.0	12.3	0.349	0.011
Festuca pratensis	0.0	0.0	0.0	0.0	13.8	0.372	0.008
Lysimachia vulgaris	0.0	0.0	0.0	0.0	14.6	0.382	0.008
Medicago falcata	0.0	0.0	0.0	1.4	16.9	0.407	0.005
Vicia cracca	0.0	0.0	1.1	0.0	19.2	0.433	0.001
Silene latifolia	0.0	1.6	1.1	0.0	19.2	0.422	0.003
Galium mollugo	0.0	0.0	0.0	0.0	25.4	0.504	0.001
Festuca rubra	0.0	3.2	2.2	0.0	25.4	0.498	0.002
Dactylis glomerata	0.0	0.0	3.2	12.5	33.1	0.546	0.001
Achillea millefolium	6.7	1.6	2.2	6.9	43.8	0.634	0.001
Kali turgidum	13.3	14.5	0.0	6.9	0.0	0.344	0.009
Polygonum persicaria	6.7	14.5	0.0	0.0	6.2	0.304	0.026
Lepidium ruderale	6.7	4.8	0.0	13.9	0.8	0.328	0.009
Tripleurospermum inodorum	33.3	14.5	0.0	27.8	3.1	0.473	0.001
Rubus caesius	13.3	0.0	2.2	2.8	13.8	0.358	0.014
Senecio jacobaea	6.7	0.0	0.0	0.0	18.5	0.415	0.004
Trifolium arvense	20.0	1.6	0.0	4.2	20.8	0.390	0.011

(Continues)

#### TABLE 3 (Continued)

Species	1	2	3	4	5	IndVal statistic	p-Value
Trifolium pratense	26.7	1.6	1.1	2.8	26.2	0.469	0.002
Holcus lanatus	26.7	0.0	0.0	0.0	13.1	0.381	0.011
Plantago lanceolata	26.7	4.8	1.1	8.3	26.9	0.496	0.002
Atriplex prostrata	0.0	17.7	0.0	11.1	0.8	0.374	0.005
Poa pratensis	0.0	8.1	6.5	2.8	22.3	0.381	0.027
Urtica dioica	0.0	1.6	28.0	0.0	14.6	0.449	0.008
Deschampsia cespitosa	6.7	4.8	33.3	1.4	12.3	0.448	0.006
Hypochoeris radicata	0.0	0.0	0.0	11.1	8.5	0.307	0.035
Pilosella officinarum	0.0	1.6	2.2	13.9	14.6	0.348	0.028
Hypericum perforatum	0.0	3.2	3.2	20.8	22.3	0.442	0.006
Tanacetum vulgare	6.7	6.5	0.0	16.7	26.2	0.462	0.008
Hieracium piloselloides	0.0	4.8	6.5	30.6	17.7	0.410	0.025
Agrostis capillaris	0.0	9.7	10.8	13.9	31.5	0.449	0.016
Picris hieracioides	0.0	0.0	3.2	20.8	32.3	0.527	0.002
Lotus corniculatus	13.3	4.8	2.2	22.2	37.7	0.549	0.001
Echium vulgare	0.0	14.5	1.1	40.3	26.9	0.528	0.002
Calamagrostis epigejos	13.3	61.3	9.7	80.6	87.7	0.892	0.001
Hordeum jubatum	6.7	12.9	0.0	12.5	0.0	0.348	0.016
Tussilago farfara	20.0	27.4	1.1	22.2	10.8	0.474	0.006
Oenothera biennis	13.3	24.2	0.0	52.8	16.2	0.547	0.001
Polygonum aviculare	73.3	38.7	0.0	34.7	2.3	0.629	0.001
Leontodon hispidus	6.7	1.6	0.0	12.5	13.8	0.355	0.011
Rumex acetosella	6.7	1.6	0.0	8.3	13.8	0.334	0.025
Cirsium vulgare	6.7	6.5	0.0	9.7	13.8	0.328	0.035
Trifolium repens	20.0	6.5	1.1	8.3	19.2	0.380	0.014
Medicago lupulina	20.0	1.6	0.0	27.8	16.2	0.448	0.002
Artemisia vulgaris	20.0	0.0	1.1	11.1	28.5	0.469	0.003
Taraxacum officinale	26.7	11.3	7.5	33.3	26.2	0.506	0.003
Cirsium arvense	26.7	8.1	2.2	19.4	34.6	0.497	0.001
Phragmites australis	6.7	21.0	6.5	26.4	28.5	0.507	0.001
Erigeron annuus	6.7	16.1	2.2	19.4	30.8	0.482	0.003
Daucus carota	0.0	25.8	4.3	44.4	40.0	0.604	0.001
Solidago gigantea	0.0	14.5	19.4	25.0	32.3	0.499	0.025
Erigeron canadensis	53.3	50.0	2.2	43.1	27.7	0.615	0.001

when there are still pioneers but the mid and late successional species are already beginning to establish, and diversity gradually falls into the late stages of succession when the pioneers are eliminated, revealing an arch-shaped pattern (Connell, 1978). In this study, we discovered that both species richness and Shannon diversity had a clear trend as succession progressed. While species richness and Shannon diversity were significantly higher in the early and mid-successional stages than in late succession, the mid-successional stage became the maximum in these response variables (an arch-shape pattern). Therefore, our study showed that remotely sensed vegetation clusters can help with ground data collection to reveal an arch-shaped pattern of species richness and

Shannon diversity as proposed by Connell (1978). Reduced competition among herbaceous and shrub species in mid-succession provides for the establishment of species such as *Senecio jacobaea*, *Trifolium arvense*, *Holcus lanatus*, *Hypochoeris radicata*, *Tanacetum vulgare*, *Leontodon hispidus*, *Rumex acetosella*, and *Cirsium vulgare* that are indicative of early and mid-successional species. Similarly, light availability (Bazzaz, 1979) and surrounding vegetation near spoil heaps (source of propagules) may support the establishment of more species through seed dispersal in the mid-successional stage (Czortek, 2023; Prach & Rehounková, 2006). On the other hand, competition among species for limited resources, particularly light availability due to canopy closure, can be the main

Response	Sum of squares	Mean square	Numerator df	Denominator df	ц	٩	Block in heap RE SD	Heap RE SD	Residual RE SD	AIC	AIC	R <sup>2</sup>	$R^2_{c}$
CWM light EIV	27.688	6.922	4	36.46	50.239	<.001	0.327	0.207	0.371	476.7	554.9	.664	.839
CWM moisture EIV	2.670	0.668	4	41.54	1.539	.209	0.354	0.415	0.659	860.2	854.2	.044	.433
CWM soil fertility EIV	7.292	1.823	4	36.79	4.237	900.	0.416	0.475	0.656	873.2	878.5	.142	.555
CWM SLA	112800.843	28200.211	4	42.49	19.752	<.001	17.471	17.108	37.785	3813.6	3886.2	.355	.546
CWM SM	15540.813	3885.203	4	26.30	1.182	.341	18.129	0.003	57.326	4078.1	4101.2	.017	.106
CWM height	100.668	25.167	4	25.41	8.180	<.001	0.603	0.270	1.754	1527.0	1544.4	.125	.234
Abbreviations: AIC (proportion of varia deviation: SLA, spe	, Akaike's Informa ability explained b cific leaf area: SM	ation Criterion; yy both fixed ar 1. seed mass.	AIC <sub>o</sub> , AIC of null ( <sup>,</sup> nd random effects)	only intercept and ran ; R <sup>2</sup> , marginal coeffici	dom effects) ent of detern	model; df, c nination (pro	degrees of freec oportion of vari	dom; F, test st ability explair	atistic; <i>p, p-</i> valuo ed by fixed effe	e; R <sub>c</sub> , conditio ects only); RE	onal coefficie ., random effe	nt of deteri ect; SD, stai	nination ndard

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cause of the decline in species diversity in the late successional stage (Prach et al., 2013). This trend was confirmed by Rawlik et al. (2018) who found that similar age stands of tree species transmitting more light through their canopies supported the presence of more understory species and higher biomass. Our results are in agreement with other studies (Alday, Pallavicini, et al., 2011; Shafi & Yarranton, 1973; Wiegleb & Felinks, 2001a). However, in contrast to our findings, a linear increase in species richness and diversity with spoil heap age was documented in some studies (Hazarika et al., 2006; Piekarska-Stachowiak et al., 2014; Pietrzykowski, 2008). Other authors found the highest diversity in the early and late stages of succession, representing a Ushaped pattern (Badraghi et al., 2023; Hilmers et al., 2018). While our study and that of Piekarska-Stachowiak et al. (2014) were conducted in the same region, it should noted that Piekarska-Stachowiak et al. (2014) used the most frequent dominant species groups in the vegetation to establish permanent plots instead of random allocation of sample plots to vegetation patches. This might be an important driver of the difference in results, as preferential sampling affects the results of vegetation analyses (Holeksa & Woźniak, 2005). Therefore, our approach of random allocation of sample plots to vegetation patches helps remove bias and provides robust findings. In general, a nearly universal pattern of diversity could be expected-the diversity of the late stage must be lower than that of some preceding stages unless the late stage is affected by disturbance allowing the establishment of pioneers in the late-successional stage (Horn, 1974).

# 4.3 | Changes in functional and phylogenetic strategies along a successional gradient

Our study revealed differences in functional diversity between obtained remote-sensed clusters which follow successional development. We found a significant difference in community-weighted means (CWM) of ecological indicator values (EIV) and functional traits (light EIV, soil fertility EIV, height, and SLA) between clusters indicating the increasing importance of competition as succession advances. The significant CWM of light EIV in late succession (i.e., 3rd cluster) suggests the influence of abiotic filtering as plant species in this stage show low demand for light during the juvenile stage; thus the elimination of plant species that perform best at optimum light and in open habitat. Similarly, through low photosynthetic rates, the latesuccessional species are usually more efficient at low light availability (Bazzaz, 1979). The difference in CWM soil fertility EIV in late succession (i.e., 3rd cluster) suggests an increasing need for soil nutrients as succession progresses. Similarly, plant height was significantly higher in late succession (i.e., 3rd cluster) which can infer that plant species at late succession are highly productive with strong competitive capacity.

SLA is an important trait that explains an acquisitiveconservative trade-off (Wright et al., 2004), which differed between our obtained remotely sensed clusters. We expect a decrease in SLA along a successional gradient (e.g., Boukili &



FIGURE 5 Mean (+SE) values of the community-weighted mean (CWM) of ecological indicator values (EIV) and functional traits describing studied vegetation among remote sensing-based clusters, assessed using linear mixed-effects models (Table 4). The same letters denote groups that did not differ at the confidence level  $\alpha = .05$  after multiple hypotheses adjustment, according to a Tukey *posteriori* test.

Chazdon, 2017; Lohbeck et al., 2013) due to its positive relationship with relative growth rate (Wright et al., 2004). However, in our study, the CWM of SLA was significantly higher in late succession (i.e., 3rd cluster). SLA variation is influenced by two traits: leaf dry matter content (LDMC) and leaf thickness (Hodgson et al., 2011; Witkowski & Lamont, 1991). While leaf thickness is positively related to light availability, LDMC is negatively related to soil fertility (Hodgson et al., 2011). Thus, decreased thickness with shading in late succession indicates a reduction in the division and expansion of palisade chlorenchyma cells (Dengler, 1980) to minimize internal shading of chloroplasts. Therefore, SLA can increase due to increased shade and soil fertility. In general, the differences in traits can be explained by variations in light and nutrient availability, both at interspecific and intraspecific levels (Grime, 2006; Paź-Dyderska et al., 2020; Poorter et al., 2005).

Functional diversity differed between obtained remotely sensed clusters. We found the lowest functional richness and highest functional dispersion in the late successional stage (i.e., 3rd cluster). Low functional richness may indicate high environmental filtering (Laliberté & Legendre, 2010), as it estimates the amount of niche space filled by all species in a community. Therefore, if plant community composition is constrained by environmental filtering, the range of available niches should be limited and we can expect a low

functional richness. Similarly, shade is an important environmental filter supporting a few unique species in the late-successional stage (i.e., 3rd cluster), thus, the low functional richness. In our study, the most frequent species in late succession-Lolium giganteum, Circaea lutetiana, Millium effusum, Poa nemoralis, Geum urbanum, and Impatiens parviflora are adapted to shade or moderate shade conditions. Functional dispersion (FDis) measures the mean distance of all plant species to the weighted centroid of the community in trait space (Anderson et al., 2006). A high value of FDis is an indication of low habitat filtering. FDis is independent of species richness but takes into account species abundance (Laliberté & Legendre, 2010). We recorded a high cover of species with distinct traits typical of forest ecosystems, for example, Circaea lutetiana, Poa nemoralis, Sambucus nigra, Milium effusum, Impatiens parviflora, and Geum urbanum in the late-successional stage (i.e., 3rd cluster) which could cause FDis to be high. The high cover of these species in comparison to the total species pool especially since these dominant cover species are adapted to shade conditions in late succession, resulted in that trend.

Phylogenetic diversity reflected the differences between our remotely sensed clusters. The late-successional stage (i.e., 3rd cluster) had significantly higher phylogenetic diversity (Faith's Phylogenetic diversity and Main pairwise distance). Given that phylogenetic



FIGURE 6 Mean (+SE) values for alpha diversity indices of studied vegetation among remote sensing-based clusters, assessed using linear mixed-effects models and a generalized linear mixed-effect model (Table 5). The same letters denote groups that did not differ at the confidence level  $\alpha = .05$  after multiple hypotheses adjustment, according to a Tukey *posteriori* test.

randomness and clustering are explained by environmental filtering (Emerson & Gillespie, 2008), under this hypothesis, abiotic conditions (i.e., temperature, precipitation, soil nutrients, and sunlight) filter species with similar trait combinations (Keddy, 1992). We could infer that environmental filters such as light and soil nutrients account for the phylogenetic nonrandomness of late-successional plant communities. Plant communities in the herbaceous layers are adapted to shade conditions while those in the shrub, understory, and canopy layer compete for sunlight. Similarly, competitive exclusion controls the plant communities in late succession because species compete for resources. Competitive exclusion can filter shade-intolerant species, thus contributing to phylogenetic convergence in late succession. Also, our findings suggest that competitive exclusion determines the species composition during the late stages of succession because environmental conditions such as light are highly heterogeneous (i.e., not homogeneously distributed) (Matsuo et al., 2021). In addition, in the late-successional stage, most light is intercepted at higher strata of vegetation, decreasing the amount of light beneath the canopy, and excluding light-demanding species from the community. As a result of the competitive effect, we have distinct plant species at the canopy layer, shrub layer, and herb layer, making the phylogenetic diversity at a similar level than predicted under a null model in late succession.

#### 5 CONCLUSIONS

Our study demonstrated that objective a priori classification of vegetation using remotely sensed data can help elucidate meaningful and ecologically interpretable division. Using the chronosequence of spontaneously developed vegetation in post-mining sites, we confirmed the applicability of remote sensing for designating study sites suitable for ecological studies. Remotely sensed characteristics differentiated early-, mid-, and late-successional stages. Species composition revealed that early-successional stages hosted species indicative of grassland and ruderal species, mid-successional stages had the highest proportion of meadow species, while late-successional stages were characterized by the presence of forest and forest edge species. These stages were reflected in remote sensing-divided clusters of study sites. Species richness and diversity followed an arch-shaped pattern: they were the highest in mid-succession and lowest in late succession. Functional composition differed significantly in late succession for light EIV, soil fertility EIV, CWM for plant height, and SLA. The late succession vegetation had the lowest functional richness and highest functional dispersion. We also found a difference in phylogenetic diversity. All these trends were in line with previous ground-based studies,

							Block in						
Response	squares	square	Numerator df	Denominator df	ц	d	neap KE SD	неар кс SD	RE SD	AIC		$R_m^2$	$R_c^2$
Faith's PD	55.944	13.986	4	33.93	16.626	<.001	0.532	0.372	0.917	1097.3	1134.1	.329	.552
Mean pairwise distance	26.099	6.525	4	33.24	10.891	<.001	0.449	0.219	0.774	931.4	950.9	.228	.455
Functional richness	1.034	0.259	4	34.47	10.297	<.001	0.092	0.076	0.158	-187.8	-179.7	.242	.516
Functional dispersion	0.006	0.002	4	39.85	3.592	.014	0.002	0.011	0.021	-1722.7	-1751.3	.077	.293
Shannon's index	3.543	0.886	4	41.24	4.242	900.	0.263	0.482	0.457	615.0	618.4	.142	.649
Species richness	33.996	8.499	4	NA	8.499	<.001	0.282	0.414	NA	2194.0	2212.3	.279	.805
Abbreviations: AIC <sub>0</sub> , AIC of coefficient of determination	null (only inter	rcept and ranc	dom effects) model; vilained by both fiv	; AIC, Akaike's Inform	ation Criteri -tel· R <sup>2</sup> mare	ion; df, degi inal coeffic	rees of freedc ient of deterr	m; F, test stal	tistic; PD, phyl	logenetic dive mility evaluation	rsity; <i>p</i> , <i>p</i> -valu	le; R <sub>c</sub> , con facts only	ditional \- RF

showing that remote sensing can help with the objective and low-cost selection of study sites for the assessment of vegetation restoration success. That way it can provide new insights into ecosystem diversity between vegetation types along successional gradients in post-mining heaps.

# AUTHOR CONTRIBUTIONS

Quadri A. Anibaba: Conceptualization (lead); data curation (lead); formal analysis (equal); methodology (lead); project administration (supporting); visualization (equal); writing – original draft (lead); writing – review and editing (lead). Marcin K. Dyderski: Conceptualization (equal); methodology (equal); writing – review and editing (supporting). Gabriela Woźniak: Conceptualization (supporting); investigation (supporting); methodology (supporting); writing – review and editing (supporting). Andrzej M. Jagodziński: Conceptualization (supporting); funding acquisition (lead); writing – review and editing (supporting).

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#### CONFLICT OF INTEREST STATEMENT

We declare that there are no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### DATA AVAILABILITY STATEMENT

The data for this study are accessible on the FigShare repository: https://doi.org/10.6084/m9.figshare.25289401.

# ORCID

Quadri A. Anibaba <sup>(D)</sup> https://orcid.org/0000-0002-5195-2920 Marcin K. Dyderski <sup>(D)</sup> https://orcid.org/0000-0003-4453-2781 Gabriela Woźniak <sup>(D)</sup> https://orcid.org/0000-0003-1936-2880 Andrzej M. Jagodziński <sup>(D)</sup> https://orcid.org/0000-0001-6899-0985

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random effect; SD, standard deviation

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Analysis of variance for alpha diversity indices of studied vegetation among remote sensing-based clusters, assessed using linear mixed-effects models (with block nested in heap as

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#### SUPPORTING INFORMATION

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Figure 1: Age distribution of remote-sensing-based clusters