RESEARCH ARTICLE

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

Quadri A. Anibaba[1], Marcin K. Dyderski[1],
Gabriela Woźniak[2], Andrzej M. Jagodziński[1]

1 *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)

Abstract

Biological invasions are one of the major challenges to the restoration of post-mining sites. Most post-mining 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.

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 18th 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 × 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 m²). 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
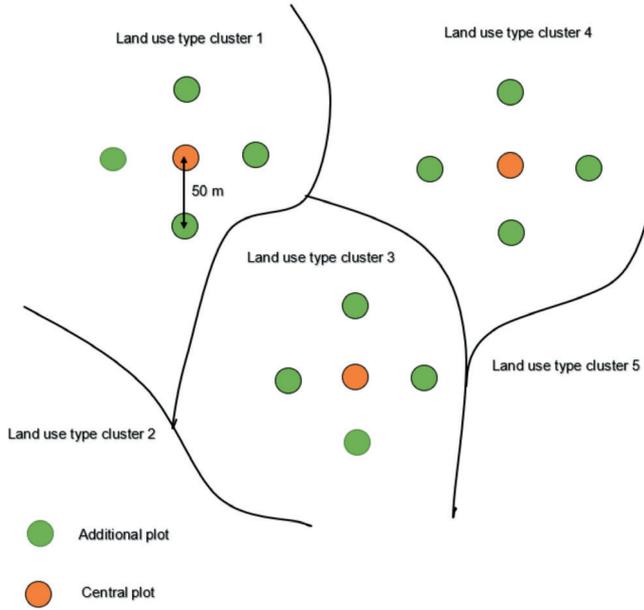
Figure 1. Scheme of study design – distribution of study plots within land use types. Additional plots are in north, south, east and west directions at 50 m from the central plot.

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

Plant traits	Code	Data type	Unit	Value (Min., Max.)	Missing data (%)
Leaf dry matter content	LDMC	Numeric	mg g^{-1}	0.3, 509.5	18.9
Seed mass	SM	Numeric	mg g^{-1}	0.001, 13737.6	5.5
Specific leaf area	SLA	Numeric	mm^2 mg^{-1}	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

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 'lme4' package (Bates et al. 2015) to develop GLMM and LMM, and the 'lmerTest' 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 of seed mass.

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).

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.

Species	Native region	Life form	Status	Frequency (number of plots)	Mean cover (%)	Pollination agent	Dispersal 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

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[*]	P
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
Alien 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

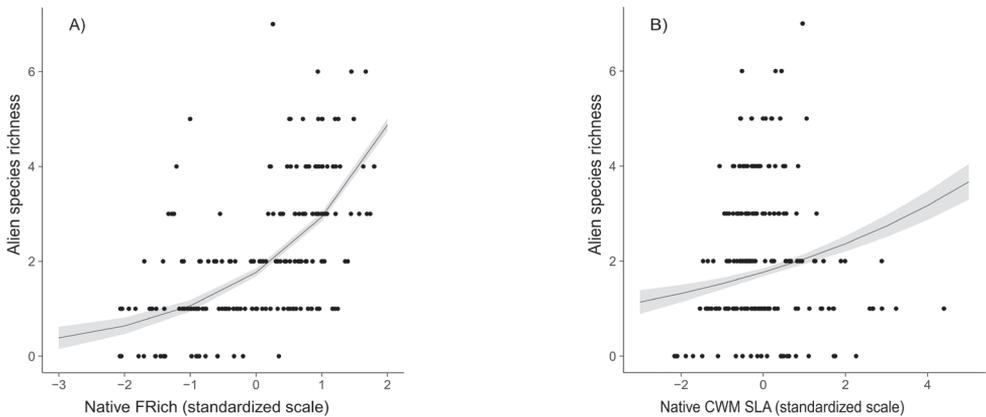[*]Z value = GLMM; t value = LMM.

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
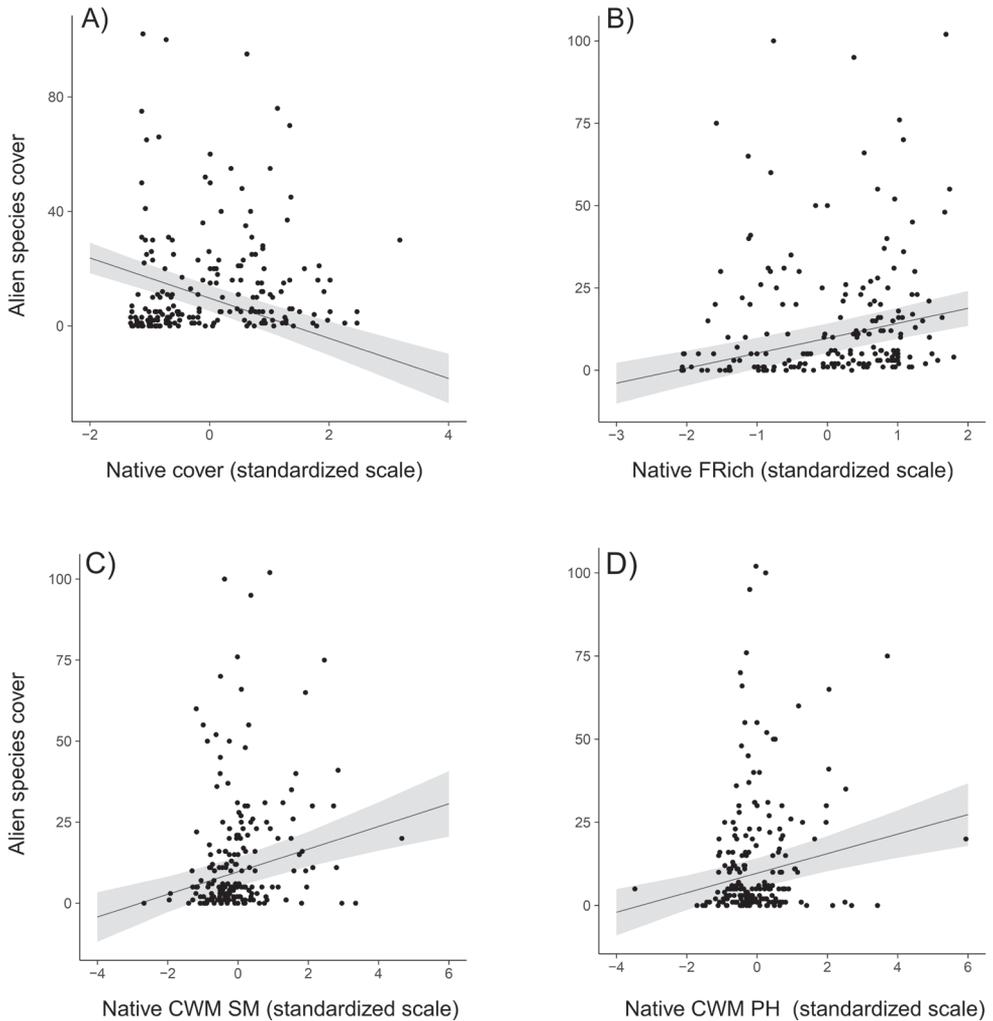
Figure 3. Alien species cover, estimated using LMM assuming a Gaussian distribution of the response variable (Table 3) as a function of **A** native cover **B** native functional richness (Native FRich) **C** native community weighted means seed mass (Native CWM SM) **D** native community weighted means 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 stage). Thus, seed mass of native species at 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 1

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
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