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

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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, the effects of a species depended on the successional stage. We found the impacts of *Calamagrostis* 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-Bąba 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-Bąba 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. gigantea*, 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* co-occur 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 man-made 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^2 (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 × 150 m. 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 3 m radius (28.3 m^2). 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.

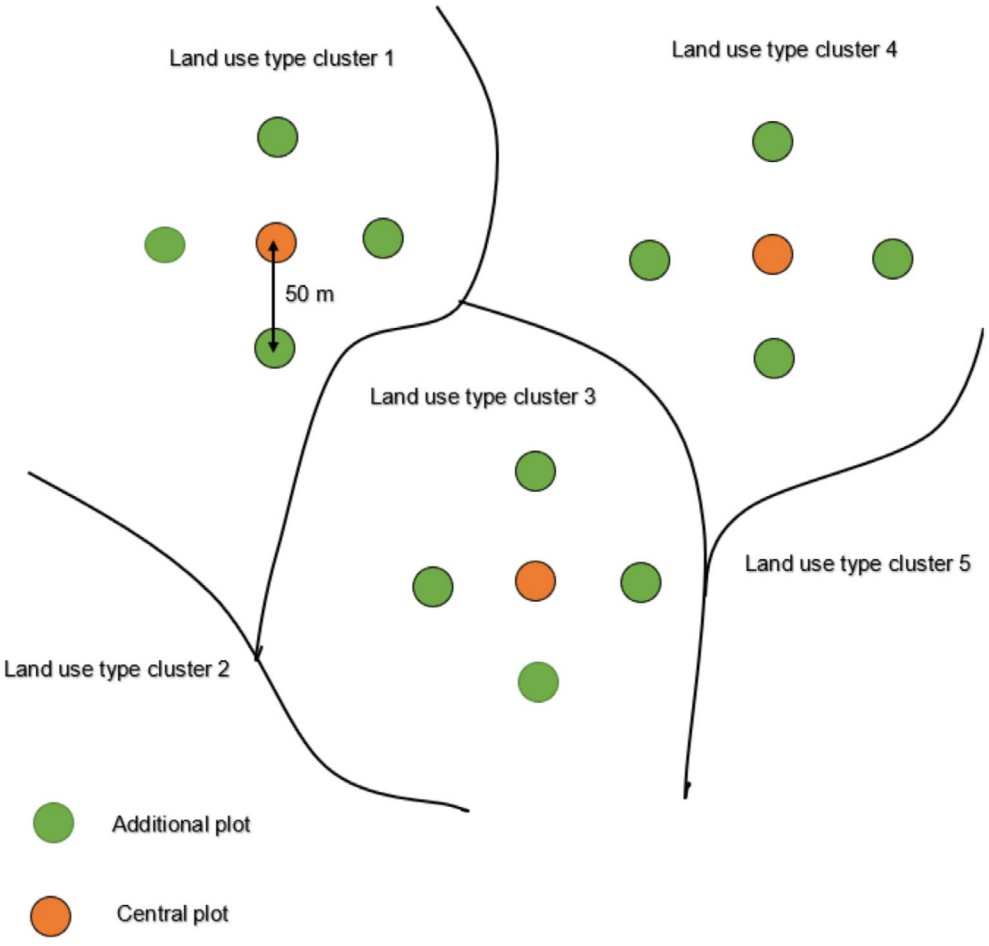


FIGURE 1 | Scheme of the study design—distribution of study plots within land use types. Additional plots are in the north, south, east, and west directions at 50 m from the central plot. Reproduced from Anibaba et al. (2023). [Colour figure can be viewed at wileyonlinelibrary.com]

2.4 | Data Processing

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 (Kleyer 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

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

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) ($cm^2 g^{-1}$)	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) ($mg g^{-1}$)	300	509.5	229.4	30.9	81.1

Categorical traits	Number of classes	Classes and their frequency	Completeness (%)
Insect pollinated	2	Yes (73.7%), no (26.3%)	95.9
Wind pollinated	2	Yes (28.9%), no (71.1%)	95.9
Self-pollinated	2	Yes (53.5%), no (46.5%)	95.9
Life form	8	Chamaephytes (4.6%), Geophytes (7.2%), Hemicryptophytes (53.2%), Hydrophytes (0.9%), Lianas (2.9%), Parasites (0.6%), Phanerophytes (15.0%), Therophytes (15.6%)	100.0

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 post-coal 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 late-successional 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

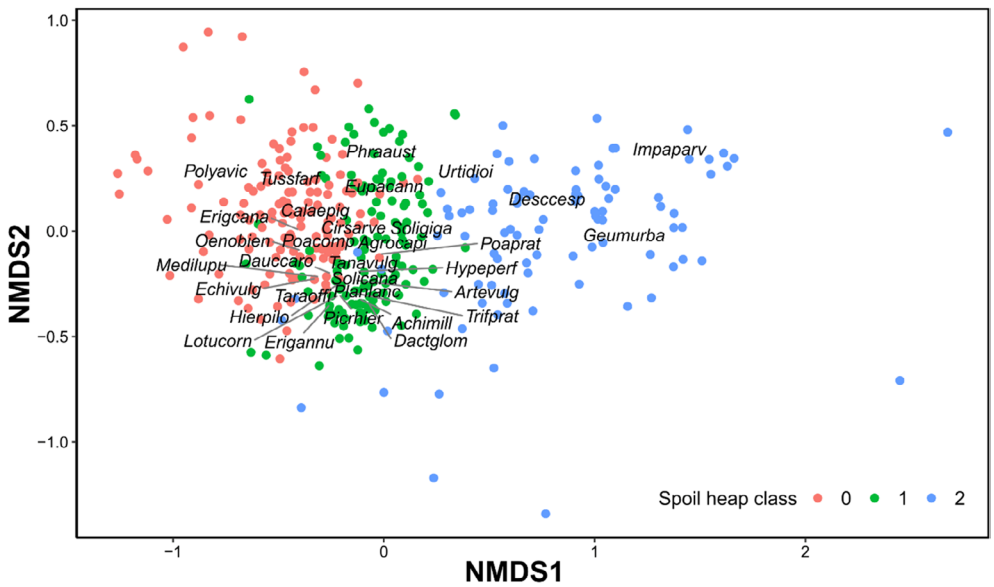


FIGURE 2 | Results of nonmetric multidimensional scaling (NMDS) analysis for all study plots showing species having a frequency (number of plots recorded) ≥40. Spoil heap class: 0, early-successional; 1, mid-successional; 2, late-successional. [Colour figure can be viewed at wileyonlinelibrary.com]

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 mid-successional 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[a]	*p*
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

[a]*Z* value for Poisson and beta GLMMs (species richness and functional richness); *t* value for Gaussian GLMMs.

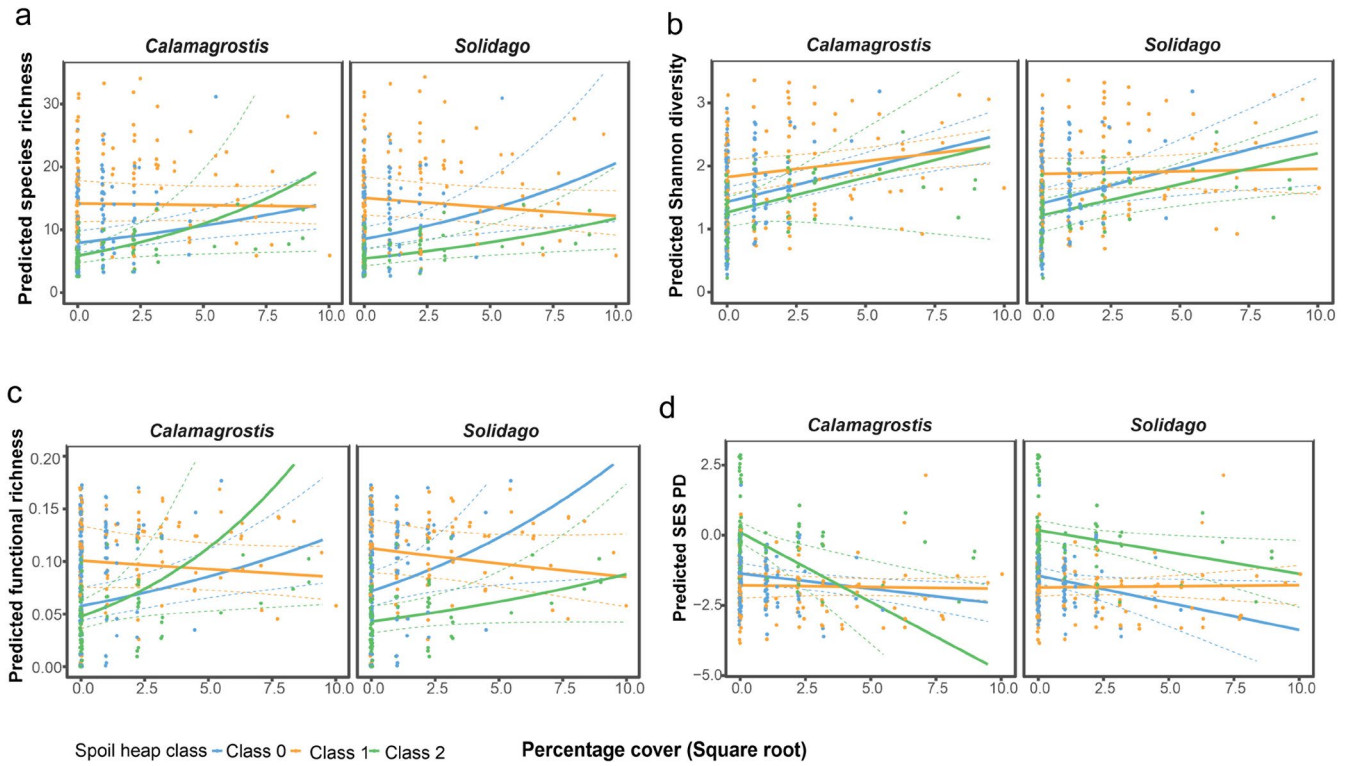


FIGURE 3 | Partial regression models with covers of *Calamagrostis*, *Solidago*, and spoil heap successional class as predictors influencing the species richness (a), Shannon diversity (b), functional richness (c), and predicted standardized effect size phylogenetic diversity (SES PD) (d). Interactions 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).

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 early-successional 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 late-successional 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).

The most parsimonious model for predicted SES PD was the interaction of *Solidago* cover and spoil heap successional class (AICc global model = 998.90, AICc null model = 1042.71, AICc best model = 996.14). We found a significant increase in predicted SES PD with *Solidago* cover under the mid-successional class. In contrast, under the early- and late-successional classes, there was a nonsignificant relationship between SES PD and *Solidago* cover (Table 3; Figure 3d).

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

Predictor	Estimate	SE	*t*/*Z* value[a]	*p*
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

[a]*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 mid-successional 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 mid-successional 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-Bąba et al. (2020) study focused on the early-successional 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 mid-successional 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.