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Research Article

Fungal community assembly during *Solidago canadensis* shoot decomposition is driven by the plant's invasion gradient

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Abstract

Solidago canadensis (L.) is an invasive plant species native to North America, but it is also widespread in Eurasia, Australia and New Zealand. Numerous authors suggest that the leaf litter of this plant decomposes rapidly. However, knowledge about the decomposition of its strongly lignified shoots, which remain in the environment for longer than one season, is limited. A comprehensive understanding of how fungal community assembly during *Solidago canadensis* shoot decomposition varies along the plant's invasion gradient and which ecological factors drive these patterns, is still lacking. We conducted a one-year litterbag study to assess the mass loss of *S. canadensis* shoot litter within the gradient of its invasion, expressed as the percentage cover of this plant on the study plots. We also identified fungi participating in this process using a morphological approach and assessed their functional diversity. Predictions, based on generalised linear mixed models, revealed that the importance of different ecological mechanisms in fungal community assembly changed over the course of the decomposition, as mass loss of *S. canadensis* shoots progressed: from the prevalence of habitat filtering and niche differentiation to interspecific competition and, subsequently, habitat filtering again. We conclude that the decomposition starts with the high activity of endophytes, which are highly adapted to particular conditions within *S. canadensis* tissues and ends with saprotrophs that are highly specialised in the decomposition of plant litter. Moreover, our results suggest that the most abundant fungi, which we identified as weak degraders, appear to be unaffected by *S. canadensis* cover. This indicates their potential to decompose the type of plant litter recently introduced to the ecosystem. Based on this finding, we wish to place the emphasis on the invasiveness of *S. canadensis*, whose litter can be degraded by native fungi already present in the ecosystem, thereby allowing large amounts of newly-introduced biomass to enter the carbon cycle. This suggests that the invasibility of Natura 2000-protected mesic meadows may increase, as native fungi readily establish novel interactions with non-native plant species. Moreover, other areas similar to them within the secondary range of *S. canadensis* may be habitats more susceptible to changes than expected before.

Key words: decomposition, fungi, functional diversity, invasion gradient, *Solidago canadensis*

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Introduction

Decomposition provides constant nutrient and energy cycling in most types of ecosystems (Berg et al. 2001). This process is conducted by many different organisms, including bacteria, different protist groups, mesofauna and fungi (Hättenschwiler

et al. 2005), which are believed to be primary decomposers of plant material (Beare et al. 1992). Fungi can play many different roles in decomposition. They impact this process directly by degrading cellulose, lignin or other chemical components of plant necromass (Berg et al. 2001). On the other hand, their impact can be visible due to indirect influence on the decomposition process through interspecies interactions like mutualism, competition and mycoparasitism (Boddy and Hiscox 2016). Nevertheless, fungi commonly change their role in the ecosystem depending on the environmental conditions or condition of their host, i.e. strains belonging to endophytic species can turn into virulent pathogens or saprotrophs of the host plant (Romero et al. 2001). On the other hand, fungi described as pathogens are detected in the decaying plant material and may play an important role in the decomposition (Behnke-Borowczyk et al. 2019).

Another factor that can influence the decomposition process of plant necromass is the population density of the plant undergoing the mineralisation, especially if the plant is a relatively new component in the ecosystem. Some invasive plant species can alter soil biota composition or biochemical properties of the soil, explaining their engineering abilities (Ehrenfeld 2003). *Solidago canadensis* (L.), a North American species invasive in Eurasia and Australia, serves as a notable example of an environmental engineer (Ren et al. 2020). The presence of this non-native plant changes the pH (Xie et al. 2023) and the extractable nitrogen, potassium and phosphorus concentration in the top layer of the soil (Ye et al. 2019). Moreover, *S. canadensis* can change the set of soil mycobiota, for instance, arbuscular mycorrhizal fungi, i.e. by changing the dominant genus (from *Ambispora* to *Paraglomus*) (Xu et al. 2024). Soil response to the invasion is not the only way that the presence of invasive plant species can alter mycobiota functioning. Day et al. (2015) showed that *Vincetoxicum rossicum* – an invasive plant in North America – can harbour fungal strains potentially pathogenic to native plants, which did not cause any harm to the invasive species representatives. Increasing the biomass of invasive species can be a driver accelerating or retarding the process of litter decomposition indirectly by the cumulative effects of metabolites produced or co-occurring organisms. Elgersma and Ehrenfeld (2011) proved that some of the dependencies within the biology of invasive species can be non-linear between different intervals of the invasion intensity, defined as increasing invaders' abundance on the study plot.

Most of the authors proved that the decomposition of *S. canadensis* is faster than that of native plants occurring in the same habitat conditions (Zhang et al. 2016; Dekanová et al. 2021). However, Pergl et al. (2023) did not observe significant differences in the rate of decomposition processes when comparing *S. canadensis* to the native grass *Calamagrostis epigejos*. Zhang et al. (2014), on the other hand, proved that the leaf litter of *S. canadensis* mixed with the leaf litter of native *Phragmites australis* decomposed faster than *S. canadensis* leaf litter alone. This implies that low cover of *S. canadensis* in areas with other vascular plants increases the mass loss. Nevertheless, Anda et al. (2022) showed that the mass loss of *S. canadensis* leaves is higher than that observed for *P. australis* shoots after the same period of time. This experiment was performed in the aquatic environment and the authors conclude that both the expansive native dominant plant and the invader change the litter quality and availability of nutrients, influencing the rate of decomposition. Despite its ecological relevance, little is known about the decomposition of *S. canadensis* shoot litter in terrestrial ecosystems. Shoots of this non-native herb are highly lignified, which makes them hard to degrade (Wiatrowska et al. 2022).

Uncertainties about the impact of dense *Solidago* populations on litter decomposition processes and the lack of direct assessments of the organisms involved in this process were the trigger for this research aimed at studying shoot necromass decomposition processes over time in plots differing in the abundance of *S. canadensis*. We believe that comparing fungi inhabiting decaying tissues of *S. canadensis* on study plots with different levels of this plant abundance (gradient of invasion) may be a suitable way to understand the invasiveness of *S. canadensis* and the recipient ecosystem's invasibility.

Since fungi can play various roles in the ecosystem and sometimes even strains belonging to the same species can have different phenotypes (Kļaviņa et al. 2023), we need to implement functional diversity components, based on trophic guilds (Nguyen et al. 2016) when assessing their role in ecosystem functioning. Three metrics of functional diversity that are widely used in ecological studies are: functional richness (FRic), functional dispersion (FDis) and functional evenness (FEve). Functional richness shows how many realised niches are present in the studied ecosystem, while functional dispersion measures the dissimilarities amongst the species' realised niches. Functional evenness, on the other hand, is used to assess if any of the niches dominate in the ecosystem, as well as how regularly the species' realised niches are distributed in an ecosystem (Villéger et al. 2008; Laliberté and Legendre 2010; Hedberg et al. 2014; Czortek et al. 2021). High values of FDis and FRic suggest niche differentiation and trait divergence, indicating that species occupy distinct functional spaces to minimise competition. Low FDis and FRic, combined with low FEve, often reflect habitat filtering, where environmental constraints select similar traits. In contrast, low FDis and FRic with high FEve may indicate competitive exclusion acting through equalising mechanisms, favouring functionally similar, but evenly-spaced species. Thus, different combinations of FDis, FRic and FEve values can signal the dominance of either filtering, niche differentiation or competitive processes in community assembly (Czortek et al. 2021). Based on this approach, we gain insight into the processes leading to the decomposition of organic matter. Developing models, based on field data, allows for a better understanding of the dynamics of the distribution of matter originating from a new plant in the environment.

This study aims to improve our understanding of decomposition processes affecting novel biomass in invaded mesic meadows of central-eastern Europe. To achieve this, we set three study aims: 1) assessment of the effect of *S. canadensis* cover in the decomposition of this plant's shoots; 2) modelling of ecological processes shaping fungal community assembly during the decomposition of *S. canadensis* and the influence of these processes on mass loss and 3) determining the composition of fungi inhabiting the necromass. We formulated the following hypotheses:

H1: *Solidago canadensis* shoot decomposition is slower in areas with higher occurrence of this non-native plant in the initial phase of decomposition than in the plots with its low abundance.

This is due to the greater proportion of recalcitrant material, such as lignin, as well as the presence of secondary metabolites (Zhang et al. 2011) and endophytic fungi associated with *Solidago* itself. These factors may lead to stronger environmental filtering in highly invaded plots, resulting not only in lower fungal taxonomic diversity but also in more functionally similar fungal assemblages.

H2: In the more advanced stages of shoot decay, decomposition is faster in plots with a higher proportion of *S. canadensis*.

As decomposition progresses, competitive interactions are likely to intensify, with *Solidago* cover promoting the proliferation of endophytes. These fungi may increasingly outcompete soil-borne decomposers through competitive exclusion, ultimately becoming the primary agents driving decomposition at these stages.

Materials and methods

Study area

We conducted our study on unmown mesic meadows in the gradient of the invasion, identified as follows: up to 25% of *S. canadensis* cover, 25–50% of *S. canadensis* cover and more than 50% of *S. canadensis* cover. We have chosen ten plots to represent each invasion gradient interval and ten control plots with 0% *S. canadensis* cover (total n = 40 plots). Plots were at least 100 m distant from each other to minimise the risk of studying the same ramet more than once. Selected mesic meadows are located in central-eastern Europe within two sites – Białowieża (52°42'11.8"N, 23°51'13.5"E) and Budy (52°43'52.2"N, 23°44'13.7"E) – approximately 10 km distant from each other. Both glades are encircled by the Białowieża Primeval Forest. Mesic meadows themselves are under the protection of Natura 2000 (habitat type code: 6410), endangered by, amongst other factors, biological invasions. The mean monthly sum of precipitation in our study area was 55.025 mm, the mean temperature was 8.235 °C and snow was present for 49 days of 2023 (Institute of Meteorology and Water Management National Research Institute, Poland 2025).

Experiment pipeline

Lignified shoots of *S. canadensis* collected at the end of the vegetation season (October 2023) were dried at a low temperature (40 °C, 72 hours) to prevent endophytic biota from dying, then they were put into fiberglass mesh bags (5 g ± 2% per bag, 15 cm × 15 cm, mesh size = 1 mm). Litterbags were arranged into sequences of four – one bag per collection date – and the sequences were arranged on plots. On each plot, we deposited three sequences – first, for the calculation of the remaining necromass of the studied material, second, to assess fungal assemblages present in the necromass and the third repetition was treated as a backup in case of loss of the two described before. We collected one repetition of each litterbag sequence every three months from each of the 40 plots. After each collection, the set designed to assess mass loss was dried (60 °C, 48 h) and weighed. We collected deposited material four times: in February 2024, in May 2024, in August 2024 and in November 2024. We assumed that, due to possible research errors, the accuracy of mass measurements may vary by up to 2%. As a result, we assume all of the effect sizes ≤ 2% as no effect of the studied predictor value.

The samples from the second set of litterbags in the laboratory were placed in sterile Falcon tubes and intensively shaken with the addition of 5 ml of deionized water. We transferred 1.5 ml of this suspension to a sterile Eppendorf tube and centrifuged it (5000 rpm, 5 min). The supernatant was discarded and the pellet was re-suspended in 100 µl of sterile water. After that, to assess fungal diversity, we visually inspected 25 µl of the suspension under the light Nikon Eclipse Ni-U optical

microscope with Nikon DS-Qi2 Mono Digital Microscope Camera. Fungal structures were counted on 50 fields of view, with the magnification 200×. The diaspores were morphotyped, and they were summarised to obtain the relative abundance of organisms represented by structures in the decomposition within one sample.

The remaining necromass was divided into three equal parts. We placed the first one on Petri plates containing malt extract agar (BTL Łódź, Poland), the second part was put into moist chambers and the third one was kept in hydroponic cultures. This approach enabled us to obtain information about the presence of different groups of fungi with different culturing requirements. Divided material was observed under the light and dissecting microscope Nikon SMZ 745 T with a DLT-Cam PRO 6.3MP USB 3.0 camera. Spores were identified to genus or species level based on Watanabe (2002), Seifert and Gams (2011), and Wergen (2018).

Statistical analyses

Statistical analyses were performed in R version 4.3.2 (R Core Team 2024). In all of the models built, the response variable was defined as a proportion of remaining litter mass within the sample to the initial mass (hereinafter "mass loss"). A matrix containing the identified forms and their abundance was used as a basis for determining functional characteristics, based on the FunGuild database (Nguyen et al. 2016, accessed January 2025). Based on that data, we used functional richness (FRic), functional dispersion (FDis) and functional evenness (FEve) calculated by using the *FD::dbFD()* function (Laliberté and Legendre 2010) as a measure of fungal functional diversity within our samples.

We calculated the generalised linear mixed models using *glmmTMB:glmmTMB()* (Brooks et al. 2017). Each model contained a random factor defined as the plot identity nested in the study site identity (Białowieża/Budy). All of the models were performed assuming a beta distribution of the response variable. The first model tested the significance of the predictor, which was the *S. canadensis* cover on the loss of this non-native's shoots necromass (eq.1). Next, models were calculated on four subsets of our data and each of them tested for the effects of functional diversity parameters on mass loss obtained during one *S. canadensis* material collection date. These models' structures were the same for each subset and consisted of mass loss as a response variable and the following predictors: eq. 2–5 functional richness, eq. 6–9 functional dispersion, eq. 10–13 functional evenness, eq. 14–17 proportion of saprotrophic fungi, eq. 18–21 proportion of pathotrophic-saprotrophic fungi, eq. 22–25 proportion of saprotrophic-symbiotrophic fungi and the proportion of pathotrophic-saprotrophic-symbiotrophic fungi (eq. 26–29). The last three models for each collection date used the number of spores of the most abundant fungal genera within samples from this collection date as a predictor (one genus per model; eq. 30–41). All of the predictors used in each model were included in the model, assuming interaction with *S. canadensis* cover expressed as an average cover within the plots belonging to the same invasion category. We calculated the marginal responses of each model using *ggeffects::ggpredict()* (Lüdecke 2018) to check the effects of each predictor separately, assuming the effects of the remaining predictors at a constant (mean) level. To check the possible spatial autocorrelation in our data, we used Moran's I autocorrelation calculated using the spdep package (Parry and Locke 2022). Based on Moran's I index, we did not observe any spatial autocorrelation between plots (Suppl. material 1).

Results

The mean mass loss after the end of an experiment (one year of decomposition) was 60.33% (± 0.51 SD) of the initial mass. Mean mass loss was 14.6% (± 0.0204% SD) of the initial mass during the first collection date, 13.7% (± 0.0913 SD) during the second collection date, 28.2% (± 0.0755% SD) during the third collection date and 39.7% (± 0.102 SD) during the fourth collection date (Fig. 1). Mass loss ranged from 15–16% at the first collection date, 12–17% at the second, 28–29% at the third and 34–46% at the fourth, with *S. canadensis* cover increasing from 0–95% (Fig. 2). The most abundant fungi were: *Alternaria* sp., *Epicoccum* sp., *Cladosporium* sp. in February, *Alternaria* sp., *Septoria* sp., *Cladosporium* sp. in May, *Alternaria* sp., *Chalara* sp., *Leptosphaeria* sp., in August and *Alternaria* sp., *Penicillium* sp., *Cladosporium* sp., in November.

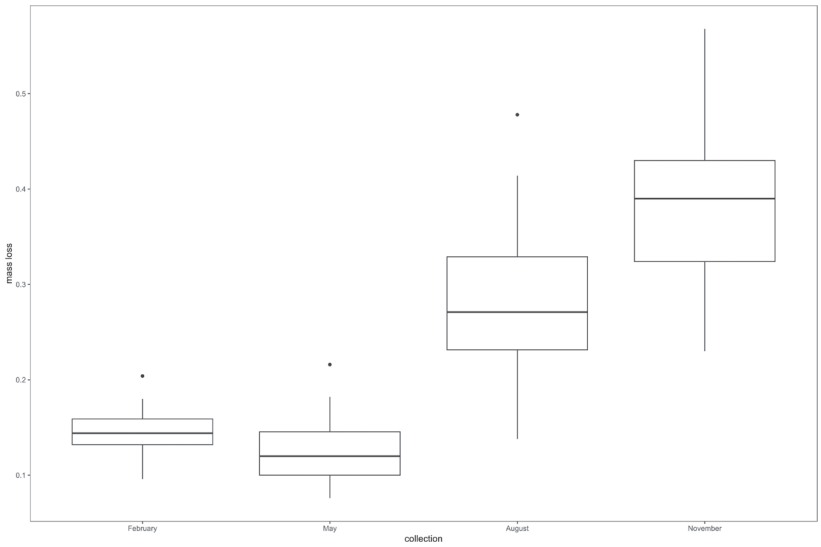


Figure 1. Mass loss within each collection date.

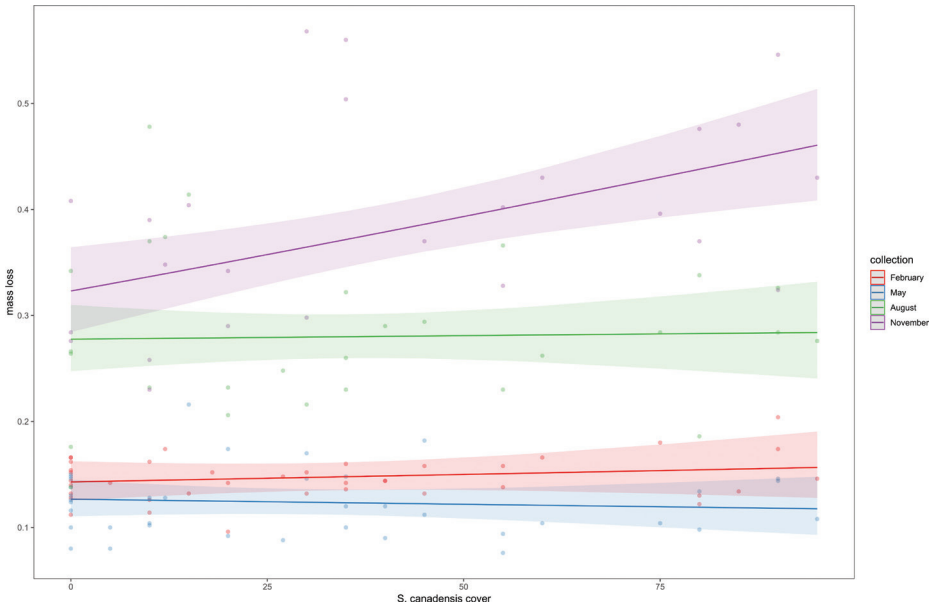


Figure 2. The influence of *S. canadensis* cover on the mass loss during decomposition, "mass loss" = proportion of mass loss to the initial mass.

During the first collection date (February 2024), FRic and FDis increased with the invasion gradient, causing a gentle slowing down of the decomposition. After six months of decomposition (in May 2024), we observed that FRic, increasing along the invasion gradient, caused a notably higher mass loss. We observed that increasing FRic along the gradient of the invasion speeded up the decomposition. On the other hand, increasing FDis and FEve with the increasing cover of *S. canadensis* decreased the mass loss. At the end of our experiment, we once again witnessed decreasing mass loss with increased FRic, FDis and FEve (Figs 3, 4).

Pathotrophic-saprotrophic-symbiotrophic fungi were the most efficient decomposers during the first three months of the decomposition, with their noticeable effect on the mass loss. In May, pathotrophic-saprotrophic and symbiotrophic-saprotrophic fungi made the decomposition process more efficient (Fig. 4). In August, the saprotrophic guild was the only one studied by us that notably increased the mass loss, while saprotrophic-symbiotrophic and pathotrophic-saprotrophic fungi substantially decreased the mass loss. Saprotrophic fungi exerted a prominent positive effect on the decomposition in November (Figs 3, 5).

Three dominant fungal genera had a negligible effect on the mass loss in February and, in May, we did not observe any effect of the invasion gradient on the mass loss caused by any of the dominant fungal genera. In August, *Alternaria* had the same substantial negative effect on the mass loss throughout the whole invasion

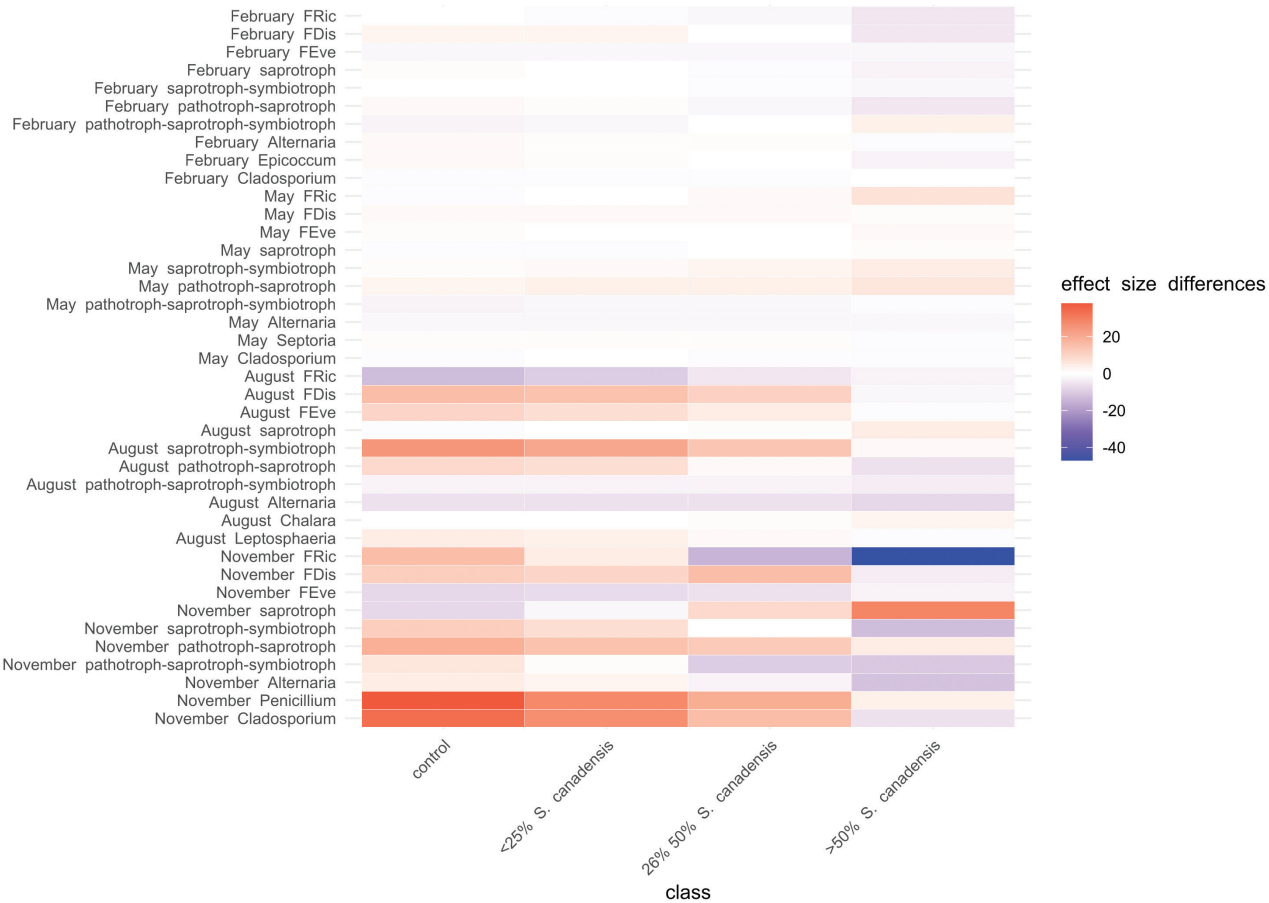


Figure 3. Differences between the predicted mass loss with the maximal value of a specific predictor and the predicted mass loss with the minimal value of the same predictor. Red bars indicate the positive impact on mass loss, blue bars indicate the negative impact on mass loss and white bars indicate no impact. The intensity of the colour indicates how great the effect size was.

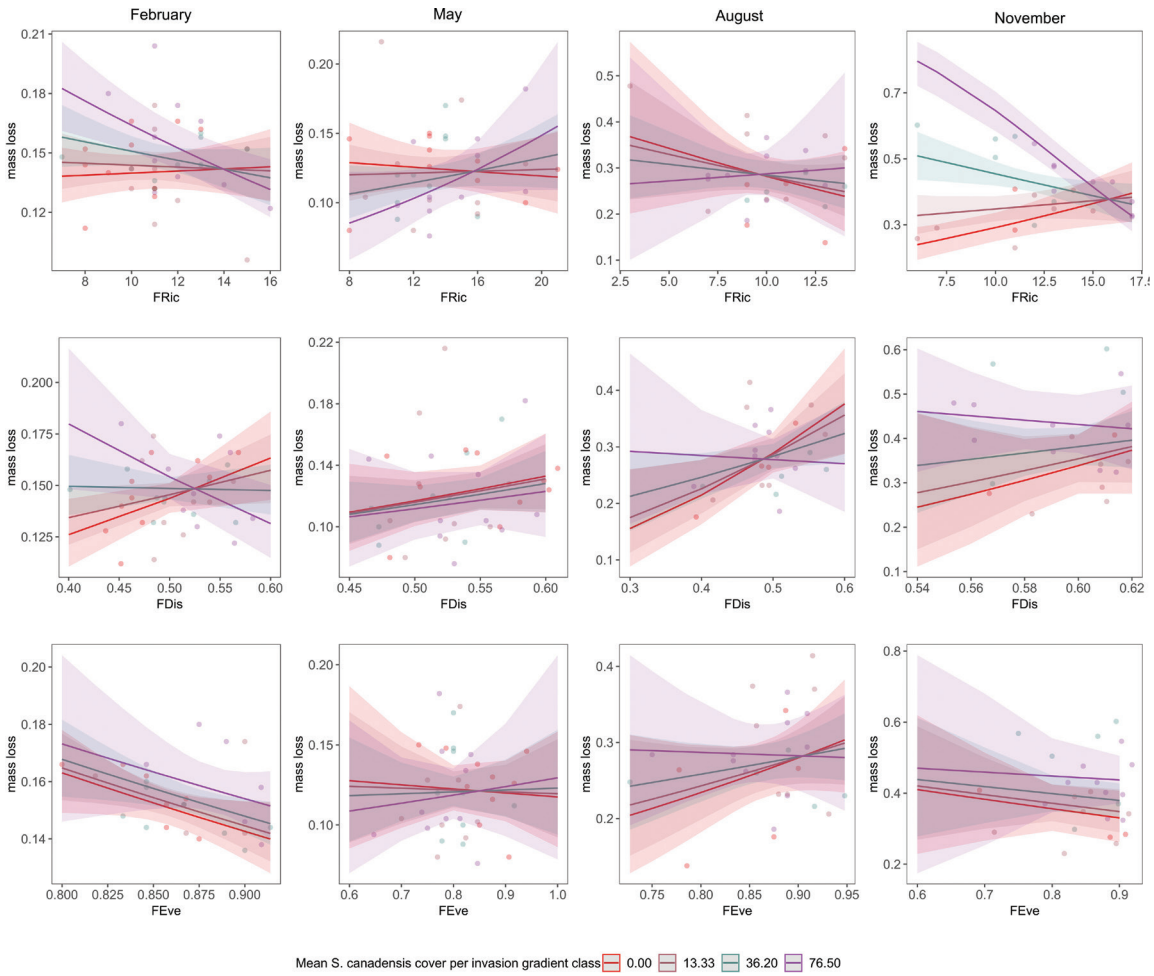


Figure 4. The influence of chosen functional diversity indices on the mass loss within each of the four collection dates. "FRic" = functional richness, "FDis" = functional dispersion, "FEve" = functional evenness, "mass loss" = proportion of mass loss to the initial mass.

gradient. *Chalara* and *Leptosphaeria* acted differently. With increasing *S. canadensis* cover, higher abundance of *Chalara* spores was positively correlated with the mass loss, while higher abundance of *Leptosphaeria* within the same conditions decreased it minimally. Finally, in November, three of the most abundant fungal genera observed during this period (*Alternaria*, *Cladosporium* and *Penicillium*) substantially decreased the mass loss with their increasing abundance with the gradient of the invasion (Figs 3, 4). Parameters of parts of the models shown in the current study are present in Table 1. Full parameters of the models are presented in Suppl. material 2.

Discussion

Decomposition of *S. canadensis* shoots is affected by the plant's cover

The effect of *Solidago* cover on the mass loss differs at various stages of decay and it is not easy to explain. In the study of Anda et al. (2023), mass loss of *S. canadensis* stems after 98 days of incubation in Balaton Lake was 14.5%, which corresponds with our results. Both experiments – ours and the one performed by Simon et al. in 2023 – differed in the type of ecosystem studied, which shows that humidity of the environment does not play a crucial role at the beginning of the *S. canadensis*

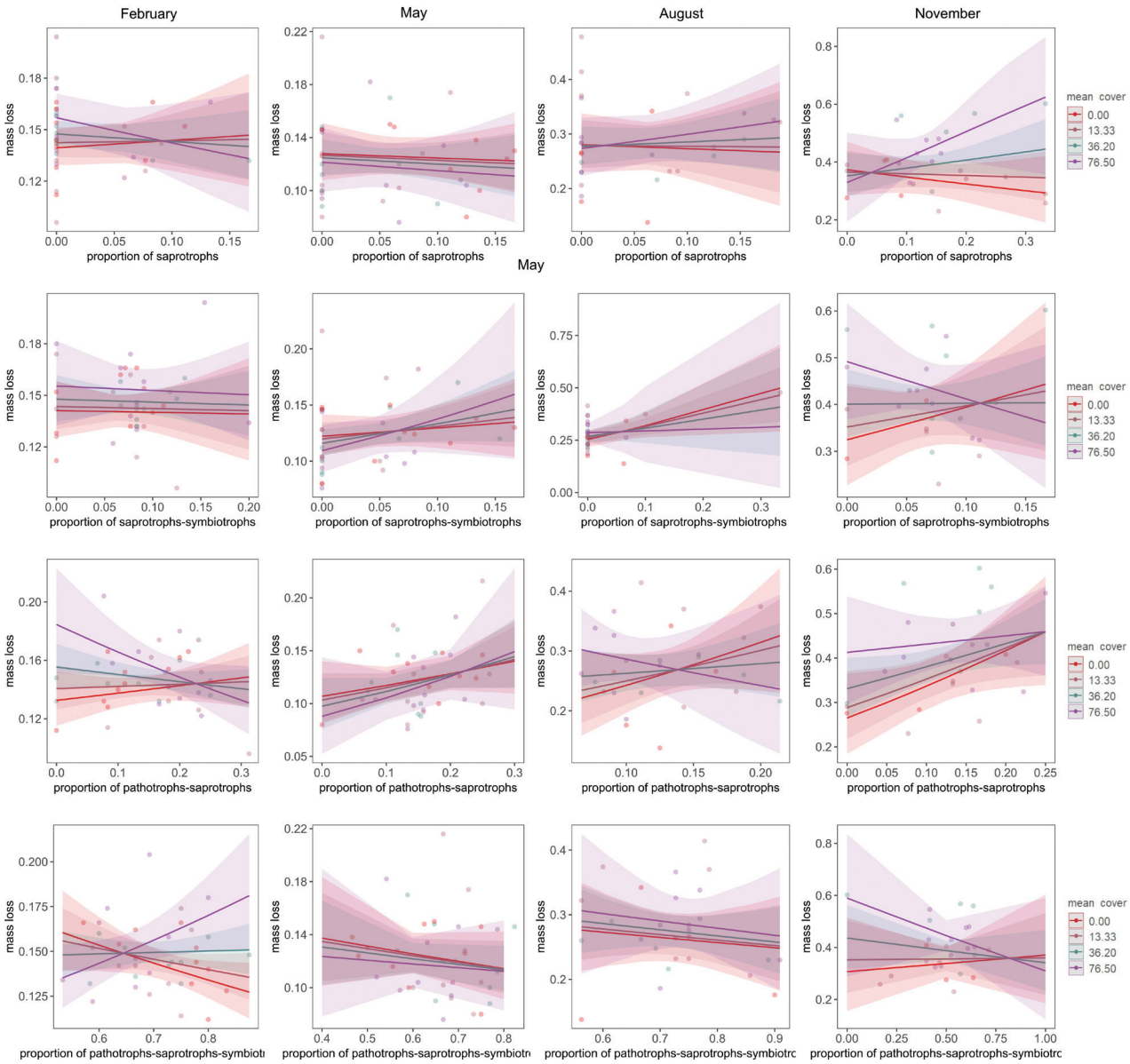


Figure 5. The influence of the proportion of chosen functional groups on the mass loss during each of the four collection dates. "FRic" = functional richness, "FDis" = functional dispersion, "FEve" = functional evenness, "mass loss" = proportion of mass loss to the initial mass.

Table 1. Final generalised linear models with a beta distribution of response variables. "solcov" = mean *S. canadensis* cover on the specific plot, "FRic" = functional richness, „FDis" = functional dispersion, "FEve" = functional evenness.

Model no.	Predictor	Estimate	SE	z-value	p	Random effect SD (site)
eq.1	Intercept	-0.954	0.103	-9.242	< 0.001	0.121
	solcov×February	< 0.001	0.003	0.051	0.959	
	solcov×May	0.002	0.002	0.975	0.329	
	solcov×November	0.004	0.002	1.505	0.132	
eq. 2	Intercept	-1.860	0.204	-9.127	< 0.001	0.078
	FRic February×solcov	-0.001	< 0.001	-1.428	0.153	
eq. 3	Intercept	-1.852	0.253	-7.332	< 0.001	0.070
	FRic May×solcov	0.001	<0.001	1.625	0.104	
eq. 4	Intercept	-0.371	0.598	-0.621	0.535	< 0.001
	FRic August×solcov	0.001	0.002	0.509	0.611	

Model no.	Predictor	Estimate	SE	z-value	p	Random effect SD (site)
eq. 5	Intercept	-1.554	0.499	-3.114	0.002	0.023
	FRic November×solcov	-0.003	0.001	-3.649	< 0.001	
eq. 6	Intercept	-2.540	0.360	-7.063	< 0.001	< 0.001
	FDis February×solcov	-0.044	0.017	-2.591	0.010	
eq. 7	Intercept	-2.758	0.810	-3.403	0.001	0.894
	FDis May×solcov	-0.005	0.037	-0.134	0.894	
eq. 8	Intercept	-2.877	0.825	-3.488	< 0.001	< 0.001
	FDis August×solcov	-0.056	0.040	-1.421	0.155	
eq. 9	Intercept	-5.227	4.754	-1.100	0.272	< 0.001
	FDis November×solcov	-0.060	0.081	-0.750	0.453	
eq.10	Intercept	-0.372	0.718	-0.518	0.604	0.007
	FEve February×solcov	0.002	0.021	0.111	0.912	
eq.11	Intercept	-1.781	0.805	-2.213	0.027	< 0.001
	FEve May×solcov	0.010	0.022	0.435	0.664	
eq.12	Intercept	-3.102	1.655	-1.874	0.061	< 0.001
	FEve August×solcov	-0.034	0.041	-0.841	0.400	
eq.13	Intercept	0.322	1.463	0.220	0.826	< 0.001
	FEve November×solcov	0.009	0.046	0.198	0.843	
eq.14	Intercept	-1.820	0.045	-40.600	< 0.001	0.006
	saprotroph February×solcov	-0.020	0.021	-0.960	0.335	
eq.15	Intercept	-1.920	0.098	-19.515	< 0.001	< 0.001
	saprotroph May×solcov	-0.004	0.028	-0.145	0.885	
eq.16	Intercept	-0.942	0.137	-6.886	< 0.001	< 0.001
	saprotroph August×solcov	0.022	0.036	0.601	0.548	
eq.17	Intercept	-0.519	0.204	-2.540	0.011	< 0.001
	saprotroph November×solcov	0.062	0.046	1.337	0.181	
eq.18	Intercept	-1.879	0.082	-22.947	< 0.001	0.006
	pathotroph-saprotroph February×solcov	-0.023	0.012	-1.824	0.068	
eq.19	Intercept	-2.124	0.157	-13.543	< 0.001	0.069
	pathotroph-saprotroph May×solcov	0.013	0.028	0.448	0.654	
eq. 20	Intercept	-1.498	0.383	-3.905	< 0.001	< 0.001
	pathotroph-saprotroph August×solcov	-0.077	0.068	-1.127	0.260	
eq. 21	Intercept	-1.020	0.238	-4.282	< 0.001	< 0.001
	pathotroph-saprotroph November×solcov	-0.035	0.035	-1.002	0.316	
eq. 22	Intercept	-1.806	0.069	-26.210	< 2e-16	0.007
	saprotroph-symbiotroph February×solcov	-0.002	0.018	-0.085	0.933	
eq. 23	Intercept	-1.972	0.086	-22.815	< 0.001	< 0.001
	saprotroph-symbiotroph May×solcov	0.025	0.034	0.753	0.452	
eq. 24	Intercept	-1.082	0.106	-10.190	< 0.001	0.010
	saprotroph-symbiotroph August×solcov	-0.037	0.076	-0.484	0.629	
eq. 25	Intercept	-0.733	0.250	-2.929	0.003	< 0.001
	saprotroph-symbiotroph November×solcov	-0.082	0.071	-1.155	0.248	
eq. 26	Intercept	-1.233	0.299	-4.123	< 0.001	0.018
	pathotroph-saprotroph-symbiotroph February×solcov	0.024	0.009	2.524	0.012	
eq. 27	Intercept	-1.628	0.441	-3.688	< 0.001	0.018
	pathotroph-saprotroph-symbiotroph May×solcov	0.003	0.017	0.191	0.849	
eq. 28	Intercept	-0.730	0.666	-1.096	0.273	< 0.001
	pathotroph-saprotroph-symbiotroph August×solcov	-0.002	0.024	-0.072	0.942	

Model no.	Predictor	Estimate	SE	z-value	p	Random effect SD (site)
eq. 29	Intercept	-0.814	0.446	-1.826	0.068	0.150
	pathotroph-saprotroph-symbiotroph November×solcov	-0.019	0.024	-0.778	0.437	
eq. 30	Intercept	-1.868	0.079	-23.769	< 0.001	0.004
	Alternaria February×solcov	< 0.001	< 0.001	-0.426	0.670	
eq. 31	Intercept	-1.831	0.052	-34.990	< 0.001	0.005
	Epicoccum February×solcov	< 0.001	< 0.001	-0.920	0.358	
eq. 32	Intercept	-1.763	0.051	-34.340	< 0.001	0.013
	Cladosporium February×solcov	< 0.001	< 0.001	0.200	0.844	
eq. 33	Intercept	-1.831	0.052	-34.990	< 0.001	0.079
	Alternaria May×solcov	< 0.001	< 0.001	-0.055	0.956	
eq. 34	Intercept	-1.900	0.108	-17.652	< 0.001	<0.001
	Septoria May×solcov	-1.971	0.105	-18.718	<0.001	
eq. 35	Intercept	-1.936	0.136	-14.229	<0.001	0.082
	Cladosporium May×solcov	< 0.001	< 0.001	-0.083	0.934	
eq. 36	Intercept	-0.793	0.184	-4.308	< 0.001	0.079
	Alternaria August×solcov	< 0.001	< 0.001	-0.172	0.864	
eq. 37	Intercept	-1.172	0.159	-7.360	< 0.001	0.121
	Chalara August×solcov	< 0.001	0.001	0.225	0.822	
eq. 38	Intercept	-1.192	0.191	-6.230	< 0.001	< 0.001
	Leptosphaeria August×solcov	< 0.001	0.001	-0.411	0.681	
eq.39	Intercept	-0.732	0.174	-4.217	< 0.001	0.111
	Alternaria November×solcov	< 0.001	< 0.001	-0.954	0.340	
eq. 40	Intercept	-0.942	0.169	-5.587	< 0.001	0.096
	Penicillium-like November×solcov	-0.001	0.001	-1.785	0.074	
eq. 41	Intercept	-0.943	0.141	-6.668	< 0.001	0.087
	Cladosporium November×solcov	-0.001	< 0.001	-2.644	0.008	

shoots decomposition maybe because *S. canadensis* populations in Poland and Hungary may possess some endobiotic microorganisms that could act similarly during the first stage of decomposition.

We observed that, during the different stages of the decomposition, expressed as different collection dates, different ecological mechanisms could prevail in shaping the fungal community assembly. However, our research hypotheses were not supported by the results. Regarding H1, in the first six months, we observed that *S. canadensis* decomposition was faster or the same in the plots densely covered by this plant and in the control plots. We observed different impacts of the *S. canadensis* cover on the mass loss in August (no impact) and in November (positive correlation), which forces us to falsify the hypothesis H2. *S. canadensis* cover probably did not have an impact on the decomposition because, as we stated before, endophytic biota had similar functions in each invasion gradient interval.

The decomposition of *S. canadensis* stems is not a uniform process; instead, the ecological mechanisms governing fungal community assembly shift markedly throughout the season and with *S. canadensis* cover showing high adaptivity of this plant to new environments. Early stages are dominated by habitat filtering, mid-stages by niche differentiation and competitive interactions and the later stages again by habitat filtering with increasing strengths of these processes with increasing *S. canadensis* cover.

Habitat filtering is crucial at the beginning of *S. canadensis* shoot decomposition

During the first three months of the decomposition, we observed that habitat filtering may be the process that shapes the fungal *S. canadensis* decomposers community since mass loss increased both with increasing fungal functional richness, functional dispersion and *S. canadensis* cover, but functional evenness did not seem to have any impact on the mass loss. In this stage, filtering could favour fungi displaying various functions (generalists). According to Chang et al. (2018) and Anžlovar et al. (2020), we conclude that shoots could be hard to colonise and decompose due to high lignin and secondary metabolite content in the initial stages of decomposition. Nevertheless, the information about the influence of *S. canadensis* secondary metabolites on fungal growth is limited to only a few, mostly pathogenic species (Zhang et al. 2011; Anžlovar et al. 2020), although we are not able to predict their impact on saprotrophic ones. Moreover, lignin could be processed and/or decomposed by other organisms that are not included in the current study, making it more available for fungi.

Competition-driven assembly of *S. canadensis* shoot decomposers in spring

From May to August, fungal community assembly could be modulated mainly by two ecological processes: niche differentiation and competition. After six months (in May), when the material was probably easier to degrade and assimilate, growing values of functional richness within the gradient of the invasion likely made the decomposition faster, but functional dispersion and evenness probably did not influence this process. Moreover, atmospheric conditions were relatively good for fungal activity (Petrović et al. 2024), since spring-times in north-eastern Poland are mostly warm with high precipitation (Institute of Meteorology and Water Management National Research Institute 2025). The large number of newly-available niches after the initial decomposition stage may have reduced the influence of both highly generalist and highly-specialised fungi, as they would lose competitive interactions with other functional groups. The most abundant fungi (*Alternaria*, *Cladosporium*), based on our dataset, did not have an impact on the mass loss during the first two stages of that process (in February and May). This is an interesting observation because these are two of the most common taxa found on all continents, in air and water (Bensch et al. 2019) and have usually been considered saprotrophs (Nguyen et al. 2016). However, it is worth noting that their presence may not necessarily mean that they are effective decomposers, but rather that they could reproduce and germinate effectively on the substrate.

Competition changes to niche differentiation during the summer

After nine months of decomposition, the competition between fungi seemed to be suppressed by the niche differentiation. Our results show that, in dense *S. canadensis*, a lot of different functional combinations could be needed to decompose the shoot litter of this plant efficiently. Nevertheless, fungal niches could not be very similar or dominated by one of them. As our results suggest, in this phase of decomposition, specialised saprotrophs appeared to be the only taxa

capable of carrying out decomposition in dense *Solidago* patches. Despite the need for saprotrophs to be specialised in degrading organic matter, they presumably had to degrade different substrates, as suggested by FDiv and FEve, which negatively affected the mass loss. We obtained interesting results for two genera of fungi that appeared in high abundance during the third sampling period (August). *Leptosphaeria* appeared to decrease in its contribution to biomass decomposition along the invasion gradient, whereas *Chalara* became increasingly significant along the invasion gradient. It seems that the specific microclimate created within dense *Solidago* patches may have a particularly strong influence on the presence of *Chalara* and its sporulation. *Chalara* is an anamorphic genus associated with multiple teleomorphs (MycoBank 2025) and the isolates observed in August may not represent the same species recorded earlier, especially since they may represent members of different fungal families (MycoBank 2025) with various ecological functions (pathogens, saprotrophs and even parasites of fungi (Wu and Diao 2023). *Leptosphaeria* appeared to decline in dense S. canadensis patches, likely due to high temperature and low humidity typical of central-eastern Europe in August and a whole bunch of secondary metabolites into idiophase were exhibited by perithecia filled with ascospores (Wergen 2018).

Habitat filtering shapes fungal community assembly after a year of decomposition

At the end of the experiment (in November), habitat filtering was presumably the mechanism that could most strongly influence the contribution of the fungal community to decomposition. The high number of ecological functions and the domination of one of them inhibited the decomposition along the gradient of the invasion. Strictly saprotrophic fungi were the only fungi detected by us that were able to degrade the *S. canadensis* shoot litter more efficiently under the high cover of this plant. Additionally, saprotrophic fungi occupied different ecological niches because higher functional evenness in the gradient of the invasion inhibited decomposition. Our field observations suggest that most of the parenchyma (which is an easier material to degrade because of its thin cell walls (Polo et al. 2020) at this point was degraded, so fungi that are not specialised plant litter degraders could not be able to perform the decomposition efficiently. On the other hand, the effect of fungi on the decomposition does not necessarily have to be negligible or negative. We detected some basidiomycetous mycelium that cannot be identified to the genus or species level, so they were not included in the current study. Nevertheless, we hypothesise that their impact on the decomposition would be higher than that of ascomycetous fungi since Basidiomycetes are known as very efficient degraders of many substrates of plant material, especially cellulose and lignin (Lundell et al. 2010). The field observations suggest the contribution of *Sphaerobolus stellatus* and *Cyathus olla* to further *S. canadensis* shoot degradation since they produce fruiting bodies on this medium.

Since the most abundant taxa in our study can be isolated as endophytes, our results can be a part of the discussion on the role of endophytes in the decomposition process. Xiao et al. (2025) showed that plant material infected by endophytes degrades faster and at the initial stage of decomposition. Some studies show the negative influence of endophytic species on decomposition (Omacini et al. 2004; LeRoy et al. 2011). We wish to underline the priming effect of potentially endo-

phytic taxa, which was visible in our data, that may weaken over time and eventually be outweighed by specialised saprotrophic genera. Most taxa we detected belonged to cosmopolitan genera and species. It is possible that we detected local strains of the same fungal species involved in the decomposition of *S. canadensis* litter in its native range. This could explain the lack of an invasion gradient effect on decomposition rates. However, detailed molecular and functional analyses of the fungal community are required to test this hypothesis and better understand the potential role of local adaptation or functional redundancy in maintaining decomposition processes across invaded habitats.

Study limitations

Next-Generation Sequencing (NGS) has become a widely adopted tool for studying fungal communities, as it reduces biases inherent in microscopic identification, such as the limitations associated with the inability of certain fungi to grow or produce spores on conventional culture media (Wu et al. 2019) or, like Basidiomycota, only within fruiting bodies that were not detected in the current study. Nevertheless, NGS approaches are not without their challenges, including the potential detection of extracellular DNA or DNA from non-target sources, which can obscure the interpretation of results (Sepulveda et al. 2020). Given these constraints and intending to emphasise the functional contributions of specific fungal taxa rather than their strict taxonomic identities in driving litter decomposition, we opted against molecular analyses in this study. On the other hand, our study reveals the need to perform metabarcoding studies of the decomposing *S. canadensis* shoots. Moreover, the mass loss can be influenced by many factors that are not addressed in the current study. First of all, physicochemical soil properties, like pH, EC, soil water content or soil structure, may influence the mass loss (Fu et al. 2022). Moreover, the experimental set-up chosen by us did not allow us to check the influence of the microclimate and plant species on our plots or that surrounding them on the decomposition. Both of these factors may influence the decomposition rate (Canessa et al. 2021; Yang et al. 2021). A study containing the molecular data, physicochemical properties of soil within the study plots and information about nutrients leaching from biological material to the soil, with comparison to our results, would fill the gaps of knowledge exposed by the current research.

Conclusions

Our study demonstrates a strong influence of *S. canadensis* cover on the fungal communities decomposing its shoots. The relative importance of ecological mechanisms structuring these decomposer assemblages was not constant, but varied temporally and across different stages of the invasion gradient. Importantly, we show that fungal communities present in the secondary range of *S. canadensis* are capable of efficiently decomposing its shoots, indicating a rapid establishment of novel interactions between native fungi and this non-native plant. We suggest that the ability of *S. canadensis* litter to be decomposed by fungal species in the introduced range represents a previously under-appreciated component of its invasiveness, allowing the species to modify ecosystem processes not only through biotic interactions, but also by altering carbon cycling pathways. Our results indicate

that the environmental engineering capacity of *S. canadensis* is stronger than previously assumed and is likely to contribute to its continued spread. The efficient degradation of its litter by resident fungal communities suggests that invasion success may be reinforced by the rapid incorporation of newly-introduced biomass into existing carbon cycles. Consequently, Natura 2000-protected mesic meadows may be more invasion-sensitive than expected, as local fungal assemblages readily form novel functional associations with non-native plant species. By extension, other habitats within the secondary range of *S. canadensis* that share similar environmental conditions may also be particularly susceptible to invasion-driven ecosystem changes.

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Additional information

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

Conceptualization: MW, PC, KK, KR. Data curation: PC, KK. Formal analysis: KK. Investigation: PC, KK, ŁK, MW, MM. Methodology: MW, KK, MM, KR, PC. Project administration: KK, PC. Resources: KK. Software: KK. Supervision: MW, PC, KK. Validation: MW, KK. Visualization: KK, PC. Writing – original draft: KK, KR, MM. Writing – review and editing: MW, PC, KK.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Moran's I autocorrelation results

Authors: Kamil Kisło, Marta Wrzosek, Marcin T. Mazurkiewicz, Łukasz Kuberski, Katarzyna Rawlik, Patryk Czortek

Data type: xlsx

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Supplementary material 2

Full parameters of generalised mixed models

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Data type: xlsx

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