



The promoting effects of soil microplastics on alien plant invasion depend on microplastic shape and concentration

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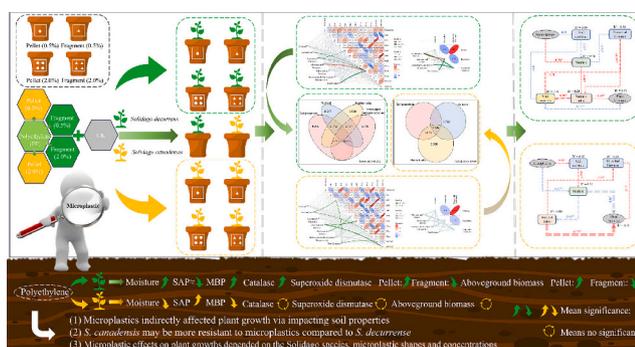
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HIGHLIGHTS

- Microplastics affect plant growth on *Solidago decurrens* more than on *S. canadensis*.
- *S. canadensis* may be more resistant to microplastics compared to *S. decurrens*.
- Microplastics may promote *S. canadensis* invasion.

GRAPHICAL ABSTRACT



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ABSTRACT

Both alien plant invasions and soil microplastic pollution have become a concerning threat for terrestrial ecosystems, with consequences on the human well-being. However, our current knowledge of microplastic effects on the successful invasion of plants remains limited, despite numerous studies demonstrating the direct and indirect impacts of microplastics on plant performance. To address this knowledge gap, we conducted a greenhouse experiment involving the mixtures of soil and low-density polyethylene (LDPE) microplastic pellets and fragments at the concentrations of 0, 0.5 % and 2.0 %. Additionally, we included *Solidago decurrens* (native plant) and *S. canadensis* (alien invasive plant) as the target plants. Each pot contained an individual of either species, after six-month cultivation, plant biomass and antioxidant enzymes, as well as soil properties including soil moisture, pH, available nutrient, and microbial biomass were measured. Our results indicated that microplastic effects on

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soil properties and plant growth indices depended on the *Solidago* species, microplastic shapes and concentrations. For example, microplastics exerted positive effects on soil moisture of the soil with native species but negative effects with invasive species, which were impacted by microplastic shapes and concentrations, respectively. Microplastics significantly impacted catalase ($P < 0.05$) and superoxide dismutase ($P < 0.01$), aboveground biomass ($P < 0.01$), and belowground/aboveground biomass ($P < 0.01$) of the native species depending on microplastic shapes, but no significant effects on those of the invasive species. Furthermore, microplastics effects on soil properties, nutrient, nutrient ratio, and plant antioxidant enzyme activities contributed to plant biomass differently among these two species. These results suggested that the microplastics exerted a more pronounced impact on native *Solidago* plants than the invasive ones. This implies that the alien invasive species displays greater resistance to microplastic pollution, potentially promoting their invasion. Overall, our study contributes to a better understanding of the promoting effects of microplastic pollution on plant invasion.

1. Introduction

Invasion of alien plant species have become a significant threat to biodiversity, food security, economies and overall, human well-being (Lovell et al., 2021; Christina et al., 2023). The successful invasion of alien plants can alter the structure and functionality of ecosystems (Wang et al., 2020a; Y. Wang et al., 2021a), through their effects on physical and chemical properties of soil, as well as on diversity, structure, activity, and function of soil biota (Herr et al., 2008; Zubek et al., 2020; Hu et al., 2021b). For example, the invasive *Solidago canadensis* increased soil moisture level (Zubek et al., 2020), while another invasive *Solidago* species, *Solidago gigantea*, lowered soil pH and increased labile phosphatase fraction (Herr et al., 2008).

Studies have revealed that global change factors, such as climate warming, land-use change, drought, among others, can influence alien plant invasion due to the creation of novel environments (Questad et al., 2021; Ren et al., 2022). According to the disturbance-mediated hypothesis, disturbance events as those caused by variability in precipitation regimes, drought periods, fertilization inputs or the presence of microplastics, may disturb the soil structure, with consequences on soil water regimes, pH and litter decomposition (Siebert et al., 2019; Zhao et al., 2021). The disturbance-induced shift in resources, highly linked with the empty niche and the diversity-invasibility hypothesis, opens up the window for the establishment of new plant species (Catford et al., 2009; Bjarnason et al., 2017). Thus, ecosystems with lower diversity and/or higher levels of disturbance tend to possess more unoccupied ecological niches that invasive species can exploit (Keller et al., 2011).

Indeed, many invasive species exhibit greater resistance to disturbances like environmental pollution and global change factors compared to native species (Zhang et al., 2014; Ren et al., 2022). For example, alien invasive plants like *Amaranthus retroflexus* and *Alternanthera philoxeroides* exert greater competitive intensity under heavy metal pollution condition than their native counterparts *Amaranthus tricolor* and *Alternanthera sessilis*, respectively (Wang et al., 2020a; Y. Wang et al., 2021a). Likewise, microplastics, a group of polymer-based particles <5 mm, as an emerging global change factor could also potentially promote the invasion of alien species (Lozano and Rillig, 2020, 2022; Deng et al., 2022). That is, at a community level, invasive species have shown greater dominance over native species when grown in soil contaminated with microplastics (Lozano and Rillig, 2020, 2022; Deng et al., 2022). Their promoting effects on alien species invasion may be ascribed to the microplastic effects indirectly (i.e., their effects on soil properties) or directly on plant growth (Iqbal et al., 2023).

Recent studies have indicated that microplastics can influence soil physicochemical properties and biota diversity and function, thus affecting plant performance. For instance, microplastics may change soil water dynamics (Kim et al., 2021), pH (Boots et al., 2019; Wang et al., 2020b; Zhao et al., 2021), organic matter contents (Romera-Castillo et al., 2018), nutrient retention, aggregation, respiration, litter decomposition (Lozano et al., 2021a), impacting plant growth (Boots et al., 2019; de Souza Machado et al., 2019; Lozano et al., 2021b) and plant community composition (Lozano and Rillig, 2020). Furthermore, the

persistence and movement of microplastics in plant-soil systems can impact plant growth throughout their life cycle, ranging from negative to positive effects. This includes processes such as seed germination and root development, nutrient uptake, physiological activity, tissue development, etc. (Zeb et al., 2022; Iqbal et al., 2023; Lozano et al., 2022).

Also, microplastics can alter the production of reactive oxygen species (ROS) in some plants (Mateos-Cárdenas et al., 2021), which plays a crucial role in regulating plant growth and development, enhancing their resistance to environmental stress (Choudhury et al., 2016). For instance, microplastics contributed to the changes in ROS levels in plants such as broccoli (*Brassica oleracea* L. var. *italica*) and radish sprouts (*Raphanus sativus* cv. Sparkler), lettuce (*Lactuca sativus*), and corn (*Zea mays* L.) (López et al., 2022; Zeb et al., 2022; Y. Zhang et al., 2022a). As the changes of ROS levels are indicated by the changes in the activities of the plant antioxidant enzymes such as catalase, peroxidase, and superoxide dismutase. Therefore, changes in the ROS levels induced by microplastics may contribute to changes in antioxidant enzymatic activities. Studies revealed that invasive plants are more tolerant to environmental stress than native species (Cai et al., 2021; Zhang et al., 2021), indicating that microplastics in soil may differently impact ROS levels in native and invasive plants, consequently influencing antioxidant enzyme activities.

To investigate the effects of microplastics on the growth of both native and invasive alien *Solidago* plants, we established a pot experiment with *S. decurrens* (native) and *S. canadensis* (alien invasive) plants, where single individual grew in pots with soil mixed with microplastics of two different shapes (pellet and fragment), at the concentrations of 0, 0.5 % or 2.0 % (w/w). We hypothesized that: (i) The presence of microplastics in the soil would induce less changes in the biomass of the invasive than the native *Solidago* species, depending on the microplastic shapes and concentrations; and (ii) The effects of microplastics on *Solidago* plant biomass would be associated with alterations in the antioxidant enzyme activities and soil nutritious levels induced by microplastics; and (iii) The invasive *Solidago* species will be more resistant to soil microplastics than the native species.

2. Materials and methods

2.1. Plant species selection and seeding preparation

Solidago canadensis, native to North America, is a plant species that was introduced to China as a horticultural plant in 1935. However, it quickly escaped cultivation and established itself in the wild, becoming one of the most dangerous invasive species in China. Indeed, *S. canadensis* is now recognized as a major threat to the terrestrial ecosystems of China (Zhang et al., 2022b; Yu et al., 2023; Iqbal et al., 2024). *S. decurrens* is the congeneric native species closely related to *S. canadensis* in China.

The seeds of the native *Solidago* plant (*S. decurrens*) were collected at the Dukou Xingli Ecological Farm, Ganzhou, China, while those of the invasive plant (*S. canadensis*) were collected at the Zhenjiang Yangtze River Ecological Park, Zhenjiang, China in 2020. The collected seeds

were stored in a refrigerator at 4 °C. Seeds were carefully nurtured and germinated under the same nature conditions in a nursery located on the campus of Jiangsu University, Zhenjiang, China in May 2021.

2.2. Microplastics and soil preparation

Low-density polyethylene (LDPE) plastics were used in the present study, as they are commonly found in the soil and constitute a considerable source of soil pollution in China. This, due their wide use in agricultural systems (e.g., mulching, silage, temporary greenhouses) to increase crop yield (Espí et al., 2006; Wang et al., 2019). LDPE plastic pellets were purchased from Zhangmutou Huahuang plastic material firm, Dongguan, China, while the plastic fragments were purchased from Shanghai Dayou Hardware Co., Ltd., Shanghai, China, and manually cut to obtain small plastic pieces. The pellets and fragments were sieved through 1.00-mm and a 0.45-mm mesh to obtain microplastic particles of 0.45–1.00 mm size. Before use, microplastics were rinsed with 70 % ethanol and then with deionized water to remove the solvent chemicals and microorganisms on their surfaces (Kim et al., 2020; Y. Zhang et al., 2022b).

2.3. Soil preparation and experimental design

Uninvaded topsoil with a loamy sand texture (82.73 ± 0.30 % sand, 15.06 ± 0.08 % silt, and 2.21 ± 0.02 % clay), exhibiting a pH of 7.69 ± 0.06, a cation exchange capacity of 10.14 ± 0.01 cmol kg⁻¹, and an organic matter content of 58.99 ± 1.42 mg g⁻¹, where neither native nor invasive plants were present, was collected from the campus of Jiangsu University, Zhenjiang, China (32° 12' N, 119° 30' E) and passed through a 2-mm sieve to remove litter, stones, roots, and debris. After this, all the soil is air-dried and preserved for future use. The soils without microplastics were served as control. The soil was mixed with the pellet or fragment microplastics at a low concentration of 0.5 % w/w (P-Low indicated for pellets and F-Low for fragments), and at a high concentration of 2.0 % w/w (P-High for pellets and F-High for fragments). The control soils were treated with the same process to provide similar disturbance. The mixed soils were in equilibrium for 14 days and being watered every three days to keep the moisture at 60 % of the soil maximum soil moisture content.

Then, in a nursery located on the campus of Jiangsu University, from July to December 2021 we conducted a full factorial experiment with ten treatments and three replicates for each treatment, resulting in 30 pots (bottom diameter 15 cm, top diameter 17 cm, and height 15 cm). Firstly, either native and invasive *Solidago* seedlings (30 days after germination), similar in size and possessing three leaves, were transplanted into each pot (one individual per pot). Subsequently, all pots were maintained in the nursery under natural environmental conditions. In summary, the ten treatments included two plant species (native or invasive *Solidago* plants) × two microplastic shapes (pellet and fragment) × two microplastic concentrations (low and high), along with a control without microplastics for each plant species.

2.4. Plant and soil sample collection

Plant and soil samples were collected after six-month cultivation. Plants were harvested and separated according to aboveground and belowground components. Before harvest, 0.1 g plant sample (leaf) was frozen and crushed using a mortar and liquid nitrogen, and then all the plant samples were preserved at 4 °C with a phosphate solution of PBS = 7.8. Soil samples were collected from each pot by using a soil core with a diameter of 2.54 cm and a depth of 10 cm. The collected soils were thoroughly mixed and sieved through a 2-mm mesh to remove visible plant debris and root matter. Plant and soil analyses were carried out within two weeks after harvest. All samples were stored in a refrigerator at 4 °C during these two weeks.

2.5. Plant and soil properties measurements

Aboveground and belowground components of each plant were dried at 60 °C for 3 days in an air blast drying oven until a constant weight was achieved. The dried samples were weighted to determine the aboveground, belowground, and total plant biomass. Levels of superoxide dismutase and peroxidase activity were analyzed in leaves according to Zhang et al. (2018). Catalase activity was assayed using a spectrophotometer, as per Azevedo et al. (1998).

Soil moisture was determined by the 105 °C oven-dry method while soil pH was determined using a glass electrode meter with a 1:5 soil: water (w/v) mixture (PHS-3E, Shanghaileici, Shanghai, China). Soil organic carbon (SOC) content was assessed using the dichromate oxidation method reported by Cui et al. (2020a). Soil dissolved organic carbon (DOC) and nitrogen (DON) were determined using a total organic carbon analyzer equipped with a total nitrogen module (Shimadzu TOC-LCPN, Shimadzu Co., Kyoto, Japan). Soil available phosphorus (SAP) was determined by the molybdate colorimetric method (Murphy and Riley, 1962; Olsen and Sommers, 1982). Microbial biomass carbon (MBC), nitrogen (MBN), and phosphorus (MBP) were determined by the chloroform fumigation-extraction method (Brookes et al., 1982; Vance et al., 1987).

2.6. Statistic analysis

Data are presented as the mean ± standard deviation. Normal distribution test and variance homogeneity test were performed for all data. If the data violated the assumptions of normality or homoscedasticity, we tried different transformations such as square root transformation, and chose the one that fulfils linear assumptions. We implemented two-way general linear model with Fisher least significant difference post-hoc analysis at a significance level of 5 % to evaluate the impact of microplastics (shape and concentration) on plant and soil properties using SAS software version 9.4 (SAS Systems, Cary, USA). Then the rest of the analyses were conducted using R software version 4.2.1 (R Core Team, 2022). We implemented the functions “fviz_pca” from the “factoextra” R package to perform principal component analysis (PCA) with permutational multivariate analysis of variance to discern differences in soil and plant properties among the treatments. Furthermore, to determine the environmental drivers affecting plant antioxidant enzyme activity and biomass with the presence of microplastics in soil, we correlated the difference in distance correction of plant antioxidant enzyme activity and biomass composition with the difference in environmental factors, by applying the functions “mantel” from the “vegan” R package for Mantel test. The variables that were significantly impacted by microplastic treatments (general linear model results) and correlated with plant performance (Mantel test results) were selected to performed further analysis. We performed variance partitioning analysis (VPA) by using the function “varpart” from the “vegan” R package, to ascertain the proportion of changes in plant performance (aboveground biomass, belowground biomass, total biomass, and the ratio of belowground to aboveground biomass) that may be explained by soil properties (moisture, MBC, and MBN), nutrient conditions (DOC, DON, and SAP), nutrient ratios (DO_{C:N}, DO_{C:P}, DO_{N:P}, and MBC:DOC) which are used to evaluate the nutrient imbalance, and antioxidant enzyme activities (superoxide dismutase, peroxidase, and catalase). Furthermore, to investigate the potential pathways through which microplastics could influence plant biomass, we also applied the functions “plsplm” from the “plsplm” R package to conduct partial least squares path modeling (PLS-PM) analysis (Cui et al., 2020b). To set the microplastics as one of the variables in the PLS-PM, we set the control as 0.01, the pellets as 2 and 3 for both concentrations, and the fragments at both concentrations as 4 and 5. The plots were generated with the “ggplot2” R package (Wickham, 2016).

3. Results

3.1. Microplastic effects on soil properties differed between native and invasive plants as a function of microplastic shapes, concentrations, and their interactions

Our results revealed that the effect of microplastics on soil properties depended on the plant species, and microplastic shapes and concentrations (Fig. 1, Table 1, and Table S1).

Microplastic treatments altered the properties of the soil with the *S. decurrens* plants, as the functions of microplastic shapes and concentrations (Fig. 1(a), Table 1, and Table S1). Both pellets and fragments increased soil moisture and microbial biomass phosphorus (MBP) but decreased the ratios of microbial biomass carbon (MBC) and nitrogen (MBN) to MBP ($MB_{C:P}$ and $MB_{N:P}$), irrespective of their concentrations (Table 1). The fragments at both concentrations and the high-concentration (2 %) pellets decreased soil available phosphorus (SAP) but increased the ratio of dissolved organic carbon (DOC) to SAP ($DO_{C:P}$), while low-concentration (0.5 %) pellets slightly increased SAP and decreased $DO_{C:P}$ compare with the control group (Table 1). Specifically, microplastic shapes significantly impacted soil moisture; meanwhile, the interaction of microplastic shape and concentration significantly altered SAP and MBP (all $P < 0.05$; Table S1).

Similarly, the presence of microplastic affected the properties of the soil associated with the invasive species *S. canadensis*, but with different effect patterns (Fig. 1(b), Table 1, and Table S1). Both pellets and fragments decreased the soil moisture, the ratios of DOC and dissolved organic nitrogen (DON) to SAP ($DO_{C:P}$ and $DO_{N:P}$), but increased SAP, regardless of their concentrations (Table 1). The pellets at both concentrations and low-concentration fragments decreased DOC and the ratio of DOC to soil organic carbon (SOC, $DOC:SOC$) (Table 1). The fragments at both concentrations and the high-concentration pellets decreased DON, but increased the ratio of DOC to DON ($DO_{C:N}$); while the low-concentration fragments increased DON and decreased $DO_{C:N}$ (Table 1). Specifically, the shape of microplastics influenced soil moisture ($P < 0.05$), SAP ($P < 0.01$), and MBP ($P < 0.05$) in native plants. For invasive plants, it affected DOC ($P < 0.01$), DON ($P < 0.01$), $DO_{C:N}$ ($P < 0.01$), $DO_{C:P}$ ($P < 0.05$), $DO_{N:P}$ ($P < 0.05$), and $DOC:SOC$ ($P < 0.05$) (Table S1). Microplastic concentration significantly influenced MBP ($P < 0.05$) in native plants and affected soil moisture ($P < 0.01$), DON ($P < 0.01$), $DO_{C:N}$ ($P < 0.01$), and $DO_{N:P}$ ($P < 0.05$) in invasive plants (Table S1). Furthermore, the interaction between microplastic shape and concentration significantly altered SAP ($P < 0.05$), $DO_{C:P}$ ($P < 0.05$),

and MBP ($P < 0.05$) in native plants. In invasive plants, this interaction influenced DOC ($P < 0.05$), DON ($P < 0.01$), $DO_{N:P}$ ($P < 0.05$), and $DOC:SOC$ ($P < 0.05$) (Table S1).

3.2. Microplastic effects on plant biomass and antioxidant enzymes depended on species character (invasive or native), microplastic shapes and concentrations

Our results indicated that microplastics affected the biomass and antioxidant enzyme activities of both *S. decurrens* and *S. canadensis* plants, with the effects being influenced mostly by microplastic shape, and in rare cases by the interaction of microplastic shapes and concentrations (Table 2 and Table 3).

Overall, the microplastic treatments significantly impacted some growth indices of the native species *S. decurrens*, with the effects varying with the microplastic shapes and concentrations (Table 2 and Table 3). Specifically, both pellets and fragments increased the activity of catalase regardless of their concentrations; the pellets increased the activity of superoxide dismutase and aboveground biomass but reduced the biomass ratio of belowground to aboveground (belowground/aboveground biomass ratio) at both concentrations, while the fragments showed contrary effect patterns (Table 2). Furthermore, only microplastic shape significantly influenced catalase ($P < 0.05$), superoxide dismutase ($P < 0.01$), aboveground biomass ($P < 0.01$), and belowground/aboveground biomass ratio ($P < 0.01$) (Table 3). The concentrations of microplastics, and their interactions with shapes showed no significant effects on the plant growth indices (Table 3). However, for the invasive species *S. canadensis*, the microplastic treatments showed no significant effects on plant growth indices (Table 2 and Table 3).

3.3. The effect pathways of microplastic effects on plant performance via changes in soil properties

Our results indicated that the different effects of microplastics on the properties of the soils associated with these two *Solidago* species contributed to the distinctive effect pathways of microplastic effects on plant performance (Figs. 2, 3, and 4, Tables S2 and S3).

Specifically, according to the results of the Mantel test (Fig. 2(a), Tables S2 and S3), the peroxidase ($P < 0.05$), superoxide dismutase ($P < 0.05$), aboveground biomass ($P < 0.01$) and total biomass ($P < 0.05$) of the native species *S. decurrens* were positively correlated with $DO_{C:P}$ (Fig. 2(a) and Table S2). Meanwhile, the aboveground biomass of *S. decurrens* was significantly positively correlated with peroxidase ($P <$

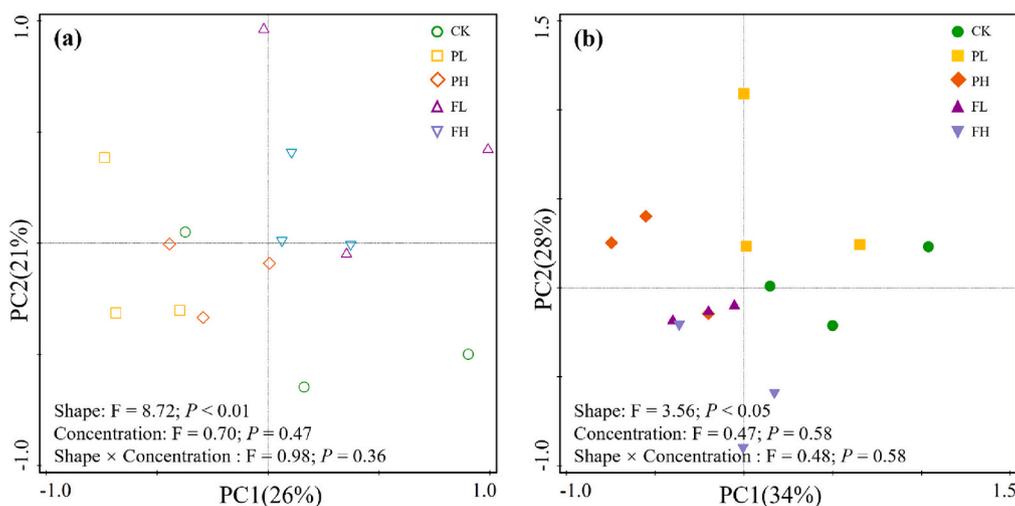


Fig. 1. Principal component analysis (PCA) of the microplastic effects on the properties of soil associated with native species (a) and invasive species (b). $n = 3$. CK: No microplastics; PL: Low concentration pellet microplastics; PH: High concentration pellet microplastics; FL: Low concentration fragment microplastics; FH: High concentration fragment microplastics.

Table 1The influence of microplastic shape and concentration on soil properties associated to native and invasive plants (Mean \pm Standard deviation was shown).

Solidago species	Soil properties	CK	Pellet		Fragments		P
			P-low	P-high	F-low	F-high	
Native species (<i>Solidago decurrens</i>)	Soil moisture (w/w %)	23.27 \pm 1.06 c	31.32 \pm 3.35 ab	34.01 \pm 1.86 a	25.53 \pm 1.16 bc	30.13 \pm 1.93 ab	S*
	pH	8.23 \pm 0.05	8.26 \pm 0.03	8.27 \pm 0.02	8.27 \pm 0.01	8.21 \pm 0.03	
	SOC ($\times 10$ mg C g ⁻¹ soil)	3.64 \pm 0.36	3.80 \pm 0.33	3.64 \pm 0.15	3.92 \pm 0.15	3.48 \pm 0.30	
	DOC ($\times 10^{-1}$ mg C g ⁻¹ soil)	4.16 \pm 0.40	4.03 \pm 0.74	4.46 \pm 0.22	4.09 \pm 0.10	3.80 \pm 0.58	
	DON ($\times 10^{-2}$ mg N g ⁻¹ soil)	4.06 \pm 0.36	6.13 \pm 0.86	4.38 \pm 0.57	5.53 \pm 1.28	5.52 \pm 0.91	
	SAP ($\times 10^{-2}$ mg P g ⁻¹ soil)	1.43 \pm 0.02 a	1.53 \pm 0.15 a	1.27 \pm 0.07 ab	0.99 \pm 0.06 c	1.13 \pm 0.09 bc	S**; S \times C*
	DO _{C:N}	8.90 \pm 1.80	6.61 \pm 0.93	10.68 \pm 1.94	8.17 \pm 1.68	7.03 \pm 1.02	
	DO _{C:P}	2.91 \pm 0.33 b	2.61 \pm 0.29 b	3.53 \pm 0.25 ab	4.16 \pm 0.34 a	3.32 \pm 0.29 ab	S \times C*
	DO _{N:P} ($\times 10^{-1}$)	3.54 \pm 0.72	4.07 \pm 0.68	3.45 \pm 0.45	5.62 \pm 1.29	4.82 \pm 0.49	
	MBC (mg C g ⁻¹ soil)	2.07 \pm 0.27	1.89 \pm 0.11	1.96 \pm 0.17	1.60 \pm 0.16	1.81 \pm 0.27	
	MBN ($\times 10^{-2}$ mg N g ⁻¹ soil)	6.75 \pm 0.10	6.14 \pm 0.71	7.54 \pm 1.98	4.85 \pm 0.83	7.83 \pm 0.93	
	MBP ($\times 10^{-3}$ mg P g ⁻¹ soil)	0.49 \pm 0.34 c	1.61 \pm 0.04 b	3.40 \pm 0.14 a	1.48 \pm 0.30 b	1.47 \pm 0.23 b	S*; C*; S \times C*
	MB _{C:N} ($\times 10$)	3.06 \pm 0.37	3.20 \pm 0.56	2.88 \pm 0.60	3.67 \pm 1.08	2.30 \pm 0.18	
	MB _{C:P} ($\times 10^3$)	0.98 \pm 0.49 a	0.12 \pm 0.01 b	0.06 \pm 0.01 b	0.11 \pm 0.01 b	0.13 \pm 0.04 b	
	MB _{N:P} ($\times 10$)	3.46 \pm 1.71 a	0.38 \pm 0.03 b	0.23 \pm 0.07 b	0.38 \pm 0.13 b	0.58 \pm 0.17 b	
	DOC:SOC (10 ⁻²)	1.14 \pm 0.01	1.10 \pm 0.25	1.23 \pm 0.10	1.05 \pm 0.03	1.13 \pm 0.24	
MBC:SOC (10 ⁻²)	5.78 \pm 0.95	5.09 \pm 0.72	5.39 \pm 0.46	4.14 \pm 0.57	5.42 \pm 1.26		
Invasive species (<i>Solidago canadensis</i>)	Soil moisture (w/w %)	32.93 \pm 0.25 a	32.39 \pm 0.54 a	23.71 \pm 0.75 b	28.34 \pm 2.51 ab	26.18 \pm 2.16 b	C**
	pH	8.25 \pm 0.07	8.26 \pm 0.02	8.32 \pm 0.02	8.21 \pm 0.07	8.27 \pm 0.05	
	SOC ($\times 10$ mg C g ⁻¹ soil)	3.11 \pm 0.16	3.22 \pm 0.10	3.59 \pm 0.17	3.48 \pm 0.05	3.22 \pm 0.24	
	DOC ($\times 10^{-1}$ mg C g ⁻¹ soil)	4.43 \pm 0.43 b	3.91 \pm 0.49 b	3.56 \pm 0.39 b	4.21 \pm 0.19 b	5.89 \pm 0.42 a	S**; S \times C*
	DON ($\times 10^{-2}$ mg N g ⁻¹ soil)	6.67 \pm 0.41 b	9.10 \pm 1.34 a	4.25 \pm 0.25 c	4.33 \pm 0.12 c	4.28 \pm 0.26 c	S**; C**; S \times C**
	SAP ($\times 10^{-2}$ mg P g ⁻¹ soil)	0.85 \pm 0.03 b	1.27 \pm 0.08 a	1.26 \pm 0.11 a	1.13 \pm 0.07 a	1.18 \pm 0.14 a	
	DO _{C:N}	6.73 \pm 0.94 bc	4.48 \pm 0.87 c	8.34 \pm 0.57 b	9.75 \pm 0.60 b	13.95 \pm 1.79 a	S**; C**
	DO _{C:P}	5.23 \pm 0.48 a	3.06 \pm 0.22 b	2.89 \pm 0.49 b	3.72 \pm 0.07 ab	5.15 \pm 0.81 a	S*
	DO _{N:P} ($\times 10^{-1}$)	7.93 \pm 0.75 a	7.23 \pm 1.11 a	3.42 \pm 0.37 b	3.86 \pm 0.32 b	3.70 \pm 0.46 b	S*; C*; S \times C*
	MBC (mg C g ⁻¹ soil)	1.88 \pm 0.08	1.98 \pm 0.34	1.75 \pm 0.26	1.63 \pm 0.06	1.39 \pm 0.11	
	MBN ($\times 10^{-2}$ mg N g ⁻¹ soil)	7.84 \pm 2.70	7.90 \pm 1.34	5.59 \pm 0.52	4.78 \pm 0.09	5.84 \pm 0.14	
	MBP ($\times 10^{-3}$ mg P g ⁻¹ soil)	2.40 \pm 0.50	0.78 \pm 0.62	0.42 \pm 0.18	1.12 \pm 0.02	1.14 \pm 0.59	
	MB _{C:N} ($\times 10$)	2.99 \pm 0.91	2.65 \pm 0.58	3.20 \pm 0.61	3.41 \pm 0.13	2.38 \pm 0.16	
	MB _{C:P} ($\times 10^3$)	0.09 \pm 0.02	1.52 \pm 1.03	0.73 \pm 0.39	0.15 \pm 0.00	0.21 \pm 0.09	
	MB _{N:P} ($\times 10$)	0.32 \pm 0.07	4.57 \pm 2.69	2.54 \pm 1.59	0.43 \pm 0.01	0.92 \pm 0.45	
	DOC:SOC ($\times 10^{-2}$)	1.44 \pm 0.20 ab	1.23 \pm 0.18 b	0.99 \pm 0.09 b	1.21 \pm 0.05 b	1.87 \pm 0.29 a	S*; S \times C*
MBC:SOC ($\times 10^{-2}$)	6.05 \pm 0.15	6.21 \pm 1.24	4.92 \pm 0.82	4.69 \pm 0.23	4.30 \pm 0.02		

CK: No microplastic; P-low: Low concentration pellet microplastic; P-high: High concentration pellet microplastic; F-low: Low concentration fragment microplastic; F-high: High concentration fragment microplastic; SOC: Soil organic carbon; DOC: Soil dissolved organic carbon; DON: Soil dissolved organic nitrogen; SAP: Soil available phosphorus; DO_{C:N}: The ratio of DOC to DON; DO_{C:P}: The ratio of DOC to SAP; DO_{N:P}: The ratio of DON to SAP; MBC: Soil microbial biomass carbon; MBN: Soil microbial biomass nitrogen; MBP: Soil microbial biomass phosphorus; MB_{C:N}: The ratio of MBC to MBN; MB_{C:P}: The ratio of MBC to MBP; MB_{N:P}: The ratio of MBN to MBP; DOC:SOC: The ratio of DOC to SOC; MBC:SOC: The ratio of MBC to SOC; the values in bold face indicate that the overall model results are significant; ns means no significance; * means significant level $P < 0.05$; ** means significant level $P < 0.01$. P values in bold indicate the variables significantly affected by microplastics (Shape (S) or concentration (C) and interaction (S \times C)).

Table 2The influence of microplastic shape and concentration on plant growth indices (Mean \pm Standard deviation was shown).

Solidago species	Growth indices	CK	Pellet		Fragments		P
			P-low	P-high	F-low	F-high	
Native species (<i>Solidago decurrens</i>)	Catalase ($\times 10^{-1}$ U min ⁻¹ g ⁻¹)	2.83 \pm 0.57 c	8.94 \pm 0.66 a	7.34 \pm 1.06 ab	4.08 \pm 0.40 bc	5.04 \pm 2.46 bc	S*
	Peroxidase ($\times 10^{-1}$ U min ⁻¹ g ⁻¹)	4.66 \pm 1.11	4.08 \pm 0.28	4.59 \pm 0.51	5.81 \pm 1.00	5.15 \pm 0.89	
	Superoxide dismutase ($\times 10^{-1}$ U min ⁻¹ g ⁻¹)	8.41 \pm 1.94 bc	13.07 \pm 0.23 a	10.44 \pm 1.32 ab	7.12 \pm 0.81 bc	6.63 \pm 1.17 c	S**
	Aboveground biomass (g)	6.89 \pm 0.75 abc	8.64 \pm 0.37 a	7.46 \pm 0.12 ab	5.30 \pm 0.90 c	6.28 \pm 0.65 bc	S**
	Belowground biomass (g)	5.10 \pm 0.76	4.05 \pm 0.89	4.43 \pm 0.61	4.56 \pm 0.88	5.94 \pm 0.42	
	Belowground/Aboveground biomass ratio ($\times 10^{-1}$ g)	7.47 \pm 0.89 ab	4.94 \pm 0.73 c	6.28 \pm 0.51 bc	8.53 \pm 0.48 ab	9.98 \pm 0.37 a	S**
	Total biomass ($\times 10$ g)	1.20 \pm 0.13	1.27 \pm 0.11	1.19 \pm 0.06	0.99 \pm 0.18	1.22 \pm 0.10	
	Catalase ($\times 10^{-1}$ U min ⁻¹ g ⁻¹)	4.56 \pm 1.82	6.50 \pm 1.22	5.59 \pm 0.83	10.31 \pm 0.27	5.45 \pm 2.13	
	Peroxidase ($\times 10^{-1}$ U min ⁻¹ g ⁻¹)	5.82 \pm 1.47	6.49 \pm 1.72	3.14 \pm 0.60	4.29 \pm 0.07	7.48 \pm 0.92	
	Superoxide dismutase ($\times 10^{-1}$ U min ⁻¹ g ⁻¹)	7.62 \pm 1.61	10.45 \pm 1.32	8.12 \pm 0.91	10.41 \pm 1.24	8.20 \pm 0.99	
Invasive species (<i>Solidago canadensis</i>)	Aboveground biomass (g)	6.30 \pm 1.13	7.57 \pm 1.82	5.74 \pm 0.22	6.80 \pm 0.84	6.13 \pm 0.18	
	Belowground biomass (g)	5.49 \pm 0.64	4.56 \pm 0.82	5.24 \pm 0.77	5.06 \pm 0.62	4.09 \pm 0.83	
	Belowground/Aboveground biomass ratio ($\times 10^{-1}$ g)	9.50 \pm 2.42	7.09 \pm 2.24	9.14 \pm 1.40	7.70 \pm 1.52	6.66 \pm 1.33	
	Total biomass ($\times 10$ g)	1.18 \pm 0.13	1.21 \pm 0.13	1.10 \pm 0.08	1.19 \pm 0.09	1.02 \pm 0.09	

CK: No microplastic; P-low: Low concentration pellet microplastic; P-high: High concentration pellet microplastic; F-low: Low concentration fragment microplastic; F-high: High concentration fragment microplastic; the values in bold face indicate that the overall model results are significant; ns means no significance; * means $P < 0.05$; ** means $P < 0.01$. P values in bold indicate the variables significantly affected by microplastics (Shape (S), concentration (C) or interaction (S \times C)).

Table 3

Microplastics shape, concentration and their interaction effects on plant indices associated to native and invasive plant species, based on general linear model results. F and P values were shown.

Solidago species	Growth indices	Shape		Concentration		Shape × Concentration	
		F	P	F	P	F	P
Native species (<i>Solidago decurrens</i>)	Catalase	8.33	*	0.12	ns	0.54	ns
	Peroxidase	1.81	ns	0.01	ns	0.49	ns
	Superoxide dismutase	14.85	**	1.42	ns	0.48	ns
	Aboveground biomass	11.6	**	0.01	ns	2.63	ns
	Belowground biomass	1.73	ns	1.49	ns	0.37	ns
	Belowground/aboveground biomass ratio	20.33	**	2.03	ns	0.14	ns
	Total biomass	1.16	ns	0.51	ns	1.70	ns
	Catalase	0.77	ns	3.24	ns	1.58	ns
	Peroxidase	1.40	ns	0.04	ns	9.67	ns
	Superoxide dismutase	0.01	ns	3.10	ns	0.01	ns
	Aboveground biomass	0.01	ns	1.25	ns	0.25	ns
Belowground biomass	0.19	ns	0.05	ns	1.34	ns	
Belowground/Aboveground biomass ratio	0.17	ns	0.12	ns	0.87	ns	
Invasive species (<i>Solidago canadensis</i>)	Total biomass	0.23	ns	1.70	ns	0.07	ns

The values in bold face indicate that the overall model results are significant; ns means no significance.

* Means significant level $P < 0.05$.

** Means significant level $P < 0.01$.

0.01) and superoxide dismutase ($P < 0.05$), and the total biomass positively correlated with peroxidase ($P < 0.05$) (Table S3). However, the correlation of *S. canadensis* plant growth properties with environmental factors showed different trends (Fig. 2(b), Tables S2 and S3). That is, peroxidase was positively correlated with DOC ($P < 0.05$) and $DO_{C:P}$ ($P = 0.05$), the aboveground biomass was positively correlated with MBN ($P < 0.05$) and the ratio of MBC to SOC (MBC:SOC), the belowground biomass was positively correlated with MBC ($P < 0.05$), and the total biomass was positively correlated with DOC ($P < 0.05$), $DO_{C:P}$ ($P < 0.05$), and MBC:SOC ($P < 0.05$) (Fig. 2(b) and Table S2). Nevertheless, there were no remarkable correlations between the plant biomass and antioxidant enzymes of the invasive species *S. canadensis* (Table S3).

Variance partitioning analysis (VPA) showed that changes in properties, nutrient, nutrient ratio of soil and plant antioxidant enzyme activities caused by microplastics explained 91.6 %, 51.7 %, 56.0 %, and 47.8 % of the variation in biomass of the native species *S. decurrens*, respectively (Fig. 3(a)). Meanwhile, only the soil nutrient and nutrient ratio explained 73.2 % and 53.6 % of the variation in the biomass of the invasive species *S. canadensis* with the presence of microplastics, respectively (Fig. 3(b)).

The influence pathway of microplastics on plant biomass remarkably differed between the native species *S. decurrens* and the invasive species *S. canadensis*. Partial least squares path modeling (PLS-PM) results showed that changes in soil moisture, nutrient, and nutrient ratio and microbial biomass caused by the soil microplastics would ultimately affect plant antioxidant enzyme activities and biomass (Fig. 4). For *S. decurrens*, microplastics had significant negative impacts on soil nutrient such as DOC, DON, and SAP, significantly impacting nutrient ratio and microbial biomass, ultimately leading to a significant reduction in plant biomass (Fig. 4(a)). Microplastics, conversely, slightly increased soil moisture, thus significantly affecting nutrient, nutrient ratio, microbial biomass of soil and antioxidant enzyme activities and biomass of plant (Fig. 4(a)). In general, plant antioxidant enzyme activities, soil nutrient, moisture, and microbial biomass positively, whereas soil nutrient ratio and microplastics negatively, contributed to the changes in plant biomass of the native species caused by microplastics (Fig. 4(c)).

Compared to the native species, the influence paths of microplastics on the plant biomass of the invasive species were significantly different. That is, microplastics, on the one hand, significantly reduced soil moisture, leading to significantly negative effects on soil nutrient. On the other hand, they displayed significantly positive effects on soil nutrient; consequently significantly positively impacting soil nutrient

ratio and plant biomass (Fig. 4 (b)). Furthermore, the soil nutrient ratio, on the one hand, had negative effects on soil microbial biomass, which subsequently affected plant biomass; on the other hand, they directly negatively influenced plant biomass (Fig. 4 (b)). Overall, microplastics, soil moisture and nutrient positively, while soil nutrient ratio and microbial biomass negatively contributed to the alterations in plant biomass of the invasive species by microplastics (Fig. 4(d)). Interestingly, the soil nutrient ratio had the most significant impacts on both species ($P < 0.05$; Fig. 4(c) and (d)). Therefore, soil nutrient ratio emerged as a crucial factor driving changes in plant biomass.

4. Discussions

4.1. Microplastic affected the plant growth of native *Solidago* species more than on the invasive species, depending on microplastic shapes, concentrations, and their interactions

Our results showed that microplastics displayed more pronounced effects on the plant growth of the native species than the invasive species, and the effects changed with microplastic shapes, concentrations, or their interactions. Specifically, microplastic treatments significantly impacted the catalase, superoxide dismutase, aboveground biomass, and belowground/aboveground biomass ratio of the native *Solidago* species; while the addition of microplastics showed no significant effects on the plant growth indices of the invasive species (Table 2). This supported our initial hypothesis that the presence of microplastics in the soil would induce less changes in the biomass of the invasive than the native *Solidago* species, but the variations depending on microplastic shapes and concentrations.

4.1.1. Microplastic effects on plant growth depended on microplastic shapes

Our results demonstrated that the microplastics impacted soil properties and plant growth indices as a function of microplastic shape and concentration, which coincides with previous studies (Lozano et al., 2021a). The microplastic shapes determine their interactions with soil particles, for example, microplastics with spherical shapes like beads exhibit less pronounced effects compared to other shapes like films and fibers, resulting in diverse impacts on soil properties and subsequently influencing plant performance (de Souza Machado et al., 2018; Rillig et al., 2019; Lozano et al., 2021b; Zhao et al., 2021). Indeed, our results revealed that the aboveground biomass of native *Solidago* plants (*S. decurrens*) was significantly affected by microplastic shapes but not by their concentrations, that is, the plants grew better with microplastics in the shape of pellet than fragment, possibly because pellets may

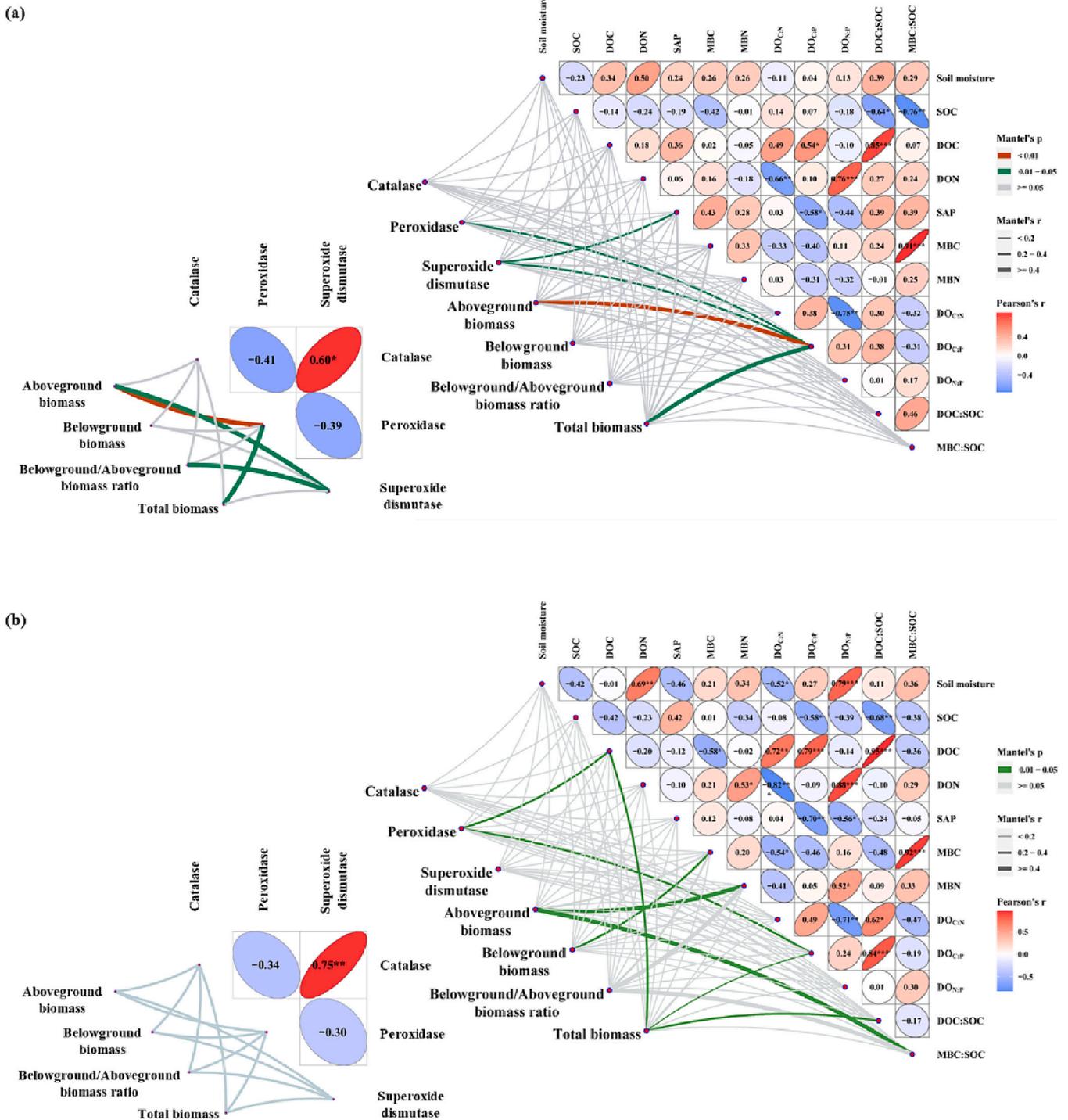


Fig. 2. Mantel test for environmental variables affecting antioxidant enzyme activity and biomass of native species (a) and invasive species (b). The grey line means no significance ($P > 0.05$); the green line means significance ($0.05 > P > 0.01$); the red line means significance ($P < 0.01$); the width of the line indicates the strength of the different correlations. The red and blue ovals indicate the strength of the correlation between the two indicators. SOC: Soil organic carbon; DOC: Soil dissolved organic carbon; DON: Soil dissolved organic nitrogen; SAP: Soil available phosphorus; $DOC_{C:N}$: The ratio of DOC to DON; $DOC_{C:P}$: The ratio of DOC to SAP; $DOC_{N:P}$: The ratio of DON to SAP; MBC: Soil microbial biomass carbon; MBN: Soil microbial biomass nitrogen; $DOC:SOC$: The ratio of DOC to SOC; $MBC:SOC$: The ratio of MBC to SOC.

provide more aeration to the soil than fragments.

4.1.2. Microplastic effects on plant growth changed with microplastic concentrations

Besides, the low-concentration (0.5 %) pellets showed more positive effects on the aboveground biomass of both *Solidago* species than the high-concentration (2.0 %). This finding agrees with previous research

on similar topics, which demonstrated that microplastic concentration below 2.0 % increased the aboveground biomass in wheat, whereas concentrations at 2.0–8.0 % triggered decreases in the aboveground biomass (Liu et al., 2021). This pattern may be attributed to the hormesis effects of pollutants, that is, low concentration of pollutants can stimulate the repair and resistance mechanism of plants, thereby promoting their growth and development; conversely, high concentration of

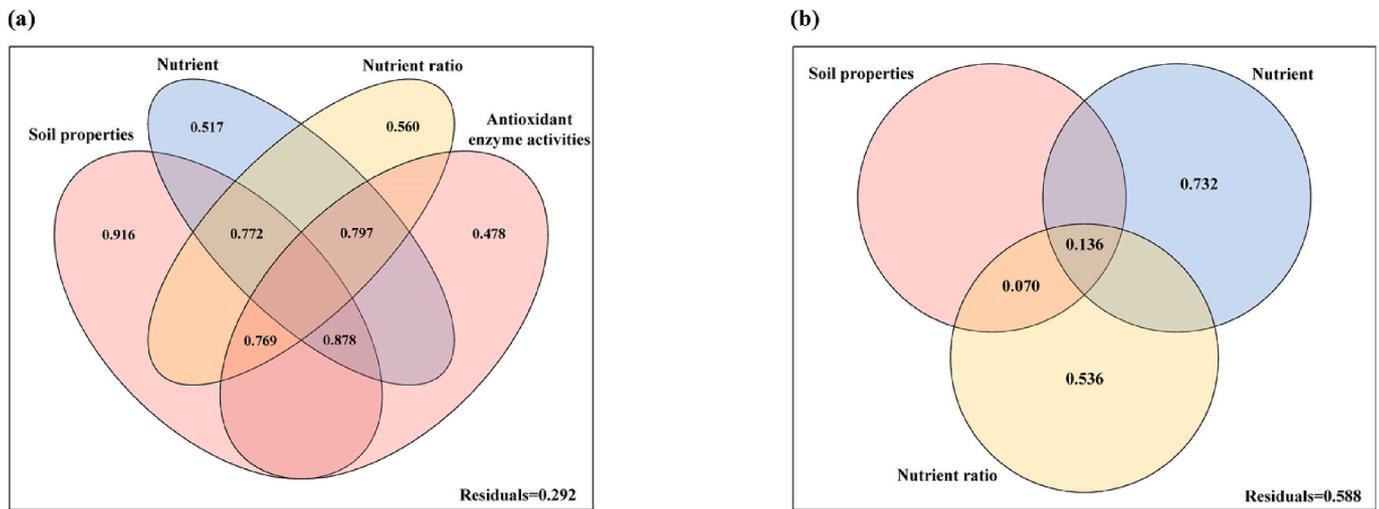


Fig. 3. Variance partitioning analysis (VPA) for plant biomass of native species (a) and invasive species (b) explained by soil properties (soil moisture, microbial biomass carbon and nitrogen), nutrient conditions (dissolved organic carbon, dissolved organic nitrogen, and available phosphorus), nutrient ratio (ratios of dissolved organic carbon, nitrogen, and available phosphorus), and antioxidant enzyme activities (catalase, peroxidase, and superoxide dismutase). Explanatory values <0 were not shown.

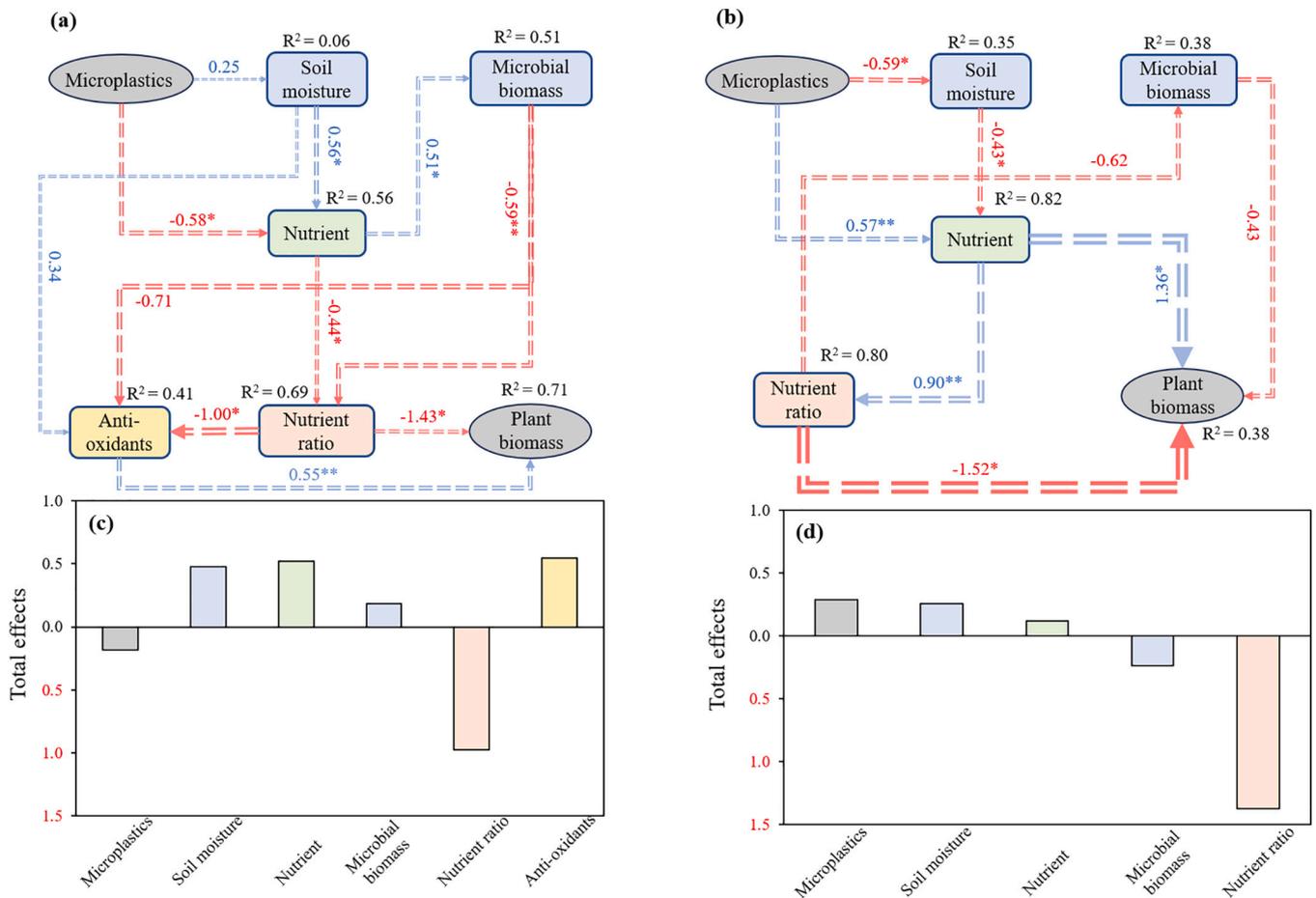


Fig. 4. The partial least squares path modeling (PLS-PM) of the microplastic effects on soil properties and growth of plant, and the results of standardized total effects of various factors. (a) PLS-PM path analysis of microplastics on native species; (b) PLS-PM path analysis of microplastics on invasive species; (c) The total impact of microplastics on native species; and (d) Total effect of microplastics on invasive species.

pollutants can exceed the plant's repair capacity, resulting in detrimental effects on plant growth (Salinitro et al., 2021). Another factor contributing to such diverse effects could be the differential impact of

microplastics at various concentrations on soil properties (de Souza Machado et al., 2018; Wang et al., 2020b; Lozano et al., 2021b).

However, neither the shape nor the concentration of microplastics

affected the growth of the invasive plant species, probably linked to the fact that these species are accustomed to encountering 'novel environments' and can rapidly adjust to such conditions (Finch et al., 2021; Liu et al., 2023a). However, high-concentration microplastics affected soil moisture associated with invasive species more than the low-concentrations did (Table 1). Higher concentration of microplastics in soil may have occupied more soil pores that otherwise could have been filled with water. Although no apparent consequences of this was found on plant biomass in the short term, it is possible that in the long term, microplastic degradation may affect soil properties (i.e., soil moisture), consequently influencing plant performance (Lozano et al., 2023). Indeed, previous results have shown that microplastics may have positive effects on invasive plant growth (Lozano and Rillig, 2020; Deng et al., 2022).

4.2. Microplastic effects on soil properties, nutrient, nutrient ratio, and plant antioxidant enzyme activities varied among plant species, contributing differently to plant growth

Our results of Mantel test, VPA, and PLS-PM indicated that the plant growth indices of both species were correlated with the changes in soil properties, nutrient, and nutrient ratio caused by microplastics, with the effect pathways changed with plant species, which supported our second hypothesis that the effects of microplastics on Solidago plant biomass would be associated with alterations in the antioxidant enzyme activities and soil nutritious levels induced by microplastics (Figs. 2, 3, and 4).

4.2.1. The correlation between the effects of microplastics on plant growth indices and on soil nutrients, and nutrient ratios varied among plant species

Mantel test results revealed that, for the native species, microplastic effects on SAP correlated with superoxide dismutase, and $DO_{C:P}$ which then correlated with peroxidase and superoxide dismutase, aboveground and total biomass (Fig. 2(a)). This is consistent with previous findings that microplastics can affect the bioavailability of essential nutrients, thereby impacting plant growth (Yan et al., 2021), and changes in soil phosphorus levels can influence antioxidant enzyme activities, and thus plant performance (Wang et al., 2021b). As for the invasive species, microplastic effects on soil properties including MBC and MBN correlated with aboveground and belowground biomass, the changes in MBC also correlated with the ratio of MBC:SOC, and then correlated with total biomass (Fig. 2b). The MBC and MBN levels in soil serve as indicators of the microbial community's capacity for nutrient cycling (Manral et al., 2023), influencing the availability of essential elements for plant growth and, thus impacting plant development. Moreover, changes in DOC induced by microplastics correlated with the peroxidase, total biomass, and DOC:SOC which also correlated with total biomass of the invasive species (Fig. 2(b)).

4.2.2. The microplastic effects on plant biomass explained by soil properties, nutrient, nutrients ratio, and plant antioxidant enzymes differently among the plant species

Our results of VPA showed that microplastic impacts on soil properties contributed plant biomass of the native species most, then followed by their effects on nutrient, nutrients ratio, and antioxidant enzyme activities (Fig. 3(a)). While, in respect of invasive species, microplastic effects on nutrient and nutrient ratio contributed to the plant biomass (Fig. 3(b)). This, on the one hand, may be attributed to the fact that *S. canadensis* can also affect soil properties, such as soil moisture, creating a comfortable ecological niche that allows it to survive. (Zubek et al., 2020). Indeed, our findings indicated that the microplastic effects on soil moisture were positively associated with *S. decurrens* but negatively associated with *S. canadensis* (Table 1), leading to distinct consequences on nutrient availability, uptake, and subsequently, plant biomass between these two species (Fig. 4(c) and (d)). On the other hand, invasive species like *S. canadensis* are more resistant to

environmental stress (Choudhury et al., 2016), which may prevent the changes in antioxidant enzyme levels. Therefore, soil properties and plant antioxidant enzymes showed no traceable impacts on plant biomass of the invasive species.

4.2.3. The effect pathways of microplastic on plant biomass changed with plant species

The PLS-PM analysis revealed distinct effect pathways of microplastics on the plant biomass of native and invasive *Solidago* species (Fig. 4(a) and (b)). Specifically, microplastics exhibited positive effects on soil moisture and nutrient, while negatively influencing nutrient ratio, contributing to the plant biomass of both species. Microplastics and their impact on microbial biomass demonstrated contrasting effect patterns. Additionally, antioxidant enzymes positively contributed to the plant biomass of the native species (Fig. 4(c) and (d)). This may be ascribed to, as discussed earlier, the differential impact of microplastics on soil moisture associated with these two species, and the distinct resistance to environmental stress of the two species. It is noteworthy that nutrient ratio emerged as the most influential factor contributing to the plant biomass of both species, highlighting its paramount importance in influencing plant growth.

4.3. Invasive *Solidago* plants were more tolerant than native ones to soil microplastics

Invasive species are known to possess more excellent resistance to environmental pressure, giving them a competitive advantage over native species (Ren et al., 2022). Based on this understanding, we hypothesized that *S. canadensis*, as an alien invasive species, might be more tolerant to soil microplastics than native species, and that they can mediate the microplastic effects on soil properties. Our findings support this hypothesis, evidenced by more pronounced effects on soil moisture and plant biomass of the native species than the invasive species.

4.3.1. *S. canadensis* may mitigate the microplastic-induced physiological and environmental stress via by affecting the soil microenvironment

Our results showed that microplastics increased the soil moisture of the native species *S. decurrens* but decreased with the invasive species *S. canadensis*. Such distinct effects in comparison with the native plant may be attributed to the higher water absorption of the invasive plant, which tends to reduce soil moisture levels (Zubek et al., 2020). This suggests that *S. canadensis* may mitigate the positive effects of microplastics on soil moisture. Likewise, the microplastic treatments in the soil significantly changed the contents of SOC and DON, as well as the ratios among available nutrient (e.g. DOC, DON, and SAP) in the soil with invasive *Solidago* plants (Table 1).

S. canadensis invasion can increase the availability of essential nutrient in the soil (Hu et al., 2021a, 2021b), and microplastics can impact soil organic matter and nutrient availability (Zhang et al., 2022a), as well as soil nitrogen contents (Rillig et al., 2021; Yu et al., 2022). Therefore, *S. canadensis* and microplastics may jointly affect soil properties, and then with consequences on plant growth. In other words, *S. canadensis* may regulate the microplastic-induced physiological and environmental stress by altering the soil microenvironment. Furthermore, invasive plants respond more rapidly to changes in soil nutrient than native plants and soil microbes (Liu et al., 2023b; Portela et al., 2023). Thus, changes in soil nutrient caused by soil microplastics showed less pronounced effects on the growth of *S. canadensis* than the native species *S. decurrens*, and consequently enhancing their tolerance to microplastic pollution, making them more resistant to microplastic pollution than the native species.

4.3.2. Microplastics induced lower levels of ROS in the invasive species *S. canadensis* than the native species *S. decurrens*

Plants increase reactive oxygen species (ROS) levels to defend against the stresses triggered by environmental factors such as drought

and heavy metals, which could damage plant cells (Yang and Ye, 2015). To mitigate such damages, plants enhance their antioxidant defence systems by increasing the activities of antioxidant enzymes like superoxide dismutase to reduce the ROS levels, especially in native species (Khattak et al., 2024). Indeed, our finding revealed that microplastics caused pronounced increases in the activities of catalase and superoxide dismutase in the *S. decurrens* plants, while no significant effects were observed in *S. canadensis* plants (Table 2). This indicated that microplastics caused higher levels of ROS in the native species, suggesting that microplastics may be more harmful to the native species when compared to the invasive species. This also suggests that *S. canadensis* plants may be more resistant to microplastic pollution than the native ones.

Such results are consistent with previous findings that invasive species are more resistant to environmental stresses, i.e. drought and high temperature (Cai et al., 2021; Zhang et al., 2021). For example, the invasive species *Sphagneticola trilobata* was reported more tolerant to high temperature than its native congener, *Sphagneticola calendulacea*, linked to the fact that high temperature caused more changes in the antioxidant enzyme activities of the native *Sphagneticola* species than in the invasive species (Cai et al., 2021).

4.3.3. The pronounced phenotypic plasticity of *S. canadensis* plants enhances their tolerance to microplastic pollution

In addition, alien invasive plants like *S. canadensis* adapt quickly to environmental changes due to their high phenotypic plasticity (Hu et al., 2021b). They can reallocate their biomass to aboveground biomass, enhancing their invasive abilities (Hiatt and Flory, 2019; Liu et al., 2022). For example, the plants of the invasive species *Ageratina adenophora* decreased their root/shoot ratio to allocate more energy to leaf mass to allow them compete with other native plants (Gong et al., 2022). In our study, microplastic-induced variation in native species was more pronounced than in invasive species (Table 2). This might be a strategy for *S. canadensis* to allocate more energy to aboveground biomass, thus enhancing their fitness and competitiveness (Du et al., 2017). These findings further support our hypothesis that *S. canadensis* plants may be more tolerant to microplastic pollution than the native species *S. decurrens*.

4.4. Potential promoting effect of soil microplastics on alien plant invasion

Microplastics had different effects on native and invasive *Solidago* plants in this study; notably, the fragmented microplastics inhibited the growth of native species *S. decurrens* but having negligible effects on *S. canadensis* plants. This suggests that soil microplastics may contribute to the success of *S. canadensis* invasion.

4.4.1. Microplastics display positive or negligible impacts on alien invasive species but negative effects on native species, thus potentially promoting invasion

Microplastic pollution can potentially promote the invasion of alien invasive species by exerting positive or negligible effects on their growth and inhibiting the growth of native species, thus enhancing the competitive advantage of the alien invasive species and facilitating their invasion. For example, microplastic fibers contributed to better growth for the invasive species such as *Calamagrostis epigejos* and *Galinsoga parviflora*, while negatively impacting the biomass of the native species like *Holcus lanatus* (Lozano and Rillig, 2020; Deng et al., 2022). In addition, microplastics even displayed legacy effects on the increase of shoot or root mass of the invasive species *C. epigejos* (Lozano and Rillig, 2022), as increased root mass can enhance their competitive advantage for nutrients over native species (Matzek, 2011; Zhao et al., 2022).

4.4.2. Microplastics may create a better soil environment for invasive plant growth than native species

Microplastics can alter soil physical and chemical properties, potentially creating a more favorable environment for the growth and

establishment of alien plants, thereby promoting their invasion. In this study, the induced changes in soil properties by microplastics were closely related to changes in plant growth (Figs. 2, 3, and 4). This is similar to the mechanism that climate change can promote the invasion of alien plants by altering the soil environment (Dai et al., 2022). Previous studies indicated that invasive species outperformed native species in microplastic-contaminated soil under drought conditions (Lozano and Rillig, 2020; Deng et al., 2022). Our findings also suggest that *S. canadensis* plants counteracted the positive effects of microplastics on soil moisture, as changes in soil water availability could impact the nutrient utilization of the native plants, thus potentially enhancing the invasive capacity of the alien invasive plants (Matzek, 2011; Hu et al., 2021b). For example, the invasive grass such as *Bromus hordeaceus* and *Bromus diandrus* can create dry conditions, allowing them to outcompete native plants for resources (Questad et al., 2021).

4.4.3. Microplastics potentially promote invasion by influencing the soil microbial interactions

Microplastics may affect the interactions among soil organisms, which could subsequently impact the invasiveness of alien plants. For instance, microplastic particles could interact with soil microorganisms, leading to changes in microbial communities and affecting the stability of soil ecosystems (Lozano et al., 2024). These changes could have complex effects on alien plant invasion. And the interactions between soil fungi and *S. canadensis* or microplastics may also enhance the invasion. For example, the growth of *S. canadensis* is positively influenced by soil fungi, especially arbuscular mycorrhizal fungi, while its neighboring native plants experience negative feedback (Dong et al., 2021). Studies have demonstrated that both *S. canadensis* and microplastics could improve the colonization, diversity, and community composition levels of arbuscular mycorrhizal fungi (Lehmann et al., 2020; Wang et al., 2020b). Specifically, *S. canadensis* increased the abundance of beneficial arbuscular mycorrhizal fungi but suppressed the unfriendly ones (Zubek et al., 2020). These processes may confer more tremendous nutrient acquisition advantages to *S. canadensis* than the native plants, thereby facilitating its invasion. However, further investigations are needed to explore the combined effects of microplastics and arbuscular mycorrhizal fungi on the invasion of alien species, considering both native and invasive plants and their interactions with arbuscular mycorrhizal fungi.

Moreover, microplastic effects on soil fungal pathogens may also potentially promote the invasion of the invasive species. As microplastics can increase the relative abundance of certain pathogenic fungi in multiple fertilization treatments (Li et al., 2021), and even serve as vectors for pathogens such as *Fusarium* and *Alternaria* (Gkoutselis et al., 2021). In addition, *S. canadensis* are more resistant to pathogens than native species (Zubek et al., 2020). Therefore, the combination of microplastics and *S. canadensis* may potentially inhibit the growth of native plants, promoting *S. canadensis* invasion. However, further studies are necessary to attain a comprehensive understanding of these interactions.

5. Conclusions

Our study contributes to a better understanding of the microplastic effects on soil properties, plant biomass, and antioxidant enzymes in native *S. decurrens* and invasive *S. canadensis* plants. We found that these effects varied depending on the microplastic shapes, concentrations, the interactions of microplastic shapes and concentrations, as well as the identities of the plant species. Furthermore, our results demonstrated that the microplastics affected the soil properties differently with the presence of native and invasive *Solidago* plants, leading to distinct effects on the plant performance. Specifically, the microplastic impacts on the plants of native species *S. decurrens* were more significant than on *S. canadensis*, suggesting that *S. canadensis* plants may exhibit greater resistance to microplastic pollution, potentially promoting their

invasion. However, the influence of soil microplastic pollution on the progress and successful invasion of alien plants remains largely unknown. Further specific research on this area is urgently needed.

CRedit authorship contribution statement

Guanlin Li: Writing – original draft. **Yi Tang:** Investigation. **Jiabao Lou:** Investigation, Data curation. **Yanjiao Wang:** Investigation. **Shiyu Yin:** Investigation. **Lianghui Li:** Formal analysis. **Babar Iqbal:** Writing – review & editing. **Yudi M. Lozano:** Writing – review & editing, Conceptualization. **Tingting Zhao:** Writing – review & editing, Writing – original draft. **Daolin Du:** Funding acquisition.

Declaration of competing 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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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