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Invasive plants can modify the soil environment through litter decomposition

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Report

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Summary

The successful colonization of invasive plants (IPs) may be facilitated by their nutrient release during decomposition, which alters soil physicochemical properties, enzyme activities, microbial metabolic processes and the diversity of soil microorganisms. This study aimed to examine the effects of co-decomposition of four Asteraceae IPs (*Conyza canadensis*, *Conyza sumatrensis*, *Erigeron annuus* and *Solidago canadensis*) along a gradient of invasion and a native plant (*Pterocypsela laciniata*) on decomposition rate, soil physicochemical properties, soil enzyme activities and the diversity of soil bacterial communities (SBCs). Leaves of *C. canadensis* with heavy invasion and *S. canadensis* with light and heavy invasion decomposed more slowly than *P. laciniata*. Leaves of *C. canadensis* with full invasion decomposed more rapidly than *P. laciniata*. *Pterocypsela laciniata* and *C. sumatrensis* had synergistic effects on each other's decomposition, whereas *P. laciniata* and *S. canadensis* displayed an antagonistic effect. Decomposition of the four IPs increased soil microbial carbon content but reduced soil fluorescein diacetate (FDA) hydrolase activity compared to *P. laciniata*. Thus, invasion degree and species identity of IPs modulate the effects of the four IPs on the decomposition rate, mixed-effect intensity of co-decomposition, soil microbial carbon content, soil FDA hydrolase activity and SBC structure.

Introduction

Invasive plant (IP) species can affect the structure and function of plant communities, particularly leading to a decrease in biodiversity (McGrath & Binkley 2009, Keet et al. 2021, Ahmad Dar et al. 2023). However, the mechanisms that facilitate their establishment are poorly understood. A significant factor contributing to the success of IPs is their capacity to interact with soil, particularly through litter decomposition. This interaction can influence soil physicochemical properties, enzyme activities and the structure of soil microbial communities, thereby facilitating the invasion process (Dekanova et al. 2021, Firmino et al. 2021, Maan et al. 2022).

The degree of IP invasion exhibits variation in invaded environments, accompanied by a gradient of succession after colonization in new habitats and the gradual formation of large mono-dominant communities (Fenouillas et al. 2021). This phenomenon is primarily attributed to the stronger growth performance, reproductive capacity, phenotypic plasticity and stress tolerance of IPs in comparison to native plants (Davidson et al. 2011). Consequently, leaves of IPs and natives may decompose together at different mixing ratios under a gradient of invasion. The decomposition rate of IPs is typically greater than that of natives, providing more nutrients for the metabolic activity and diversity of soil microorganisms (particularly decomposers), which in turn facilitates the successful colonization of IPs (Dekanova et al. 2021, Firmino et al. 2021, Maan et al. 2022, Vujanović et al. 2022). The invasion degree of IPs may affect soil physicochemical properties, soil enzyme activities and the metabolic activity and diversity of soil microorganisms via decomposition processes. Several IPs, particularly those belonging to the Asteraceae family, can occur in the same area (Wang et al. 2023). Thus, there is a need for studies that examine the association between the invasion degree and decomposition processes of multiple Asteraceae IPs. However, current progress in this field is relatively limited.

This study aimed to elucidate the effects of the co-decomposition of four Asteraceae IPs, namely *Conyza canadensis* (L.) Cronq., *Conyza sumatrensis* (Retz.) Walker, *Erigeron annuus* (L.) Pers. and *Solidago canadensis* L., along a gradient of invasion, and the native Asteraceae plant *Pterocypsela laciniata* (Houtt.) Shih on the decomposition rate, soil physicochemical properties, soil enzyme activities and diversity of soil bacterial communities (SBCs). The four IPs are capable of establishing expansive, monodominant communities with minimal latency following the successful invasion of habitats in China. Consequently, the four IPs have been

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considered as malignant invasive species in China. The four IPs and *P. laciniata* show similar growing-season characteristics: their maximum growth naturally occurs between April and August in China. The four IPs and *P. laciniata* are found in similar habitats, including agro-ecosystems, wastelands and near main roads in China, and they reach similar heights of up to c. 2–3 m. *Pterocypsela laciniata* can coexist with one or more of the four IPs in the same ecosystem in China.

The following questions were investigated: (1) Is there a greater decomposition rate of the four IPs in comparison to *P. laciniata*? (2) Does decomposition of the four IPs increase soil enzyme activities and SBC alpha-diversity? (3) Do the decomposition rate of the four IPs, soil enzyme activities and SBC alpha-diversity increase as the invasion degree of the IPs increases?

Materials and methods

Study design

Leaves of the four IPs and *P. laciniata* were collected in Zhenjiang (32.1633–32.2092°N, 119.4565–119.5293°E), China, in May 2022.

Decomposition of the four IPs and *P. laciniata* was replicated through a polyethylene litter-bag experiment conducted from 1 November 2022 to 3 May 2023 (c. 182 days) in a greenhouse in Zhenjiang (32.2061°N, 119.5128°E). Six grams of air-dried leaves of the four IPs and/or *P. laciniata* were placed in each polyethylene litter-bag (dimensions: 10 × 15 cm; mesh size: c. 0.425 mm) as follows: (1) 6 g of leaves of *P. laciniata* (imitating conditions without invasion; PL); (2) 6 g of mixed leaves with 2 g of *C. canadensis* and 4 g of *P. laciniata* (imitating *C. canadensis* with light invasion; CCL); (3) 6 g of mixed leaves with 3 g of *C. canadensis* and 3 g of *P. laciniata* (imitating *C. canadensis* with moderate invasion; CCM); (4) 6 g of mixed leaves with 4 g of *C. canadensis* and 2 g of *P. laciniata* (imitating *C. canadensis* with heavy invasion; CCH); (5) 6 g of leaves of *C. canadensis* (imitating *C. canadensis* with full invasion; CC); (6) 6 g of mixed leaves with 2 g of *C. sumatrensis* and 4 g of *P. laciniata* (imitating *C. sumatrensis* with light invasion; CSL); (7) 6 g of mixed leaves with 3 g of *C. sumatrensis* and 3 g of *P. laciniata* (imitating *C. sumatrensis* with moderate invasion; CSM); (8) 6 g of mixed leaves with 4 g of *C. sumatrensis* and 2 g of *P. laciniata* (imitating *C. sumatrensis* with heavy invasion; CSH); (9) 6 g of leaves of *C. sumatrensis* (imitating *C. sumatrensis* with full invasion; CS); (10) 6 g of mixed leaves with 2 g of *E. annuus* and 4 g of *P. laciniata* (imitating *E. annuus* with light invasion; EAL); (11) 6 g of mixed leaves with 3 g of *E. annuus* and 3 g of *P. laciniata* (imitating *E. annuus* with moderate invasion; EAM); (12) 6 g of mixed leaves with 4 g of *E. annuus* and 2 g of *P. laciniata* (imitating *E. annuus* with heavy invasion; EAH); (13) 6 g of leaves of *E. annuus* (imitating *E. annuus* with full invasion; EA); (14) 6 g of mixed leaves with 2 g of *S. canadensis* and 4 g of *P. laciniata* (imitating *S. canadensis* with light invasion; SCL); (15) 6 g of mixed leaves with 3 g of *S. canadensis* and 3 g of *P. laciniata* (imitating *S. canadensis* with moderate invasion; SCM); (16) 6 g of mixed leaves with 4 g of *S. canadensis* and 2 g of *P. laciniata* (imitating *S. canadensis* with heavy invasion; SCH); (17) 6 g of leaves of *S. canadensis* (imitating *S. canadensis* with full invasion; SC). Polyethylene litter-bags were buried in pastoral soil at a depth of c. 2 cm in planting pots (top diameter: 30 cm; height: 24 cm), with one polyethylene litter-bag per planting pot. The pastoral soil was not sterilized. Three replicates were performed per treatment (3 replicates × 17 treatments (i.e., *P. laciniata* + 4 species of IPs × 4 degrees of invasion) = 51 planting pots/polyethylene litter-bags).

Following experimental treatment, all polyethylene litter-bags were collected. Decomposed leaves were subjected to a moderate washing process and air-drying procedure to analyse the variables associated with decomposition. Soil samples were collected from a depth of c. 1 cm adjacent to polyethylene litter-bags and passed through a 2-mm sieve to measure soil variables and SBC structure.

Determination of decomposition variables, soil variables and SBC structure

The cumulative mass loss (CML), decomposition coefficient (k), expected k of mixed leaves and mixed-effect intensity of co-decomposition (MEIC) were analysed.

The pH, moisture, electrical conductivity, total organic carbon, soluble organic carbon and microbial carbon in soil were assayed. Activities of several soil enzymes involved in the soil carbon cycle were examined, including polyphenol oxidase, fluorescein diacetate (FDA) hydrolase, cellulase, β-glucosidase, β-xylosidase and sucrase.

Illumina PE250 was employed to analyse the SBC structure. The primers 341F and 806R were employed to perform amplification of the V3–V4 region of the 16S rRNA genes of the SBC (Wear et al. 2018). Further analysis was conducted using previously described methods (Liu et al. 2024).

The determination methods for decomposition variables, soil variables and SBC structure are described in Appendix S1, Table S1.

Statistical analysis

Multiple comparison with Tukey's test was employed to statistically analyse the differences in the studied variables between the various treatments. Correlation patterns between CML and k, soil variables and SBC alpha-diversity were estimated via the application of principal component analysis (PCA) with a permutational multivariate analysis of variance (PERMANOVA) test. Two-way analysis of variance (ANOVA) was used to estimate the effects of invasion degree and plant species on CML and k, soil variables and SBC alpha-diversity; $P \leq 0.05$ was considered statistically significant. Statistical analyses were conducted using IBM *SPSS Statistics* (26.0).

Results

The CML and k of *C. canadensis* with heavy invasion and *S. canadensis* with light and heavy invasion were less than those of *P. laciniata* ($P < 0.05$; Figs 1a,g,h & 2a,b,e,f), whereas those of *C. canadensis* with full invasion were larger than in *P. laciniata* ($P < 0.05$; Figs 1a,b & 2g,h). There were no significant differences in the CML and k between *P. laciniata*, *C. sumatrensis* and *E. annuus* regardless of invasion degree (Figs 1 & 2). The CML and k of *S. canadensis* were less than those of the other three IPs, especially with light and heavy invasion ($P < 0.05$; Fig. 2a,b,e,f).

The MEIC of *P. laciniata* and *C. sumatrensis* was positive; the MEIC of *P. laciniata* and *S. canadensis* was negative ($P < 0.05$; Appendix S1, Fig. S1f,l). The MEIC of *P. laciniata* and *C. canadensis* was positive with light and moderate invasion but was negative with heavy invasion ($P < 0.05$; Appendix S1, Fig. S1c). The MEIC of *P. laciniata* and *E. annuus* was positive with moderate invasion but was negative with light and heavy invasion ($P < 0.05$; Appendix S1, Fig. S1i).

Decomposition of *C. canadensis* and *S. canadensis* increased soil pH ($P < 0.05$; Appendix S1, Figs S2a & S3a). Decomposition of

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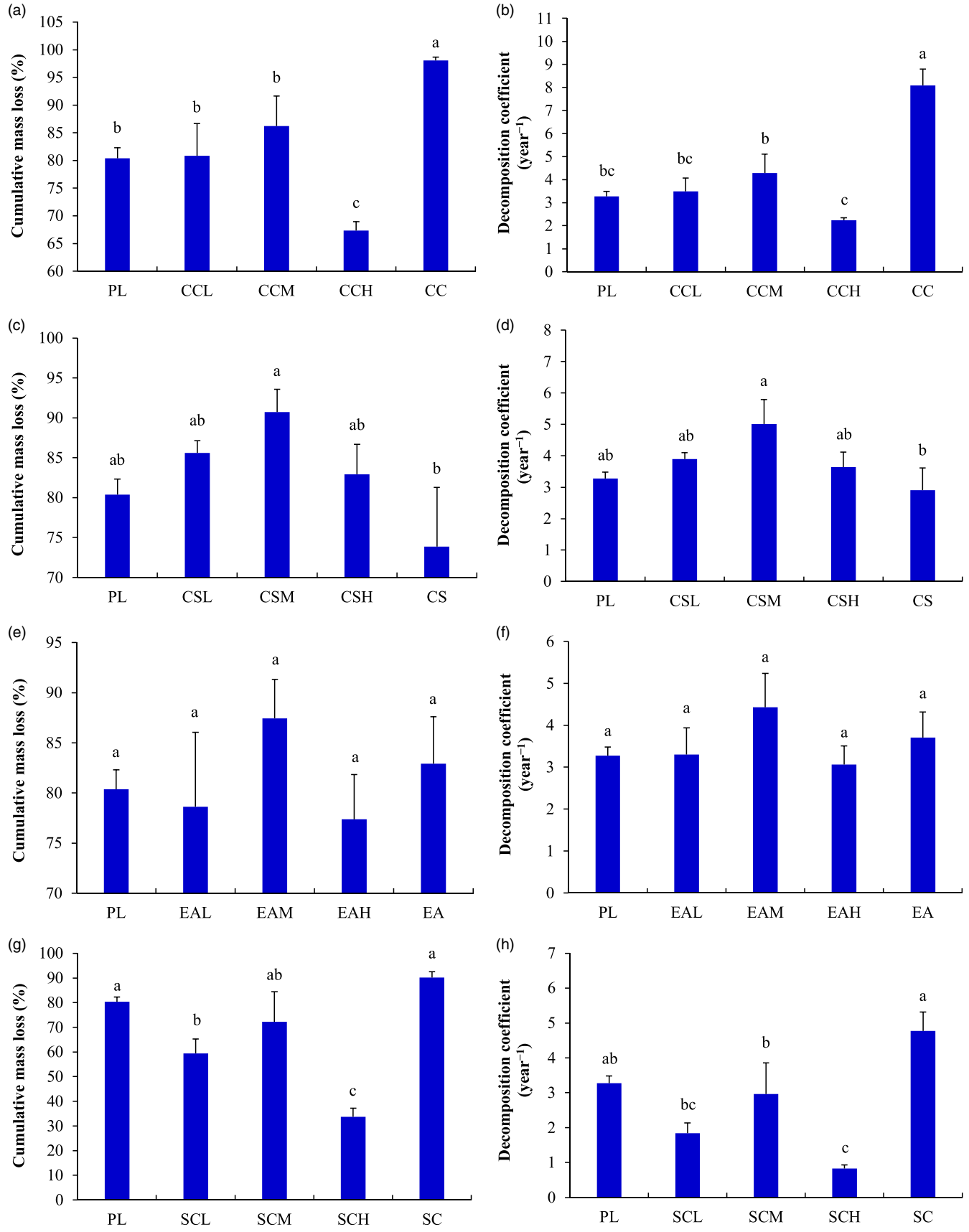


Figure 1. (a–h) Differences in the cumulative mass loss and decomposition coefficient between the native plant *Pterocypsela laciniata* (Houtt.) Shih and the same species invasive plant with a gradient of invasion. Data (means ± standard errors; n = 3) with different letters indicate statistically significant differences. PL = *P. laciniata*; CCL = *Conyza canadensis* (L.) Cronq. with light invasion; CCM = *C. canadensis* with moderate invasion; CCH = *C. canadensis* with heavy invasion; CC = *C. canadensis* with full invasion; CSL = *Conyza sumatrensis* (Retz.) Walker with light invasion; CSM = *C. sumatrensis* with moderate invasion; CSH = *C. sumatrensis* with heavy invasion; CS = *C. sumatrensis* with full invasion; EAL = *Erigeron annuus* (L.) Pers. with light invasion; EAM = *E. annuus* with moderate invasion; EAH = *E. annuus* with heavy invasion; EA = *E. annuus* with full invasion; SCL = *Solidago canadensis* L. with light invasion; SCM = *S. canadensis* with moderate invasion; SCH = *S. canadensis* with heavy invasion; SC = *S. canadensis* with full invasion.

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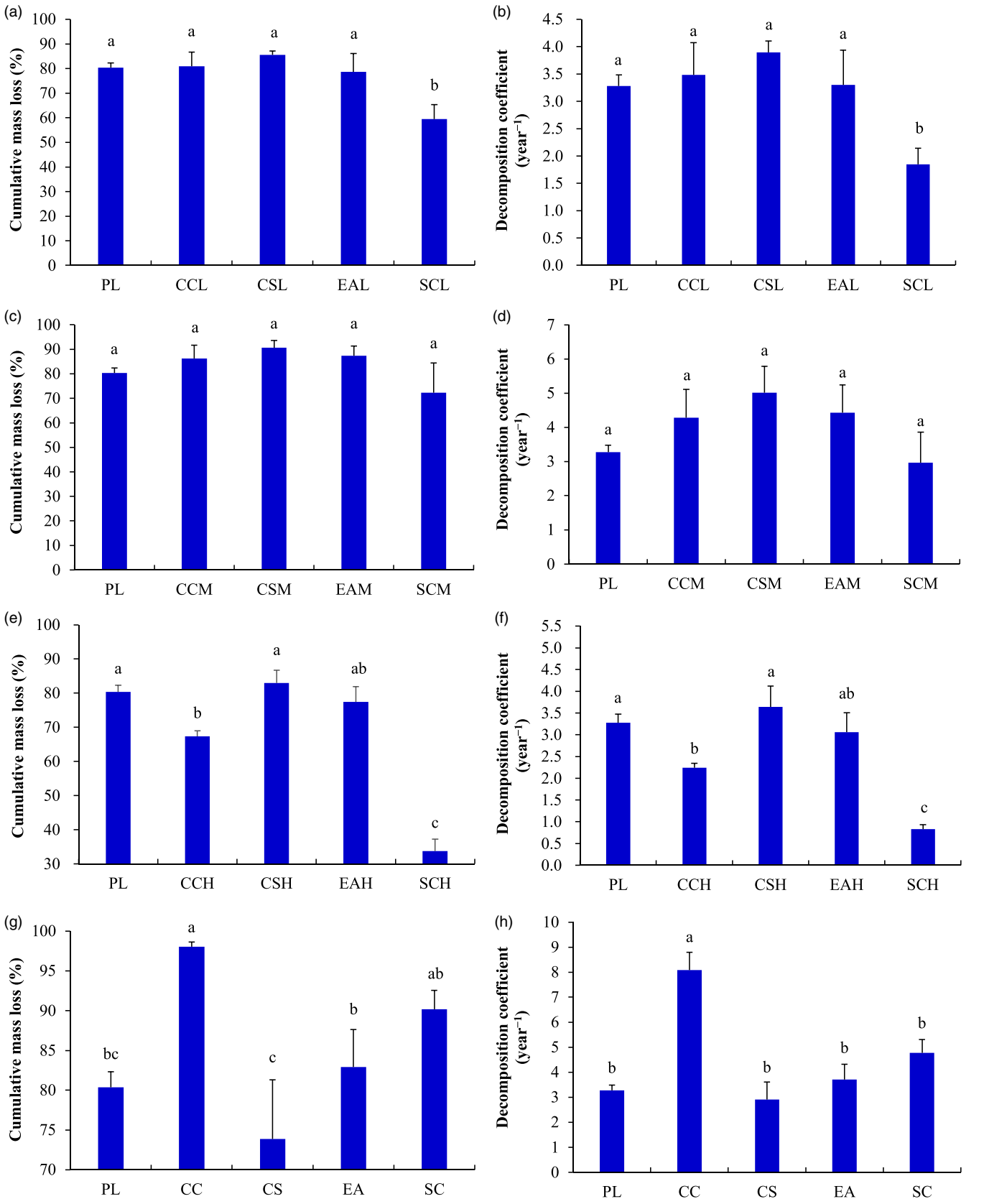


Figure 2. (a–h) Differences in the cumulative mass loss and decomposition coefficient between the native plant *Pterocypsela laciniata* (Houtt.) Shih and different invasive plants with the same invasion degree. Data (means ± standard errors; n = 3) with different letters indicate statistically significant differences. Abbreviations are the same as in Fig. 1.

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the four IPs irrespective of invasion degree generally increased soil microbial carbon content above that of *P. laciniata*, and the maximum content of soil microbial carbon was observed under decomposition of *S. canadensis* ($P < 0.05$; Appendix S1, Figs S2f, S3f, S4f & S5f). Decomposition of *C. sumatrensis* and *E. annuus* irrespective of invasion degree (except for *E. annuus* with moderate invasion) reduced soil FDA hydrolase activity more than that of *P. laciniata* ($P < 0.05$; Appendix S1, Figs S4j & S5j).

Decomposition of the four IPs resulted in changes in SBC beta-diversity (Appendix S1, Figure S6) and in the presence of numerous dominant biomarkers of SBCs (Appendix S1, Fig. S7).

The CML and k of *P. laciniata* and the four IPs were closely correlated with electrical conductivity, moisture, total organic carbon and soluble organic carbon contents and polyphenol oxidase activity in soil (Appendix S1, Fig. S8).

Decomposition of the four IPs did not significantly affect SBC alpha-diversity ($P > 0.05$; Appendix S2, Figs S9–S16 & Table S2).

Discussion

We show that invasion degree and species identity of IP appear to be the most significant factors influencing decomposition rate of *C. canadensis* and *S. canadensis*. This may be attributed to variance in soil physicochemical properties, especially electrical conductivity, moisture and total organic carbon and soluble organic carbon contents, under conditions of decomposition of the two IPs. This phenomenon may also be attributed to changes in SBC beta-diversity and the emergence of distinct dominant biomarkers of SBCs resulting from the decomposition of the two IPs. Nevertheless, the decomposition rates of *C. sumatrensis* and *E. annuus* were comparable to those of *P. laciniata* regardless of invasion degree, possibly because the percentages of soluble and recalcitrant substances in the leaves of the three plant species are similar. Thus, invasion degree and species identity of IP are not the most significant factors influencing the decomposition rate of *C. sumatrensis* and *E. annuus*. The nutrient cycling facilitated by litter decomposition may be of greater importance to the successful invasion of *C. canadensis*, particularly in the context of full invasion, than that of the other three IPs.

Leaves of *S. canadensis* decomposed more slowly than those of the other three IPs, particularly with light and heavy invasion; this could be related to alterations in SBC metabolic activity and SBC beta-diversity and the emergence of numerous dominant biomarkers of SBCs associated with the decomposition of *S. canadensis*. Thus, the role of nutrient cycling mediated by litter decomposition may be less prominent in the successful invasion of *S. canadensis*, especially with light and heavy invasion, than in the cases of the other three IPs. Therefore, species identity of IP emerges as a pivotal factor influencing the decomposition rate of the different IPs.

The MEICs of IPs and natives may be altered as a consequence of the litter of IPs and natives being mixed along an invasion gradient. Co-decomposition of *P. laciniata* and *C. sumatrensis* could be synergistic, whereby the two species decompose more rapidly when present together, regardless of invasion degree. Conversely, co-decomposition of *P. laciniata* and *S. canadensis* could be antagonistic, with the two species decomposing more slowly together regardless of invasion degree. This phenomenon is largely attributable to the interspecific facilitation or interference of chemical substances contained in mixed litter, respectively (Barbe et al. 2018, Kouadio et al. 2023). Thus, *P. laciniata* can facilitate the invasion of *C. sumatrensis* via accelerated nutrient cycling, which is mediated by a synergistic effect of co-decomposition irrespective of invasion degree. This may result in *P. laciniata* actively cooperating with or even creating favourable conditions to facilitate *C. sumatrensis* invasion. Conversely, *P. laciniata* can impede the invasion of *S. canadensis* by slowing nutrient cycling, which is mediated by antagonistic co-decomposition irrespective of invasion degree.

The exudation of secondary metabolites by IPs can alter soil physicochemical properties during decomposition (Ahmad Dar et al. 2023). Decomposition of *C. canadensis* and *S. canadensis* resulted in a higher soil pH than that of *P. laciniata*, possibly through the release of alkaline or other substances into the soil conducive to alkalization (e.g., anions) during decomposition (McGrath & Binkley 2009). Alternatively, this outcome could be ascribed to a diminution in the generation of H^+ via a reduction in the secretion of acidic substances present in the leaves of *C. canadensis* and *S. canadensis* (Zhong et al. 2022).

In general, IPs can increase soil carbon content by increasing inputs of carbon-containing substances to the soil (Vujanović et al. 2022). Decomposition of the four IPs irrespective of invasion degree generally increased soil microbial carbon content more than did decomposition of *P. laciniata*. The maximum content of soil microbial carbon was observed under decomposition of *S. canadensis*, especially with light, heavy and full invasion. Soil microbial carbon content may be enhanced under decomposition of the four IPs, with no discernible impact of invasion degree, and this is especially the case for *S. canadensis* under light, heavy and full invasion. A potential for greater microbial carbon sequestration in the soil is evident, particularly through the utilization of carbon by soil microorganisms during the decomposition of the four IPs, particularly *S. canadensis*.

IPs can also affect soil enzyme activities and SBC structure (Keet et al. 2021, Woods et al. 2021). The release of carbon- and nitrogen-containing substances throughout decomposition facilitates this process, providing the vital nutrients required for the metabolism of soil microorganisms. Soil FDA hydrolytic capability was reduced under conditions of the decomposition of *C. sumatrensis* and *E. annuus*. This decline can be attributed to a decrease in nutrient availability and/or an increase in the rate of microbial metabolism in the soil under conditions of the decomposition of the two IPs. Furthermore, decomposition of the four IPs resulting in changes in SBC beta-diversity was demonstrated through the presence of numerous dominant biomarkers of the SBCs compared to with decomposition of *P. laciniata*. Differences in leaf quality of the four IPs and *P. laciniata* may lead to some species differentiation of the SBCs (Santonja et al. 2017, Keet et al. 2021). Selective inhibition or facilitation caused by altered amounts, types and complexities of nutrients (e.g., carbon/nitrogen-containing and other recalcitrant substances) in the soil throughout the decomposition of the four IPs could also be responsible for this observation (Dekanova et al. 2021). Thus, some SBC taxa may persist while others may die over time due to decomposition of the four IPs. Decomposition of the four IPs mainly affected SBC structure rather than alpha-diversity.

Decomposition of plants can affect soil physicochemical properties, enzyme activities and SBC structure (Firmino et al. 2021, Ahmad Dar et al. 2023). The decomposition rate of *P. laciniata* and the four IPs evidently affects electrical conductivity, moisture, total organic carbon and soluble organic carbon contents and polyphenol oxidase activity in the soil. The soil physicochemical properties and enzyme activities probably affect the

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release of substances, especially carbon-containing substances, from leaves during decomposition, and this in turn affects resource use and access to nutrients metabolized by the SBCs (Keet et al. 2021).

Conclusions

Decomposition of the four IPs, irrespective of invasion degree, generally increased soil microbial carbon content compared to decomposition of *P. laciniata*, especially under conditions of decomposition of *S. canadensis*. Consequently, decomposition of the four IPs irrespective of invasion degree, and especially that of *S. canadensis*, may contribute to microbial carbon sequestration. Our findings showed that although IPs can have negative ecological impacts, their role in microbial carbon sequestration should be considered in management strategies, especially in wastelands and wilderness areas.

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/S0376892925100131.

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Competing interests. The authors declare none.

Ethical standards. Not applicable.

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