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The invasive plant species *Solidago gigantea* increases litter decomposition rates by altering soil characteristics

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Abstract Alien invasive species impact native plant communities, not only through direct negative effects on native species but also by altering nutrient cycling and availability. However, the mechanisms driving these changes—such as differences in litter decomposition rates and litter quality, or increased overall decomposition rates within invaded stands—remain unclear. This study examines how *Solidago gigantea*, an invasive species in Europe and Asia, affects decomposition. A climate chamber experiment tested whether *S. gigantea* litter decomposes faster than litter from co-occurring native species. The study examined whether differences in decomposition rates could be attributed to litter quality (using C/N ratio as a proxy) or to variations in soil microbiota (via inoculum from invaded vs. non-invaded plots). A field experiment measured overall decomposition rates in invaded and non-invaded plots using tea bags and wooden spatulas buried for 2–16 weeks. Soil moisture, carbon, and soil fauna activity were also assessed for their influence on decomposition. *S. gigantea* litter decomposed significantly faster than native graminoid species (decomposition rates of 0.91 and 0.33 g g^{-1} day^{-1} resp.), despite its higher C/N ratio (39.6 and 27.9 resp.). Invaded stands consistently had higher decomposition rates, which was attributed to abiotic changes, including reduced soil moisture and increased soil carbon, rather than to biotic changes in soil fauna or microbiota activity. These findings highlight *S. gigantea*'s substantial impact on nutrient cycling in invaded ecosystems. However, the extent—and potentially the direction—of these effects likely depends on the invaded plant community. Grass-dominated and wetter communities may experience the greatest increases in nutrient cycling, potentially enhancing primary productivity.

Keywords Soil carbon · Primary productivity · C/N ratio · Leaf litter quality · Nutrient availability · Bait lamina strips

Introduction

Alien invasive species are widely recognized as a significant threat to native biodiversity (Hejda et al. 2009; Gaertner et al. 2009; Mollot et al. 2017). Research indicates that the absence of pathogens and

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herbivores specific to these species in the areas they invade can provide them with a competitive edge over native plants (Klironomos 2002; Wolfe 2002; Kulmatiski et al. 2008; Engelkes et al. 2008). In addition to these advantages, invasive species often possess inherent competitive strengths (Vilà and Weiner 2004) due to characteristics such as allelopathic effects (Kalisz et al. 2021), clonal reproduction (Lloret et al. 2005; Speek et al. 2011) and rapid growth rates (Van Kleunen et al. 2010).

Characteristics of ecosystems often change after invasion of alien species, with impacts on both community structure (Hejda et al. 2009; Gaertner et al. 2009) and whole ecosystem functioning (Vilà et al. 2011; Eviner et al. 2012). Community structure changes includes shifts in ecological interactions such as host use, pollination and herbivory (Goodenough 2010), changes in species' relative abundance, and local extinctions (Bellard et al. 2021). Ecosystem functioning changes through invasion include shifts in primary productivity (Vilà et al. 2011) and nutrient cycling (Ehrenfeld et al. 2001; Vanderhoeven et al. 2005; Castro-Díez et al. 2014).

These ecosystem-level changes occur through several mechanisms, such as nutrient uplift by deep-rooted species (Dijkstra and Smits 2002; Blank and Young 2002; Jobbágy and Jackson 2004), enhanced asymbiotic atmospheric nitrogen (N) fixation (Ley and D'Antonio 1998) or increased phosphorus (P) availability via soil acidification or enhanced phosphomonoesterase production (Chapuis-Lardy et al. 2006). Invasive plants can also alter soil moisture (Le Maitre 2004; Huddle et al. 2011), soil biota composition and diversity (Callaway et al. 2004; Jordan et al. 2008), and litter decomposition processes (Ehrenfeld 2003; Allison and Vitousek 2004; Liao et al. 2008). Decomposition rates themselves are primarily dependent on climate, the decomposing organisms and litter quality (Coûteaux et al. 1995).

Climate variables—such as temperature, rainfall and humidity—are the most important drivers of variation in decomposition on large regional scales (Berg et al. 1993). On a smaller scale most variation in decomposition rates can be attributed to differences in microclimate, the soil microbial community (Cleveland et al. 2014) and meso- and macrofauna in the soil (Frouz 2018), and to leaf litter quality, i.e. traits such as C/N and C/P ratios and lignin concentrations (Aerts 1997; Canessa et al. 2021). Invasive species can impact the local microclimate by e.g., altering hydrology and soil moisture content (Le Maitre 2004; Huddle et al. 2011). Invasive species can also alter both the invaded soil microbial community (Jordan et al. 2008; Weidenhamer and Callaway 2010) and decrease or increase detritivorous soil fauna (Abgrall et al. 2019), leading to a lower or higher litter decomposition. Furthermore, the litter from the alien species can build up its own unique decomposer communities, leading to a higher decomposition rate (Lin et al. 2019; Veen et al. 2019). Lastly, leaf litter traits differ among species and leaf quality—and therefore decomposition rate—is often higher in fast-growing plant species (Cornelissen and Thompson 1997), which many invasive species are. These invasion-induced changes in nutrient availability can further accelerate decomposition (Güsewell and Gessner 2009), enhance primary productivity and ultimately reinforce invasion through positive feedback (Hobbie 2015). However, Delgado-Baquerizo et al. (2015) demonstrated that soil characteristics can be more influential than litter quality in determining nutrient release during decomposition. While many studies have focused on the role of high-quality litter inputs following invasion, the effects of invasion-induced changes in soil characteristics on decomposition remain largely understudied.

Solidago gigantea is an alien invasive species in Europe and parts of Asia, originating from North America. *S. gigantea* is an eurytopic plant, invading many different plant communities such as ruderal vegetation, riverside habitats as well as grasslands and forest edges (Török et al. 2003; Weber and Jakobs 2005; Güsewell et al. 2005), where it competes mainly with grasses and other forbs. Once *S. gigantea* is established, it often becomes dominant due to its clonal growth and high competitive ability forming dense stands (Weber 2011). Besides its direct negative effects on the local plant communities through competition (Pal et al. 2015), *Solidago* species can indirectly impact the invaded ecosystems through transforming both biotic (Liao et al. 2013) and abiotic (Baranová et al. 2017) properties of the soil. For instance, *Solidago* species affect aboveground arthropod communities at different trophic levels (de Groot et al. 2007), e.g., pollinators (Moroń et al. 2009) and ants (Trigos-Peral et al. 2018). However, belowground mesofauna does not seem to change after *Solidago* invasions (Sterzyńska et al. 2017; Klimek et al. 2020). *S. gigantea* is also known to alter soil pH (Herr et al. 2007) and nutrient availability, like those of nitrogen (Scharfy et al. 2009) and phosphorus (Chapuis-Lardy et al. 2006; Stefanowicz et al. 2017), although both the strength and direction of these soil alterations depend on the initial conditions of the invaded area (Dassonville et al. 2008; Goossens et al. 2024). However, the mechanisms by which nutrient availability is altered in invaded ecosystems remain unclear. One possible explanation is the increased nutrient release from faster-decomposing litter produced by invasive species, as demonstrated for the closely related *S. canadensis* (Zhang et al. 2016; Dekanová et al. 2021). This faster decomposition may be attributed to higher litter quality, such as a lower C/N ratio. Alternatively, nutrient release may be enhanced by shifts in soil decomposer activity or increased overall decomposition rates within invaded stands, driven by changes to the local microclimate (Trigos-Peral et al. 2018). Although *S. gigantea* alters it soil characteristics and the local microclimate, no studies have examined its possible effect on decomposition and nutrient cycling.

In this study, we aimed to investigate whether decomposition rates changed following the invasion of *S. gigantea*, potentially influencing nutrient availability. Our first hypothesis was that litter from *S. gigantea* decomposes faster than that of native plants due to its higher quality, characterized by a lower C/N ratio. Our second hypothesis was that the decomposition rate of organic material—rooibos and green tea in our experiment—is higher in field sites dominated by *S. gigantea* compared to non-invaded areas. Additionally, we aimed to assess whether variations in field decomposition rates could be linked to differences in soil moisture, carbon levels, or changes in meso—and macrofauna or soil microbial activity between invaded and non-invaded sites.

Materials & methods

Both a climate chamber experiment and a field experiment were carried out. For the climate chamber experiment, leaf litter from both *S. gigantea* and co-occurring native species (Supp Table 1) were incubated on Petri dishes to test whether litter decomposition rates differed between the invasive and native species. Two types of inocula were used (one from an invaded site and another one from a paired non-invaded site) to evaluate the effect of soil microbiota on decomposition rates. The C/N ratio in leaf litter was measured to assess whether there was a difference between *S. gigantea* and native species. For the field experiment, tea bags with green tea and rooibos were incubated along with wooden spatulas to test the effect from a possibly changed soil after invasion on decomposition rates (Keuskamp et al. 2013). Bait lamina strips were placed to measure the activity from both the meso- and macrofauna (Eisenhauer et al. 2014). Lastly, abiotic factors such as soil moisture and soil carbon were measured.

Site selection

In total 30 paired plots were chosen; plot pairs consisted of an invaded plot and a paired non-invaded plot within 2 to 5 m of each other. Neither the invaded, nor the non-invaded plot contained any other invasive species. The collection of leaf litter and the field experiment were done at the same three nature areas, all located in the Flemish part of Belgium: Liedekerkebos, Doode Bemde and Bos van Aa. These locations were chosen in order to have a wide variety in habitat types, such as grasslands, forest edges and river edges (Table 1). In all three locations, *S. gigantea* was present in dense patches with densities ranging up to 400 stems per m^2. Plots were 1 m^2, with invaded plots placed in the centre of the *S. gigantea* stands to prevent edge effects, while the paired non-invaded plots were chosen based on similar conditions as their associated invaded plot (e.g. habitat type, sun exposure and altitude). All three locations have an oceanic climate with warm summers and cool winters. During the field experiment (Fall 2023–Winter 2024), average temperatures were 2.2 °C above the long-term mean, with 13.4 °C in Fall 2023 and 6.3 °C in Winter 2024. Rainfall was also above average, totalling 283.7 mm in Fall 2023 and 310.7 mm in Winter 2024—78.3 mm above the typical values.

Field experiment

To test whether decomposition rates of organic matter differed between invaded and non-invaded plots, rooibos tea bags, green tea bags and wooden spatulas ($150 \times 18 \times 1.6$ mm) were put underground in both invaded and non-invaded plots in the top 5 cm of

Table 1 Biotic and abiotic characteristics of the sampled nature areas

Site	# of plot pairs	Soil texture	Dominant plant communities		Moisture content fall (%)	Moisture content winter (%)	Carbon content (%)
Liedekerkebos	10	Sandy loam	Moist—wet grasslands & forest edges	NI	34.4 ± 2.4	51.2 ± 0.3	8.2 ± 0.4
				I	26.7 ± 2.3	50.1 ± 0.6	8.7 ± 0.5
Doode Bemde	9	Loam	Riverside megaphorb	NI	9.9 ± 2.2	34.1 ± 2.0	6.4 ± 0.4
				I	7.5 ± 1.5	32.1 ± 1.4	6.4 ± 0.4
Bos van Aa	11	Not applicable*	Dry—moist grasslands & forest edges	NI	8.2 ± 1.4	30.1 ± 2.0	3.7 ± 0.3
				I	5.1 ± 1.1	33.9 ± 1.8	4.4 ± 0.4

The last four columns are averaged statistics with their standard error of the non-invaded (NI) and invaded (I) plots. Soil texture was always the same for paired plots. *Soil texture for Bos van Aa is not applicable since the original soil is not present any longer, due to its use as a landfill in the past

the soil in a horizontal position (Didion et al. 2016). Nylon tea bags with a mesh size of 0.25 mm were filled with 1.51 (±0.06) g of tea and were labelled (Mori 2022). A mesh size of 0.25 mm allowed microorganisms and mesofauna to reach the tea, but prevented macrofauna to do the same (Setälä et al. 1996). Since the weight of the wooden spatulas was not adequately constant, each spatula was weighed and labelled. To test the meso- and macrofauna activity in the soil, bait lamina strips were placed in the centre of all plots underground vertically with the top 1 cm visible above ground. Bait lamina strips were 3D printed following the design of Vorobeichik and Bergman (2023) and filled with a substrate that consisted of 70% microcrystalline cellulose, 27% wheat bran and 3% active charcoal and dried afterwards at 40 °C for one hour (Eisenhauer et al. 2014). Tea bags and wooden spatulas were put underground early October 2023 and collected after 2, 4, 8 and 16 weeks. A total of 480 tea bags (60 plots × 2 different teas × 4 collection moments per tea) and 240 wooden spatulas (60 plots × 4 collection moments) were placed (Supp Figure 1).

After collection, tea bags and wooden spatulas were dried at 70 °C for three days. Dirt was removed and tea within the tea bags and the wooden spatulas were weighed. A total of 60 bait lamina strips (1 per plot) were collected after two weeks and directly evaluated in the field. Bait lamina strips have two different sizes of holes—in order to distinguish soil macro—and mesofauna activity (Vorobeichik and Bergman 2023)—and scores were calculated separately for both sizes. Each hole of a strip was given a score based on how much of the substrate was gone—1 if a part of the substrate was gone for the entire length of the hole, 0.5 if only part of the substrate was gone—and all individual scores were added up to get the score per bait lamina strip, with a maximum of 16 large and 32 small holes (Eisenhauer et al. 2014; Vorobeichik and Bergman 2023).

Moisture in the invaded and non-invaded plots was measured using the HydroSense II Handheld Soil Moisture Sensor with the CS659 portable soil–water probe attached to it. Measurements were done at six different moments in time at all plots—once at the setup, at all four collection moments and once after the experiment was concluded at the end of March 2024. For each plot at each moment, three moisture measurements were done and averaged. For the analysis, the first measurement at setup (fall) and the fourth measurement at collection (winter) were used as these were respectively the driest and wettest measurements. Soil carbon was measured for all plots by collecting a soil sample (0–10 cm deep) per plot which was dried beforehand for three days at 70 °C. Samples were afterwards burned in a muffle oven at 500 °C for four hours incinerating all organic compounds. The difference in weight before and after was then used to calculate the carbon percentage in the soil (Wotherspoon et al. 2015).

Climate chamber experiment

During the setup of the field experiment in early October 2023, leaf litter and soil samples were collected at all 60 plots. Leaf litter was taken from mature plants, as close to the bottom as possible, without feeding marks and without much discolouration (less than

5% brown or yellow discolouration), from many different individuals when possible. At all invaded plots, *S. gigantea* leaves were collected, while at all non-invaded plots leaves were collected from both the native plant species that was the most abundant within the plot and, if present, from *Holcus lanatus*, *Tanacetum vulgare* and *Artemisia vulgaris*. These three species are widely spread in Belgian grasslands and forest edges, hence they were used as standard species. In total, 77 litter samples were collected, 47 of which were native plants (Supp Table 1).

Plant litter was then stored at 5 °C for one to three days and dried at 70 °C for three days before being crushed using a coffee grinder until pieces were smaller than 5 mm^2. Soil samples were also stored at 5 °C after collection and were later used to make the inoculum by mixing 50 g of soil with 500 ml of water and letting it rest for an hour and shake it every 15 min (Quested et al. 2002). The supernatant was then filtered using 1 mm and 0.25 mm sieves in order to exclude macrofauna from the inoculum (Setälä et al. 1996). Inoculum was made for every plot separately.

Petri dishes (9 cm diameter) were filled with ± 28 g of dried quartz sand (type M31, Sibelco NV, Belgium) with no traceable organic components or N and P. A 0.1 mm mesh was placed on top to prevent the leaf litter from mixing with the sand. 0.2 g dried leaf litter was placed onto the mesh and 10 ml inoculum was added to the dish. For every litter sample collected, two Petri dishes were filled, one with the inoculum from its own plot and one with the inoculum from the paired invaded/non-invaded plot. Petri dishes were placed in a climate chamber to incubate at 25 °C and 50% moisture. Water was added twice a week until the water level was right above the sand. Petri dish lids were only partly sealed to ensure sufficient gas exchange. In total 616 separate Petri dishes were used (77 different litter samples × 4 collection moments × 2 types of inoculum per litter sample, Supp Figure 2).

Leaf litter was collected after 1, 2, 4 and 8 weeks and dried at 70 °C for three days after collection. Sand was carefully removed before weighing the leaf litter. Litter was weighed together with the mesh and the mesh's weight was later subtracted. The mesh's weight was calculated by determining the mesh's surface area using a scanner and ImageJ version 1.54 and calculating the relative weight/surface area of a clean mesh.

In order to measure organic C and N%, the plant material was dried, powdered, homogenized and weighed (about 1 mg) in tin cups. C and N fraction of the material was then measured using a Eurovector elemental analyzer EA 3100, according to Nieuwenhuize et al. (1994).

Statistics

The remaining mass from both litter and tea bags experiments were used to calculate decompositions rates constants k_1 and k_2 following Eq. 1 (Cornwell and Weedon 2014).

$$PercentageMassRemaining = \alpha * e^{-k_1 * t} + (1 - \alpha) * e^{-k_2 * t} \tag{1}$$

Equation 1 is a discrete parallel function where α is the labile fraction, (1−α) is the recalcitrant fraction, k_1 and k_2 the respective decomposition rates constants and t is the incubation time. The labile fraction α is rapidly broken down during the initial incubation period, while the recalcitrant fraction 1–α takes much longer to break down. This means that on shorter time periods, litter decomposition is mainly described by k_1 (Keuskamp et al. 2013). Decomposition constants were calculated using the 'fit_litter' function from the 'litterfitter' package (Manzoni et al. 2012; Cornwell and Weedon 2014). Due to sand mixing with the litter, about a quarter of the four weeks incubations and about half of the eight weeks incubations had to be excluded. Decomposition constants for three leaf litters were removed since the 'fit_litter' function could not converge on a consistent result.

To test whether litter decomposition in the climate chamber experiment differed between native graminoids, forbs and *S. gigantea* and if litter quality also had an effect on decomposition, a mixed linear model—lmer-function from the package 'Lme4' (Bates et al. 2015)—was performed with k_1 as a response variable and functional group (litter from *S. gigantea*, native forbs or native graminoids), C/N ratio of the leaf litter and their interaction as fixed factors. Inoculum type (invaded or non-invaded) was added as a third fixed factor to test whether the microbial community from invaded stands altered decomposition rates. k_1 was log transformed to improve the fit. For one plot, the most abundant native plant species was *Vicia cracca* (Supp Table 1) and since this was the only legume in the dataset, we opted to omit this data point from the analysis since legumes belong to their own separate functional group. Plot pairs were added as a random factor. Assumptions were checked visually using a histogram to check normality of the residuals, a Q–Q plot to check for normal distribution and a standardized residuals plot to test for homogeneity of variances. The vif-function from the 'car' package (Fox and Weisberg 2019) was used to test correlation between variables. Afterwards, specific differences in decomposition rates between native forbs, graminoids and *S. gigantea* were determined using the emmeans package for a post-hoc test (Lenth 2022).

Differences in leaf chemical traits between native forbs, graminoids and *S. gigantea* were also tested with linear mixed models, with C%, N% and C/N ratio as response variables and functional group as fixed factor and plot pair as random factor to account for where leaves were gathered from. Specific differences in leaf traits between native forbs, graminoids and *S. gigantea* were calculated with the emmeans package. The effect of invasion on decomposition variables in the field and on abiotic soil characteristics was analysed similarly, with the decomposition rates from rooibos, green tea and the wooden spatulas, bait lamina strips scores (separated for large and small holes), soil carbon and soil moisture (fall and winter) as response variables. Invasion status of the plot (invaded or non-invaded) was used as fixed factor. As random factors plot pairs, nested in location were added to ensure pairwise comparisons within plot pairs. Location was added to control for differences between the three nature areas. Assumptions were checked as described before. For both rooibos tea and soil carbon a 1/y transformation was done to improve fit. Since the effect of location was negligible for rooibos, the use of a mixed model was unnecessary and a paired t-test was performed instead, where the effect of invasion on rooibos decomposition was checked, paired within plot pairs. Normality was checked with a Shapiro–Wilk test.

Lastly, we analysed whether the strength of changes in soil carbon and moisture (during fall and winter) depended on the initial conditions of the invaded plot. Linear mixed models were performed with the difference between invaded and non-invaded plots (Δ) for soil carbon and moisture as response variable and the soil carbon or moisture of the non-invaded plot (as a proxy for the initial conditions of the invaded plot) as a fixed factor. Location was again added as a random factor. Assumptions were checked as described above.

All analyses were performed in R version 4.2.1 (R Core Team 2022). Figures were made with ggplot from the ggplot2 package (Wickham 2016), and edited in Inkscape 1.2.1.

Results

Climate chamber experiment

With a climate chamber experiment, we tested whether litter decomposition rates differed between the invasive and native species. Decomposition rate constants k_1 (Fig. 1) were significantly different between the investigated functional groups (*S. gigantea*, native forbs and native graminoids; Table 2). Native graminoids had significantly lower decomposition rate constants than both *S. gigantea* and native forbs (Supp Table 2). Decomposition rates were not different between *S. gigantea* and native forbs. Furthermore, we evaluated the effect of soil microbiota on decomposition rates (Fig. 1) and showed that decomposition rates were not different between inocula from invaded and non-invaded plots (Table 2). k_2 values, the decomposition rate constant of the recalcitrant fraction, were very low—mostly < 0.001—compared to k_1 values—mostly > 0.05.

To assess whether there was a difference between *S. gigantea* and native species, litter quality as N and C was measured. *S. gigantea* leaves contained significantly less N and more C than both native forbs and graminoids (Fig. 2A, B), resulting in a significantly higher C/N ratio (Fig. 2C, Table 3, Supp Table 2). The C/N ratio itself had no general effect on decomposition rate (Table 2), only for graminoids a clear negative effect was found (Fig. 2D, Supp Table 2).

Field experiment

Decomposition rates constants k_1 from the rooibos tea bags (Fig. 3) were significantly higher within the invaded plots compared to the non-invaded plots (Table 3). The decomposition rates from green tea bags and wood (Fig. 3) were not different for invaded and non-invaded plots (Table 3). k_2 values were again very low, for both invaded and non-invaded plots.

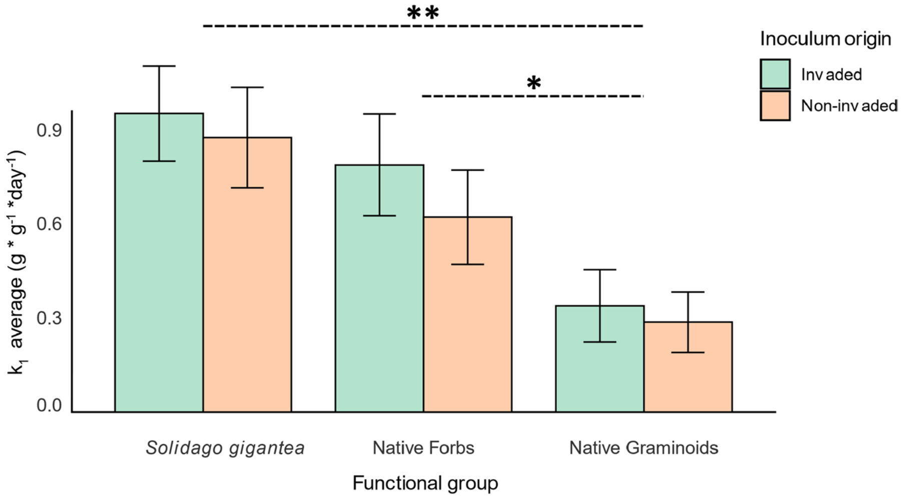

Fig. 1 Mean decomposition rate constants k_1 of leaf litter for different functional plant groups, based on their weights after decomposing for 1, 2, 4 and 8 weeks at 25 °C and 50% moisture. Used inoculum for incubation is showed in colour. For the species comprising the functional groups, see Supp Table 1. $n = 30$ (*Solidago gigantea*), 26 (native forbs) and 20 (native graminoids) for each type of inoculum. Error bars show the standard error. Significant differences in leaf decomposition between functional groups is shown by: P-value $= 0.05 > * > 0.01 > ** > 0.001 > ***$. Results of statistical analyses are shown in Table 2 and Supp Table 2

Table 2 Statistic results (effect size, Chi-square, *P*-value, marginal and conditional R^2) from linear mixed models showing: (first row) the effect of inoculum type, functional group, C/N ratio and their interaction on leaf decomposition rate, (three last rows) how soil carbon and moisture are affected by invasion depending on the invaded sites initial conditions (= as measured in the non-invaded paired plot). Significant P-values are indicated in bold.

Response variable	Fixed factor	Effect size[a]	χ^2	*p*	Marg. R^2	Cond. R^2
k1 leaf litter	Inoculum origin	–	0.44	0.51	0.13	0.14
	Functional group	–	12.1	**0.002**		
	C/N ratio	–	0.0002	0.99		
	Funct. gr. x C/N ratio	–	7.3	**0.025**		
Δ carbon	Initial carbon %	−0.82	16.0	**< 0.001**	0.42	0.79
Δ moisture fall	Initial carbon %	–	2.0	0.16		
	Initial moist. content (fall)	−0.63	20.0	**< 0.001**	0.53	0.84
Δ moisture winter	Initial carbon %	−0.02	12.9	**< 0.001**	0.35	0.36
	Initial moist. content (winter)	−0.49	13.4	**< 0.001**	0.46	0.83

Effect sizes are only shown when significant. Δ's are obtained by subtracting the value of the non-invaded plot from the value of the invaded plot

[a] Effect sizes of functional group and C/N ratio on decomposition of leaf litter are not given here. For the differences between functional groups see Supp Table 2

Invasion also did not alter soil biota activity, as could be seen from the bait lamina strips, for both large and small holes (Fig. 3, Table 3).

S. gigantea significantly increased total soil carbon content in invaded plots, when compared to non-invaded plots (Fig. 3, Table 3). The strength of this increase depended on the initial carbon content of the soil (as measured in the non-invaded plot), where soils with lower initial carbon content saw larger increases (Fig. 4A, Table 2). Moisture content at the end of the growing season (early fall) was decreased significantly in invaded sites (Fig. 3 and Supp

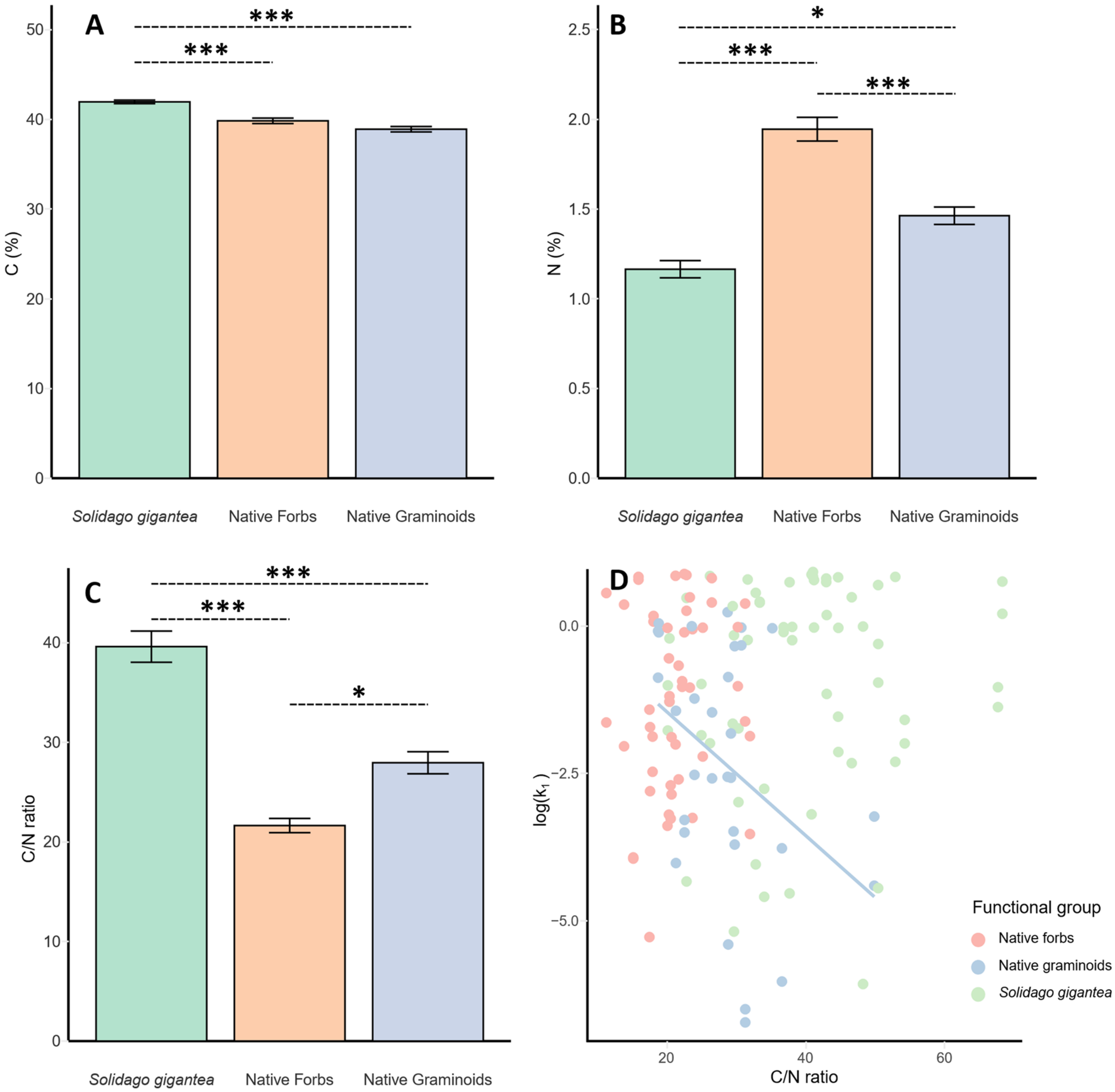

Fig. 2 Leaf chemical traits for native forbs, graminoids and *Solidago gigantea* (leaf C% (2A), leaf N% (2B), and leaf C/N ratio (2C)) and their influence on leaf decomposition rate (2D). For the species comprising the functional groups, see Supp Table 1. $n=30$ (*Solidago gigantea*), 26 (native forbs) and 20 (native graminoids). Error bars show the standard error. Significant differences between functional groups are shown by: *P*-value $= 0.05 > * > 0.01 > ** > 0.001 > ***$. Results of statistical analyses are shown in Tables 2d, 3a–c and Supp Table 2

Figure 3, Table 3), where the wettest locations were most impacted (Fig. 4C, Table 2). During the wet season (winter), no overall effect of *S. gigantea* on soil moisture content was found (Fig. 3, Table 3). However, difference in moisture seemed to be negatively related to both the initial carbon and moisture content of the plots (again, as measured in the non-invaded plots, Fig. 4D, E, Table 2).

Table 3 Statistic results (effect size, Chi-square and *P*-value) from linear mixed models showing: (above) the effect of *Solidago gigantea* invasion on different decomposition variables and on abiotic soil characteristics, (below) the differences in leaf chemical traits between different functional groups (native forbs, native graminoids and *S. gigantea*). Significant P-values are indicated in bold

Response variable	Fixed factor	Effect size	χ^2	*p*
	Plot type (Non-invaded – Invaded)			
k_1 rooibos		0.039	-1.73^a	**0.045**
k_1 green tea		–	0.29	0.59
k_1 wood		–	0.14	0.71
BLS large holes		–	1.76	0.18
BLS small holes		–	1.51	0.22
Soil carbon (%)		0.02	4.13	**0.04**
Moisture fall		0.07	15.9	**< 0.001**
Moisture winter		–	0.01	0.93
	Functional group			
C/N ratio		$–^b$	76.1	**< 0.001**
C (%)		$–^b$	34.8	**< 0.001**
N (%)		$–^b$	58.0	**< 0.001**

Effect sizes are only shown when significant. *BLS* Bait lamina strips

[a] *t*-value given for paired *t*-test

[b] Effect sizes only given for individual differences between functional groups (Supp Table 2)

Discussion

Our findings demonstrate that *Solidago gigantea* influences decomposition, affecting nutrient cycling and availability, through multiple mechanisms, highlighting the complex, previously underexplored ways invasion can alter ecosystems. Firstly, the results supported our first hypothesis: while *S. gigantea* leaves decomposed more rapidly than those of native graminoids, they did not decompose faster than those of native forbs (Fig. 1). This result is closely aligning with the findings of Scharfy et al. (2011), who compared six invasive forbs (including *S. gigantea*) with six native forbs and six native grasses. They found no overall differences between invasive and native species, but grasses decomposed significantly more slowly than forbs, and invasives tended to decompose faster than grasses. However, this accelerated decomposition cannot be attributed to higher litter quality, as *S. gigantea* leaves contained lower N levels and higher C content than native plants, resulting in a higher C/N ratio (Fig. 2A–C).

Interestingly, our results also suggest that a higher C/N ratio does not invariably slow decomposition, as this relationship was observed only for native graminoids (Fig. 2D). This discrepancy may indicate that other litter characteristics -such as phenolic compounds, lignin content or minerals beyond nitrogen- play a stronger role in regulating decomposition of the forbs in our study (Hobbie 2015). These findings are somewhat surprising, as they contrast with Chomel et al. (2016), who reported consistently reduced decomposition with high C/N ratios across the studies they reviewed. Evidence regarding other traits remains mixed: tannins and phenols, although understudied, showed no consistent effect on decomposition, though they may become more important in later stages (> 2 months) than covered in our experiment (Loranger et al. 2002; Chomel et al. 2016). Conversely, Vargas et al. (2006) found phenols to be equally important as C/N in explaining decomposition rates. Lignin content is also widely used as a proxy for litter quality, but for non-woody species with low lignin, such as in our case, C/N ratio is generally considered a more reliable predictor (Taylor et al. 1989).

We thus anticipate that *S. gigantea* can either increase or decrease N availability in invaded communities, as observed in the field by Goossens et al. (2024), with the direction and magnitude of this effect depending on factors such as the plant composition of the invaded community. In forb-dominated communities, N availability could decline over the long term due to the substantially higher C/N ratio of *S. gigantea* litter compared to most native forbs. Conversely, in grass-dominated communities, where the disparity in C/N ratios is less pronounced (though still significant), the faster decomposition rate of *S. gigantea* litter may play a more critical role, potentially increasing soil N through accelerated decomposition.

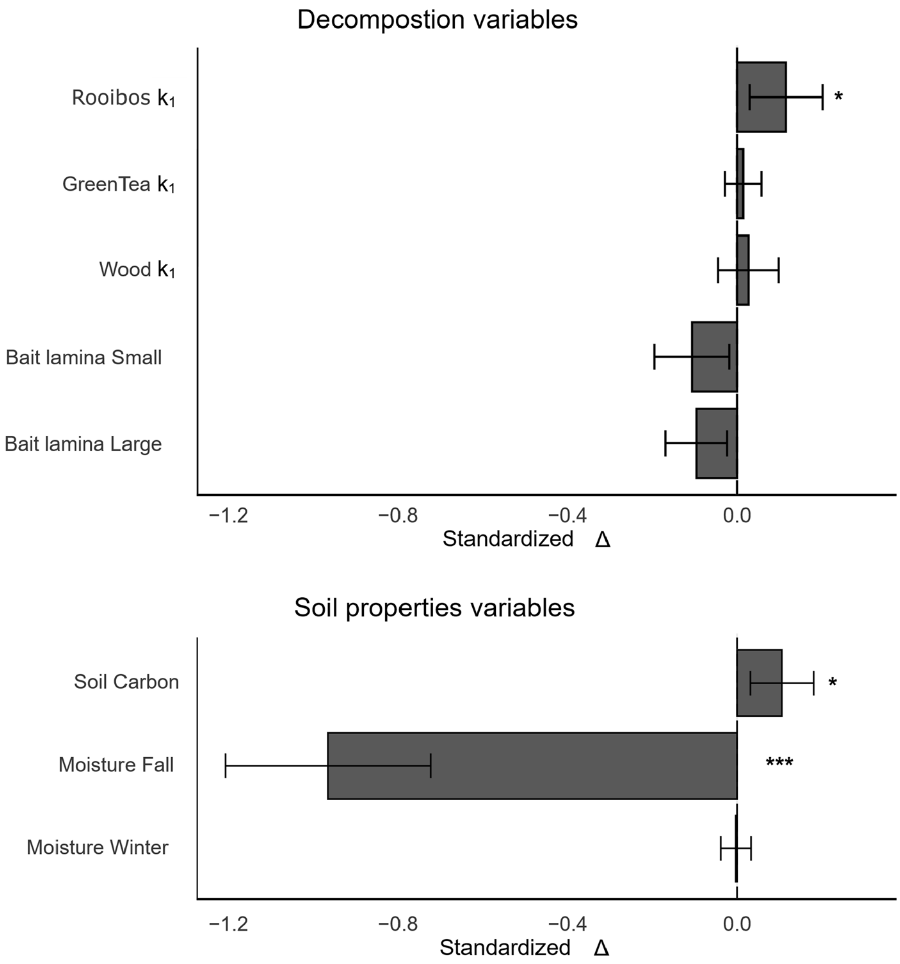

Fig. 3 Mean differences between invaded and non-invaded plots for different variables. Δ is obtained by subtracting the value of a variable at the non-invaded plot from the value of the invaded plot. Data was standardized by dividing the Δ values by the maximum value of that variable. Error bars show the standard error. Significance is shown by: P-value $= 0.05 > * > 0.01 > ** > 0.001 > ***$. Results of statistical analyses are shown in Table 3

A second way *S. gigantea* affects nutrient cycling and availability is by increasing overall decomposition rates in invaded areas (Fig. 3). This novel result, providing direct evidence that organic matter decomposes faster in invaded than in non-invaded sites, reveals a previously underappreciated pathway by which *S. gigantea* alters nutrient cycling beyond litter quality effects. On average, rooibos tea in invaded sites decomposed 12.9% (±9.6%, standard error) faster than in non-invaded sites. We show that this increased decomposition is likely due to alterations of various abiotic factors, rather than changes in biotic factors like soil microbiota, meso- and macrofauna activity (Fig. 3). For instance, *S. gigantea* reduced soil moisture during the growing season, similar to other *Solidago* species (Trigos-Peral et al. 2018), which can influence litter decomposition (Canessa et al. 2021). Because decomposition rates typically peak at moderate moisture levels (Cortez 1998), this reduction in soil moisture may accelerate litter decomposition in wetter locations due to soil oxygenation after lowering the water table (Laiho 2006; Straková et al. 2012), where the decrease in soil moisture is also most pronounced (Fig. 4C). Furthermore, soil carbon was increased in invaded areas, although this effect was most noticeable in less developed soils with low soil carbon, as in Dassonville et al. (2008) and Frouz (2024), such as those in Bos van Aa (Fig. 4A, Table 1). This increase in soil carbon could indirectly also impact decomposition outside of the growing season, since soils with higher carbon levels can hold more moisture (Hugar et al. 2012). This probably explains why plots on less developed soils—and thus low soil carbon (Frouz 2024)—show a larger discrepancy in moisture content during winter between invaded and non-invaded plots (Fig. 4D) as, again,

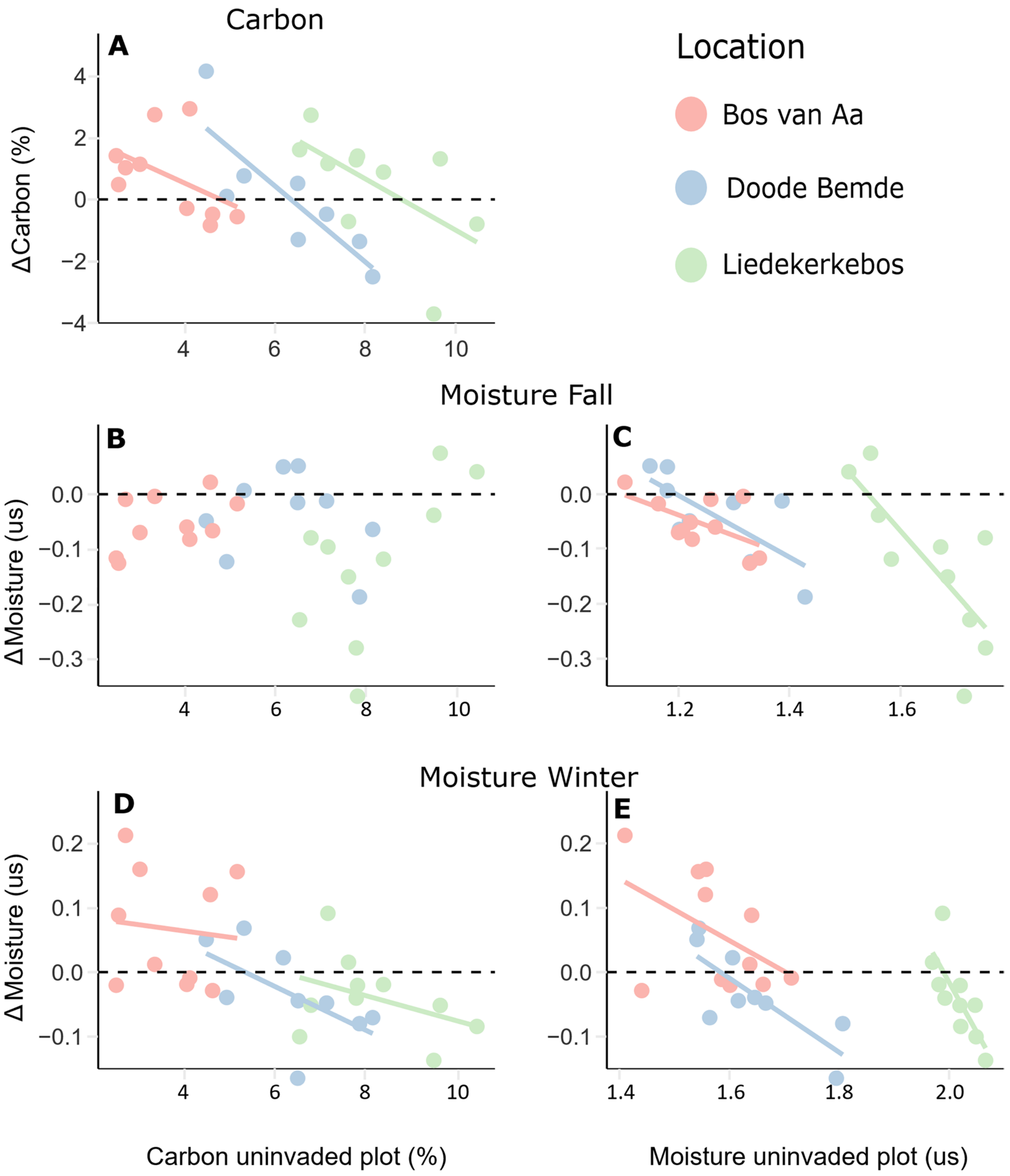

Fig. 4 Showing the differences (Δ) in soil carbon (4A) and moisture (4B-E) between invaded and non-invaded plots in function of the soil carbon (4B & D) or moisture (4C & E) of the non-invaded plots (as a substitute for the initial carbon or moisture content). Differences are obtained by subtracting the value of a variable at the non-invaded plot from the value of the invaded plot. Moisture is displayed relative to a dry standard measurement, meaning that a value of e.g. 1.5 us is a moisture level of 1.5 times the dry standard measurement. Data points above the dotted line have increased soil carbon/moisture in invaded plots, and vice versa for data points below the dotted line. Location is showed in colour. Lines show significant relationships ($P < 0.05$). Results of statistical analyses are shown in Table 2

can be seen for Bos van Aa (Table 1). We propose that the decreased soil moisture during the growing season and the increased soil carbon are both driven by the high primary productivity of *S. gigantea* and the fast-growing native plants commonly associated with these invaded stands (Vilà et al. 2011; Goossens et al. 2024). Elevated evapotranspiration, linked to higher primary productivity, reduces soil moisture, while increased litterfall and the rapid decomposition of this litter contribute to higher soil carbon levels (Liao et al. 2008; Gentile et al. 2011; Bowden et al. 2014). Additionally, the fast decomposition rates of invasive species' litter can further decrease soil moisture by preventing the formation of a thick leaf litter layer, which would otherwise aid in moisture retention (Veen et al. 2019).

Consistent with Klimek et al. (2020) we found that neither soil microbiota nor meso- and macrofauna activity were affected by *S. gigantea* invasion (respectively Figs. 1 & 3). Klimek et al. (2020) proposed two possible explanations why these faunal groups may not be affected by *S. gigantea* invasion. First, *S. gigantea* did not alter soil chemical properties in their study, and thus did not affect soil fauna feeding activity. However, we found that *S. gigantea* did alter soil chemical properties in our study which was in line with other studies reporting consistent invasion-induced changes in soil chemistry (Chapuis-Lardy et al. 2006; Scharfy et al. 2009; Goossens et al. 2024). The second explanation of Klimek et al (2020) was that *S. gigantea*'s dense vegetation may increase soil moisture and reduce soil temperature, counteracting the expected decline in soil fauna activity due to lower plant diversity. However, our results indicate that soil moisture actually decreased after invasion, likely due to increased transpiration, although this could still lead to lower soil temperatures. While invasion may alter the community composition of both soil microbiota and fauna (McTee et al. 2017; Zhang et al. 2019), overall decomposer activity appears largely unaffected, and no home-field advantage is supported for invasion of *S. gigantea*.

The invasion of *S. gigantea* did not significantly affect the decomposition rates of green tea or wooden spatulas (Fig. 3), which might be related to differences in decomposition dynamics between rooibos and green tea linked to the duration of the experiment. Green tea decomposes much more rapidly than rooibos (Keuskamp et al. 2013), with a rapid decline in mass within the first 14 days (Duddigan et al. 2020) which made it difficult to capture its full decomposition curve. To overcome this study limitation, including an additional collection moment within the first week could have facilitated differentiating decomposition rates of green tea between invaded and non-invaded plots. Similarly, additional collection moments, such as at six and twelve months, might have revealed an impact of invasion on wood decomposition, given its slower decay rate. Extending the experiment's duration would also allow for analyzing k_2 decomposition values, which are typically more reliable over longer timescales (Keuskamp et al. 2013).

Our study focused on the decomposition of fresh green leaves rather than senescent or fallen leaves, as not all herbaceous plants produce senescent leaves simultaneously—or at all. However, senescent leaves decompose more slowly, likely due to their higher C/N ratios (Li et al. 2021). This could also explain the even higher C/N ratios of 65 (±1) reported for *S. gigantea* by Zhang et al. (2016). Furthermore, increased C/N ratios only had a negative effect on litter decomposition for graminoids, but not for forbs. Possibly this is due to other chemical components, such as lignin, (hemi)cellulose and phenolics (Melillo et al. 1982; Chomel et al. 2016) influencing decomposition in forbs more strongly than C/N ratios do, although Zhang et al. (2008) show that C/N ratios (and other nutrient contents) are generally more important for decomposition than other chemical compounds.

Conclusion

Our findings indicate that the invasion of *S. gigantea* affects nutrient cycling and availability by altering decomposition rates within invaded stands. Moreover, we propose that the impact of invasion on nutrient availability and community composition varies depending on the characteristics of the invaded plant community and its abiotic components. Specifically, we identify the following mechanisms:

(i) In many grass-dominated communities, nutrient turnover is likely to accelerate, potentially stimulating primary production. This effect is probably less pronounced in forb-dominated plant communities. Enhanced primary production may provide a competitive advantage to invasive plants and fast-growing native species, creating a positive feedback loop (Michalet et al. 2023).

(ii) Furthermore, the combination of higher primary production and the absence of a persistent litter layer due to increased decomposition, can reduce soil moisture. This effect is particularly impactful in wetter areas, where drier soils can further accelerate decomposition.

(iii) In less developed soils, which are typically less productive with more specialist plant species, invasion can lead to significant increases in soil carbon and thus accelerated soil development. This process may result in the loss of associated specialist flora.

We recommend that future research on the effects of invasive species on nutrient cycling account for the variability in invasion impacts, considering the characteristics of the invaded plant community and its interactions with soil biotic and abiotic factors.

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Author contributions EPG and HOV conceived the ideas and designed methodology; EPG and FVP collected and analysed the data; EPG led the writing of the manuscript, and all authors contributed critically to the drafts.

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Data availability Data and R codes will be made available upon request.

Declarations

Conflict of interest There are no competing interests to be declared.

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