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ORIGINAL PAPER

Solidago gigantea invasion homogenizes soil properties and native plant communities

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Abstract *Solidago gigantea*, a notorious invasive species in Europe and Asia, has been shown in previous studies to impact soil properties such as nutrient availability and pH. However, the strength and direction of these alterations have varied across studies. Additionally, the species reduces species richness in invaded communities, though the susceptibility of different plant communities to invasion remains unclear. To address these inconsistencies, we investigated invasion effects on soil properties and plant communities across various soil types, nitrogen and pH levels, and plant communities. Soil samples were collected from invaded and nearby uninvaded plots, with measurements taken for extractable nitrogen, pH, and moisture content. Plant species richness, diversity, Sorensen similarity, mean Ellenberg indicator values and some community mean plant traits were compared between invaded and uninvaded plots. Lastly, *S. gigantea* stand density and size in invaded plots were quantified. *Solidago gigantea* significantly altered soil extractable-N and pH, with the extent and direction of changes depending on initial soil conditions. Alterations were most pronounced in acid, N-poor soils. Species richness and diversity consistently decreased in invaded plots. However, this decline was not due to direct competition with native species but to the replacement of specialized, local plant communities with less diverse, fast growing generalist communities adapted to fertile habitats. *Solidago gigantea* acts as an invasive ecosystem engineer, modifying soil conditions after introduction. This not only facilitates its spread but also leads to lasting effects that can persist even after its removal. Further studies on other invasive species are needed to establish general patterns due to their varied effects on ecosystem properties.

Keywords Invasive alien species · Nitrogen availability · Field study · pH · Ellenberg · Legacy effects · Functional traits

Introduction

Invasive species have been shown to be a major threat to native biodiversity (Hejda et al. 2009; Gaertner et al. 2009; Mollot et al. 2017; Brondizio et al. 2019). Many studies have shown that the absence of species-specific pathogens (Klironomos 2002; Kulmatiski et al. 2008) and herbivores (Wolfe 2002; Engelkes et al. 2008) in their introduced range can

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aid them to outcompete native flora, as stated by the enemy release hypothesis (Mitchell and Power 2003). Besides these advantages, invasive species are often naturally strong competitors (Vilà and Weiner 2004) thanks to traits as clonal reproduction (Lloret et al. 2005; Pyšek and Richardson 2007; Speek et al. 2011), high phenotypic plasticity (Davidson et al. 2011), allelopathy (Kalisz et al. 2021) and a high growth rate (Van Kleunen et al. 2010).

For many invasive species it is largely unknown to which extent they are the cause of the decline in biodiversity and alteration of soil properties (invasive species as drivers of ecosystem change, Bauer 2012; White et al. 2013), or if they are only the result of already degraded habitat (invasive species as passeengers of ecosystem change, Didham et al. 2005; Hansen and Clevenger 2005; Huebner 2021). Some studies indeed show for invasive plants that they can alter soil properties like nutrient availability (Hawkes et al. 2005; Dassonville et al. 2007), pH (Vanderhoeven et al. 2005) or soil microbe community (Belnap et al. 2005; Peltzer et al. 2009; Grove et al. 2017), possibly creating positive feedbacks that reinforce further invasion of conspecifics (Zhang et al. 2019). Though, the strength and even the direction of these alterations may depend on multiple environmental factors, such as the soil type, nutrient availability, pH and species richness of the invaded site (Ehrenfeld 2003). There is thus a need for studies where the impact of exotic plant invasions on both soil properties and plant communities is measured over large ranges of soil types, nutrient availabilities and vegetation types (Scharfy et al. 2009).

A classic example of such a notorious invasive species in Europe is *Solidago gigantea* Aiton. It invades different habitats by both seed dispersal and rhizome propagation (Weber 2011). This is one of the few invasive species that can even be found in oligotrophic heathlands were it can possibly still become invasive due to the high amount of rhizomes it produces (Güsewell et al. 2006). In its introduced range, *S. gigantea* displays a higher production of rhizomes, greater biomass and stem density compared to its native range in North America (Jakobs et al. 2004; Güsewell et al. 2006; Pal et al. 2015). This contrast may be attributed to native populations being predominantly diploid, while invasive populations are exclusively tetraploid (Schlaepfer et al. 2010). Despite both native and introduced ranges supporting stands with exceptionally high stem densities, the impact of S. gigantea on plant species richness appears significantly greater in the introduced range. It competitively excludes native species in direct correlation to the density of its own stand, exacerbating the reduction in species diversity (Pal et al. 2015). Besides this, *S. gigantea* seems to be more plastic in its introduced range (Jakobs et al. 2004), occurring in a wide range of environments affecting many different plant communities, e.g. wetlands and gallery forests (Török et al. 2003; Güsewell et al. 2005), forest plantations (Török et al. 2003) and disturbed sites (Török et al. 2003; Weber and Jakobs 2005).

Solidago gigantea seems to alter soil composition, however which properties it effectively alters and in which direction remains unclear. Previous studies present conflicting findings regarding the impact of *S. gigantea* on soil mineral concentrations and pH. These range from decreased pH (Herr et al. 2007), phosphorus (Stefanowicz et al. 2017) and nitrogen (Scharfy et al. 2009) concentrations to increased pH (McGrath and Binkley 2009), phosphorus (Chapuis-Lardy et al. 2006; Herr et al. 2007) and other mineral (Vanderhoeven et al. 2005) concentrations. Conversely, some investigations indicate no discernable effect on pH (Scharfy et al. 2009), phosphorus (Scharfy et al. 2010) or nitrogen (Scharfy et al. 2010; Stefanowicz et al. 2017; Bobuľská et al. 2019) concentrations. Besides the uncertainty of *S. gigantea*'s effect on soil composition, it has not yet been studied if differing plant communities are equally impacted by its invasion.

The aim of this study was to infer how the impact of plant invasions on soil nutrient availability, pH and plant community characteristics (diversity, mean Ellenberg indication values, community mean traits) depends on the abiotic and biotic components of the invaded area itself. Thereto, *S. gigantea* was chosen as a model invasive species. We used a novel experimental setup where both its abiotic impact on pH, moisture content and total extractable nitrogen and its biotic impact on native species richness, diversity and composition were examined along a large range of plant communities and soil types with varying nitrogen availabilities and pHs. We hypothesized that *S. gigantea* will alter soil nitrogen availability and pH, but that both the strength and direction of this effect depend on the initial soil conditions of the invaded area. Similarly, we hypothesized that plant communities of high species richness and diversity and with a more specialized species composition will be most negatively impacted by *S. gigantea*, through replacement of specialized species by taller, generalist species with high growth rate. Lastly, we hypothesized that the strength of these effects would depend on *S. gigantea* stand density, with denser stands having stronger impacts. If the invasion effects of *S. gigantea* depend on the initial conditions of the invaded site, this can demonstrate the need for studies where the impacts of invasions are investigated over different soil conditions and vegetation types. Secondly, it can support nature managers in deciding which areas are most sensitive to invasion.

Materials & methods

Site selection

Stands of *S. gigantea* were investigated in three Belgian nature reserves in order to cover different soil types and habitats, e.g. wet grasslands, open forests and forest edges, and heathland (Table 1). Stand sizes of *S. gigantea* ranged from < 1 m^2 up to 30 m^2 (and one very large stand, slightly larger than 6000 m^2), with densities of < 10 up to more than 400 stems per m^2. Stands also occurred along multiple abiotic gradients from low to high pH, nitrogen availability and soil moisture content (Table 1). In the centre of each *S. gigantea* stand a 1 m^2 plot was chosen to avoid edge effects, along with an associated 1 m^2 plot within the neighbouring uninvaded vegetation zone, two to six meters apart from the invaded plot, for a total of 56 plots (nine or ten plot pairs per nature area). Uninvaded plots were carefully chosen to occur within the same habitat type, altitude and sun exposure as their associated invaded plot. No other invasive species were present in or nearby any of the plots.

Vegetation composition

During the second half of April 2022, all native species within the invaded and uninvaded 1-m^2 plots were identified and their respective cover was assessed using the Braun-Blanquet cover-abundance scale (Braun-blanquet 1932) transformed to ordinal values (OTV, ordinal transform values between one and nine) according to van der Maarel (1979). Native species diversity of the plots (thus excluding *S. gigantea* itself in the invaded plots) could then be calculated using the Shannon Wiener diversity (SWD) index H' (Shannon and Weaver 1949) where the relative frequency of each species in the community was calculated from these OTVs (Eq. (1)):

$$H' = -\sum_{i=1}^{S} p_i \cdot \ln\left(p_i\right) \; with \; p_i = \frac{OTV_i}{\sum_{i=1}^{S} OTV_i} \tag{1}$$

where S = the total number of species within a plot. In order to assess changes in native species composition we calculated the Sorensen Similarity Index between all plot pairs, based on species cover (Chao et al. 2005). To infer how native species comsition changes after invasion, we calculated weighted average functional trait values for vegetative plant height, specific leaf area (SLA) and relative growth rate (RGR) of

Table 1 Biotic and abiotic characteristics of the sampling led sites

	# of plot pairs	Soil texture	Dominant plant communities	pH	Soil extractable nitrogen (mg kg^{-1} dry soil)	Moisture content (%)
Liedekerkebos	10	Sandy loam	Moist–wet grasslands	5.8 ± 0.9	15.5 ± 6.0	28 ± 9.6
Haachts Broek	9	Clay–heavy clay	Open deciduous forest–wet meadows	5.4 ± 0.8	16.6 ± 5.2	33 ± 5.8
Averbode bos en heide	9	Sand–loamy sand	Forest edges—Heathland	5.6 ± 1.1	17.7 ± 7.2	17 ± 8.4
			Total range of soil property:	4.0–7.7	9.0–75.9	6.3–44.5

Mean values with their standard deviation of the uninvaded plots are shown. Soil texture was always the same for paired plots. Soil extractable nitrogen is KCl-extractable inorganic N ($NH_4^+ + NO_3^- + NO_2^-$)

all native species within each plot with their OTV as weight. Functional trait data was retrieved from the TRY Plant Trait Database (Kattge et al. 2020). Since functional trait data was not available for all species in our dataset, plots were excluded from the analysis when data was only available for less than 40% plant coverage. A higher threshold would ensure a more accurate plot representation, but would also result in a lower amount of plots to analyse. We thus chose this threshold as a trade-off. To further analyse species composition, weighted average Ellenberg values for fertility (N), moisture (F) and acidity (R) were also calculated for each plot, with Ellenberg data available for all species in our dataset (Ellenberg 1991; Persson 1981; Hill 1999; Seifan et al. 2010; Hedberg et al. 2014; Di Biase et al. 2023). For the invaded plots, total stand size (m^2) and stem density of *S. gigantea* were measured (stems·m^{-2}). Due to the heterogeneity in stand shapes, stand size was approximated as the product of the longest cross-section of the stand and the length of its perpendicular bisector. Stem density was measured as it is both a good predictor for the impact of *S. gigantea* on native species (Ledger et al. 2015; Pal et al. 2015) and it can be used to infer how well-suited the habitat is for *S. gigantea* itself (Nagy et al. 2020).

Soil sampling and chemical analyses

In the middle of each plot a soil sample (0–10 cm deep) was taken at the end of March 2022, in order to measure moisture content, pH-KCl and total extractable nitrogen ($NH_4^+ + NO_x$, from here on N_{ext}). Soil textures, defined as in Van Ranst & Sys (2000), were retrieved from the detailed digital soil map of Flanders on geopunt (soil map of Flanders on geopunt) (Geopunt 2022).

To determine N_{ext}, 3 g of wet soil sample was mixed with 30 ml of 0.2 M KCl solution and shaken for one hour. pH-KCl was also measured in the soil extracts. Afterwards, this suspension was filtered using a Whatman GF/C filter and NH_4^+, and $NO_3^- + NO_2^-$ concentrations were measured with a Bran + Luebbe quAAtro (De Caluwe and Van Logtestijn 1998). Additionally 3 g of soil was dried for 72 h at 70 °C to determine soil moisture content, which was used to calculate soil extractable-N in mg N·kg^{-1} dry soil.

Statistical analyses

Abiotic (N_{ext}, moisture content and pH-KCl) and biotic (species richness and diversity, functional traits and Ellenberg values) differences between invaded and uninvaded plots were analysed using paired t-tests (function t.test) after the normality assumption was checked with the Shapiro–Wilk test (function shapiro.test). Differences in non-normally distributed parameters were analysed using a paired samples Wilcoxon test (function wilcox.test). Secondly, to infer whether the effect of invasion by *S. gigantea* depended on the initial conditions and on how dense the invasive stand was, we fitted mixed linear regressions for all above-mentioned variables, except for the functional trait data. Biotic and abiotic differences (as described above) between plot pairs were used as response variables. Stand density and the initial value of the soil parameter -as measured in the uninvaded plot- were inserted as fixed factor, together with their interaction term. Soil type was inserted as random factor (the three different nature reserves are located on different soil types so these were not inserted separately as random factor). One outlier was removed from the dataset used for the model assessing the influence of *S. gigantea* on N_{ext}, after detection with the Grubbs's test from the R package outliers (Komsta 2022) ($P = 1.96.10^{-9}$, $N = 113.6$ mg kg^{-1} dry soil—more than twice as much as the second highest value). Initial N_{ext} concentrations, as measured in the uninvaded plot, were also log-transformed in order to improve fit and reduce heteroscedasticity. Multicollinearity between the two fixed values was analysed using VIF (Variance Inflation Factor) values with the VIF function from the R package car (Fox and Weisberg 2019) with a cut-off of < 3. Lastly, a mixed linear regression was made for the effect of soil type and stand density (and their interaction) on the Sorensen Similarity Index of paired plots. For all mixed models normality and heteroskedasticity were checked with visual plots, and respectively with the Shapiro–Wilk and Breusch-Pagan test with the function bptest from the R package lmtest (Zeileis and Hothorn 2002). Conditional and marginal R^2 from the mixed models were calculated with the function R.squaredGLMM from the R package MuMIn (Bartón 2022).

The effect of stand size instead of stand density was considered, but the former was always less significant than the latter in explaining differences between invaded and uninvaded plots. Since stand size and stand density were correlated (mixed model, $P<0.001$, marg. $R^2=0.33$; Extended Data Fig. 1), we could not use both as fixed factors in our mixed models.

Data analyses was performed in R version 4.2.1 (R Core Team 2022). Figures were made with the function ggplot from the ggplot2 package (Wickham 2016), coloration using the package RColorBrewer (Neuwirth 2022), and edited in Inkscape 1.2.1 (Inkscape Project 2020).

Results

The presence of *S. gigantea* had a strong impact on soil and vegetation characteristics, and the strength and direction of the effect strongly depended on the initial soil conditions (Table 2). *Solidago gigantea* increased pH and extractable N in soils of initially low pH and low N availability, but decreased these soil variables in soils with initially higher pH and N availability (Fig. 1a, b). The effect on pH also seemed to depend on stand density, with denser stands exacerbating the effects of invasion (positive coefficient for stand density and negative coefficient for the interaction term; Table 2). Moisture content was not significantly altered by *S. gigantea* (Fig. 1c, Table 2).

Solidago gigantea decreased both species richness and diversity of the invaded plant communities (Fig. 2a-b), and this effect was stronger in dense stands and species-rich communities (Table 2). On average, invaded stands contained 2.6 species fewer and had their SWD index reduced by 26%. *Solidago gigantea* did not just outcompete some native species, but rather altered species composition completely. The Sorensen Similarity Index of paired plots shows that species composition in invaded plots is different from non-invaded plots, with denser stands being more dissimilar from their paired non-invaded plots (Fig. 2c; Table 2). Average Ellenberg N and R values of the plant communities indicate that invasion of *S. gigantea* promoted species from fertile and neutral to alkaline habitats, and this promotion was strongest in the nutrient-poor and acid sites, respectively (Fig. 3a, b, Table 2, Extended Data Tables 1, 2). Ellenberg F values show that invasion of *S. gigantea* also promoted species from intermediate moisture in both relatively wet and relatively dry sites, where the effect was again strongest in sites of more extreme moisture regimes (Fig. 3c, Table 2, Extended Data Table 3). Stand density had a significant effect on how Ellenberg N and F values of the community were altered, where denser stands exacerbated the effect on Ellenberg N and lowered Ellenberg F values (Table 2). Invaded communities consist on

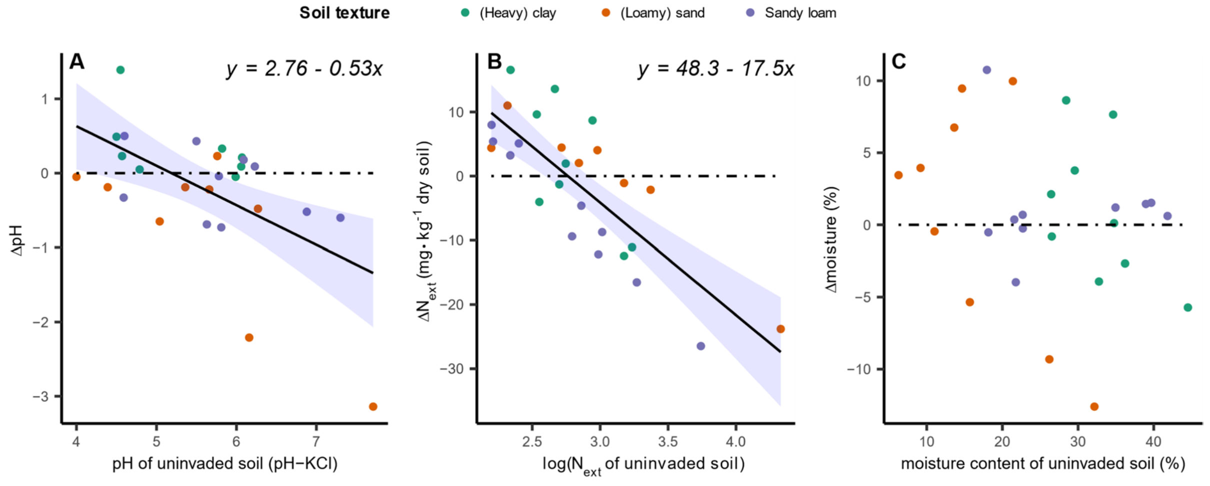

Fig. 1 Abiotic alterations by *S. gigantea* in function of the initial soil parameters. **A** difference in pH between the invaded and uninvaded soil. **B** difference in available nitrogen between the invaded and uninvaded soil. **C** difference in moisture content between the invaded and uninvaded soil. Equations are from linear models with x-axis as only explanatory variable

Table 2 Statistics for paired tests and Mixed model ANOVA results

Response variable	Paired tests		Fixed factors of mixed linear models									
			Initial value of the variable (IV)			*S. gigantea* stand density (SD)			Interaction IV × SD			
	t-value	*P*-value	*F*-value	Effect size	*P*-value	*F*-value	Effect size	*P*-value	*F*-value	Effect size	*P*-value	R^2
Soil pH	172[a]	0.27	18.7	**−0.15**	***	3.0	**0.015**	.	4.8	**−0.003**	*	**0.40**
N_{ext}	0.64	0.26	73.4	**−18.4**	***	0.5	–	0.50	0.5	–	0.48	**0.62**
Moisture	−0.68	0.51	2.3	–	0.13	0.0	–	0.93	1.5	–	0.23	–
Species richness	6.69	***	4.6	**−0.25**	*	18.3	**−0.015**	***	0.06	–	0.81	**0.39**
Species diversity	5.75	***	1.7	–	0.19	18.2	**−0.003**	***	0.24	–	0.62	**0.38**
Sorensen diversity	–	**–**	–	–	–	14.7	**−0.002**	***	–	–	–	**0.26**
Ellenberg R	100[a]	*	18.9	**−0.59**	***	2.4	–	0.12	1.5	–	0.23	**0.42**
Ellenberg N	−3.6	***	21.3	**−1.29**	***	20.9	**−0.039**	***	6.4	**0.008**	*	**0.65**
Ellenberg F	0.24	0.41	42.5	**−0.42**	***	6.7	**−0.001**	**	0.71	–	0.40	**0.72**

Effect sizes are written in bold, when they were significant

Paired tests show whether *S. gigantea* has a significant unidirectional effect on the response variable. Both fixed factors show which variables can influence both strength and direction of this effect. *P*-values are indicated as follows: 0.1 > . > 0.05 > * > 0.01 > ** > 0.001 > ***. Effect sizes are only given when significant. Marginal R^2 is given. The effect on soil pH remained significant when the two paired plots with the largest pH changes ($\Delta pH < -2$, Fig. 1a) were omitted. Similarly, all effects of stand density remained significant when the plot with stand density > 400 stems·m^{-2} was omitted

[a] *V*—value given of the paired samples Wilcoxon test

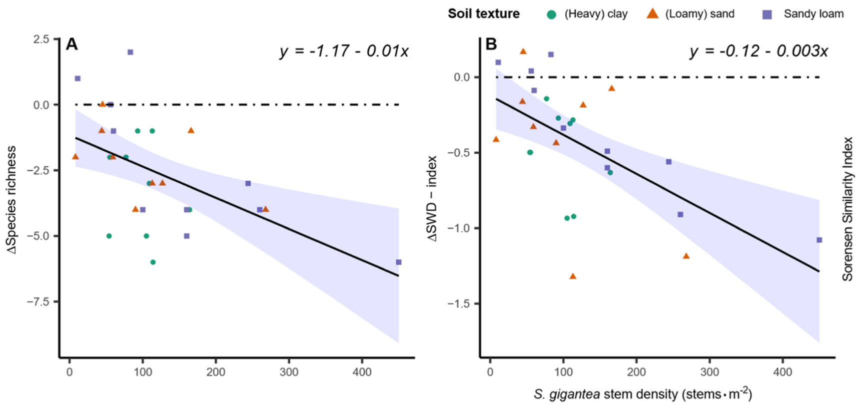

Fig. 2 Biotic alterations by *S. gigantea* in function of invasive stand density. **A** difference in species richness between the invaded and uninvaded plot. **B** difference in Shannon Wiener diversity (SWD) index between the invaded and uninvaded plot. **C** Sorensen similarity of paired invaded and uninvaded plots. Equations are from linear models with x-axis as only explanatory variable

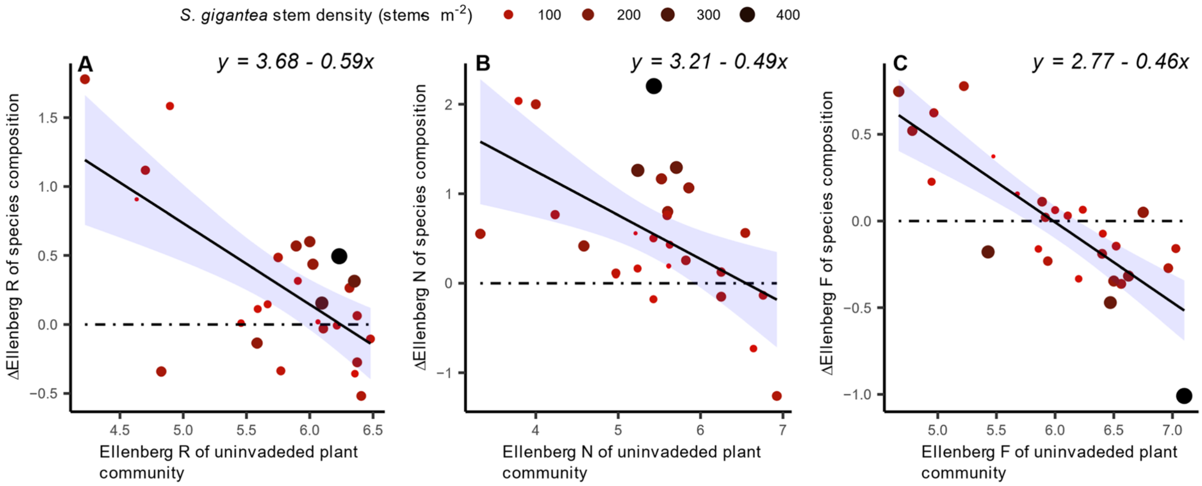

Fig. 3 Plant community alterations by *S. gigantea* in function of the initial communities. **A** difference in averaged Ellenberg R value between the invaded and uninvaded community. **B** difference in averaged Ellenberg N value between the invaded and uninvaded community. **C** difference in averaged Ellenberg F value between the invaded and uninvaded community. Equations are from linear models with x-axis as only explanatory variable

average of taller plants (P-value < 0.01, Fig. 4) with a higher relative growth rate (RGR) (P-value < 0.05, Fig. 4), and a tendency for a higher specific leaf area (SLA) (P-value = 0.066) (Fig. 4).

Discussion

Solidago gigantea as a driver of abiotic ecosystem change

Solidago gigantea is indeed a eurytopic plant, i.e. able to invade many different plant communities on different soil types (Török et al. 2003; Weber and Jakobs 2005; Güsewell et al. 2005). This can

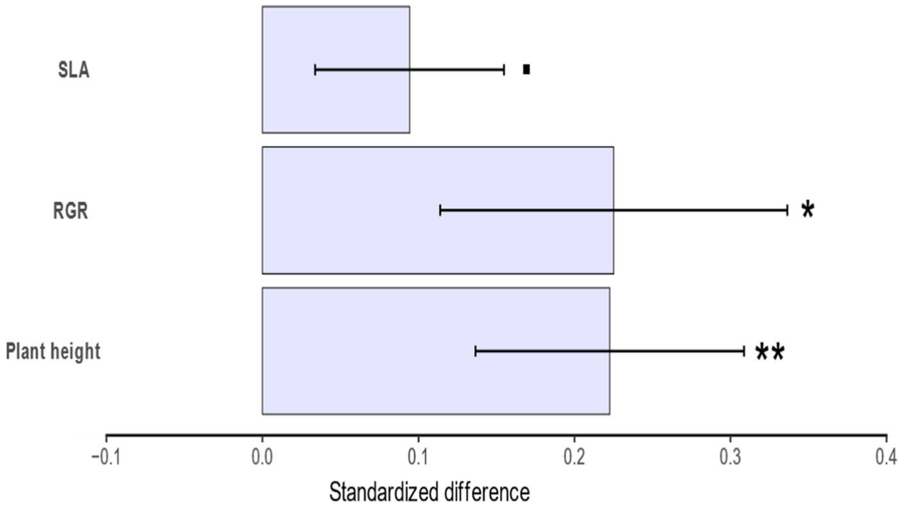

Fig. 4 Plant community alterations by *S. gigantea*, illustrated by changes in some community mean trait values of invaded plots. The traits include specific leaf area (SLA), relative growth rate (RGR) and plant height of the vegetative part of the plants (hence, flowering stems are not included). Differences in community mean traits were calculated by subtracting the averaged trait value of the species in each uninvaded plot from those in its paired invaded plot. Differences shown here are averaged between all plots. Standard errors of 27, 13 and 19 paired plots are shown for SLA, RGR and plant height respectively. Standardization was done for each averaged trait value by dividing by the maximum value of that trait value. Standardized differences > 0 indicate that the community mean trait values of the invaded plots were higher than that of the uninvaded plots. *P*-values from paired t-tests are indicated as follows: 0.1 > . > 0.05 > * > 0.01 > ** > 0.001 > ***. All differences in functional trait values were normally distributed

be seen as no clear trends or maxima in stand density were observed along the full ranges of all abiotic parameters of the sampled plots (Extended Data Fig. 2a, c). Though throughout this range of plant communities and soil parameters, *S. gigantea* showed to have a consistently homogenizing effect on its environment in our studied sites, both biotic and abiotic. As *S. gigantea* could both increase or decrease soil pH and N_{ext}, depending on the initial soil conditions (Fig. 1a, b), studies that examined soils with either only rather low or only high pH or N_{ext} found a unidirectional effect, respectively increasing or decreasing pH and N_{ext} (Vanderhoeven et al. 2005; Herr et al. 2007; Scharfy et al. 2009). Other studies that examined soils on larger pH or N_{ext} ranges, but did not take the initial soil conditions into account would indeed not find a significant impact of *S. gigantea* on these soil parameters (Scharfy et al. 2009, 2010; Stefanowicz et al. 2017). This homogenizing effect might be a more consistent effect of invasive species as this was already proposed for another notorious invasive plant species in Europe: *Fallopia japonica* (Dassonville et al. 2007). Further research is needed, where the effects of invasion by other exotic species are examined over large ranges.

How does *S. gigantea* alter these soil conditions? The increased N availability in invaded plots on nutrient poor soils might be explained by the faster decomposing litter and rapid nutrient cycling of *S. gigantea*, as has been shown for other invasive species (Ehrenfeld 2003; Allison and Vitousek 2004). In the case of *S. gigantea*, it has been shown that its leaf litter decomposes faster than of native graminoids, which could alter soil nutrient availability, especially when invading grass-dominated habitats (Scharfy et al. 2011). Although nutrient uplift (Jobbágy and Jackson 2004) has been suggested for multiple other deep-rooting invasive species (Vanderhoeven et al. 2005; Dassonville et al. 2007), this is probably not the case for *S. gigantea* since it does not root much deeper than many other native herbs (Vanderhoeven et al. 2006). On nutrient richer soils these effects might be reversed when *S. gigantea* has lower quality litter with lower N immobilization than the original native plant community (Scharfy et al. 2009). While not subject to our investigation, *S. gigantea* might have a similar complex effect on

P availability through similar mechanisms. As suggested by Herr et al. (2007), *S. gigantea* might lower soil pH in more alkaline soils by active acidification of the rhizosphere. The mechanisms for increased pH in acid soils are not clear, but multiple propositions exist: the preferential uptake of nitrate over ammonium by invasives (Ehrenfeld et al. 2001) or faster leaf decomposition from invasive species (Finzi et al. 1998) can increase pH. Lastly, invasive species can take up cations differently with differing turnover times, resulting in an increased pH (Reich et al. 2005). Our results indicate that *S. gigantea* has no direct effect on soil moisture (Fig. 1c), however it is possible that *S. gigantea* evapotranspirates more due to its high growth rates. These altered moisture contents could then alter e.g. litter decomposition. More research is needed though, where moisture contents are repeatedly measured throughout the growing season instead of point measurements in March.

Solidago gigantea as a driver of biotic ecosystem change

Solidago gigantea decreased native species richness and diversity (Fig. 2a, b; Hejda et al. 2009), with denser stands having larger impacts (Table 2; Pal et al. 2015). Our results add that plant communities with highest species richness were most negatively impacted, which seems in contrast with the generally accepted hypothesis that more diverse communities have higher invasion resistance (Kennedy et al. 2002; Tilman 2004). However, our results do not necessarily implicate that more diverse communities are more easily invaded, but rather that once invaded, biodiverse communities will generally suffer higher species losses than less biodiverse communities. More importantly, we found that *S. gigantea* did not just decrease species richness and diversity by outcompeting some native species, but by actually replacing whole plant communities by other, less diverse and less specialist plant communities (Figs. 2c, 3a–c and 4). Similarly to its effects on the abiotic soil conditions (see above), *S. gigantea* homogenized plant communities, promoting generalist species of fertile soils that can cope with the competition pressure, while species adapted to more extreme moisture and pH levels steadily disappear. The transition from invaded communities to more fertile ones is evident in the elevated Ellenberg N values (Table 2). Additionally, these invaded communities showcased a prevalence of competitive plants, as indicated by their taller average height, higher RGR, and SLA (Fig. 4). This correlation underscores how these functional traits align positively with community fertility (Extended Data Fig. 3). The main issue is thus that *S. gigantea*, itself a eurytopic species, can invade many different plant communities where it replaces the locally adapted, specialist flora consistently with the same generalist vegetation, often composed of ruderal species like *Juncus effusus*, *Rubus fruticosus*, *Urtica dioica* and *Galium aparine*, regardless of the invaded habitat type.

As *S. gigantea* alters both the abiotic soil conditions and the species composition, it is important to understand to which extent species composition is altered directly -through competition (Pal et al. 2015)- or indirectly, where soil alteration is the main cause of species replacement. We can make some assumptions through the quantification of the effect sizes of *S. gigantea* on the soil properties pH and N_{ext}. If these effect sizes, despite being significant, are only very small, then we could assume that the changes in native species composition are mostly due to direct competition effects. However, the slopes of our mixed models show that the effects of the original soil pH and N_{ext} on the change in respectively pH and N_{ext} by *S. gigantea* are quite large (Fig. 1a, b; respective coefficients of slope: -0.51 ± 0.13 and -1.08 ± 0.19, standard errors given), indicating that the effect sizes of *S. gigantea* on these soil properties are large. For instance, when invading acid oligotrophic soils *S. gigantea* can increase N availability and raise pH, which in turn can expel locally adapted oligotrophic plant species. The indirect effect here could thus be strong enough to alter plant communities, even without the direct competition effect of the invader. Although *S. gigantea* has been shown to easily invade disturbed habitats (Török et al. 2003; Weber and Jakobs 2005), and thus fits the model of a "passenger" of ecosystem change (Didham et al. 2005; Hansen and Clevenger 2005; Huebner 2021), we here show that it also fits the model of a "driver" of ecosystem change (Bauer 2012; White et al. 2013). We propose *S. gigantea* should be considered an invasive ecosystem engineer, which have faster growth rates and larger impacts in sub-optimal habitats—sub-optimal for the invasive species itself that is- than other invasive species (Cuddington and Hastings 2004), by altering these habitats. To further infer how important the direct and indirect effects of invasives such as *S. gigantea* are, more research is needed. As we show here, the exclusion and replacement of native species by invasive species is a complex mix of different effects.

While there have been studies exploring strategies for managing *S. gigantea* invaded grasslands and their biotic restoration (Nagy et al. 2020; Szymura et al. 2022), these do not investigate whether abiotic restoration is needed after invasion and how this should be done. This is an important knowledge gap since certain plant invasions can leave long lasting legacy effects on soil nutrient cycling (Elgersma et al. 2011). There is thus a clear need for long-term field experiments where soil conditions and/or plant communities can be manipulated to infer the long-term abiotic impacts of *S. gigantea* on nature restoration projects after invasive plant control.

Study limitations

As discussed by Chapuis-Lardy et al. (2006), a fundamental problem of field invasion studies is the lack of certainty that no pre-invasion differences in biotic and abiotic soil properties were present, making invasion locally more feasible. Though, we have shown that *S. gigantea* can grow and expand equally successful in a large range of abiotic soil properties (Extended Data Fig. 2a–c), indicating the unlikeliness that these differences between invaded and uninvaded plots are the cause of invasion, but that the invasion of *S. gigantea* is rather the cause of these differences.

It is possible that stand size is related to their age, with older stands being larger. We initially aimed to include this factor into our study, but as the invasion of *S. gigantea* was never documented this information was not available. Furthermore, analyzing stand age through herb-chronology proved to be unfeasible, because rhizomes older than 4 years were too decomposed to distinguish growth rings.

Conclusions

Our results show that the impact of an invasive plant species, such as *S. gigantea*, can vary strongly among invaded sites with differing plant communities and soil characteristics. There is thus a clear need in invasion ecology for studies examining the different effects of invasion on varying soils, rather than the effects of many different invasive species on a few locations. An invasive plant species might not have a unidirectional effect, but a rather complex impact depending on the biotic and abiotic conditions of the invaded area. Especially nutrient-poor, acid soils and more specialized and diverse plant communities are disproportionately impacted (at least by *S. gigantea*). Noteworthy, these are also the habitat types which are already relatively rare and vulnerable to change. Additionally, since many plant invasions can have long lasting effects on soil properties, even after their removal, clearing an invaded site from its invader may not be sufficient to restore the initial soil characteristics and plant community.

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Author contributions EPG and HOV conceived the ideas and designed methodology; EPG, WM collected the data; EPG, WM analysed the data; EPG led the writing of the manuscript; EPG, WM, HOV contributed critically to the drafts and all authors gave final approval for publication.

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Data availability The data that support the findings of this study will be uploaded to Figshare.

Declarations

Conflict of interest The authors declare that there are no competing interests.

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