

Research Article

A community resembling semi-natural meadow is as resistant to goldenrod invasion as highly productive commercial grassland

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Abstract

Alien goldenrods (*Solidago* and *Euthamia*) invade improperly managed grasslands causing serious environmental problems. The general knowledge regarding habitat resistance against invasion does not allow predicting whether species-rich semi-natural meadows or highly productive artificially sown grasslands are more resistant to invasion by goldenrods. To test the differences in resistance, an experiment was conducted. A community resembling a semi-natural, species-rich meadow and a commercial grassland was created in containers in 2018 using seed mixes, with open soil serving as the control. Three goldenrod seedlings representing particular species (*Solidago canadensis* L. s.l., *S. gigantea* Aiton, and *Euthamia graminifolia* (L.) Nutt.) were planted in the test containers with the different communities in 2019. The vegetation was cut once per year during the first and second years of the experiment. In September of the third year, the number of goldenrod ramets, the height of the tallest goldenrod ramet, and the flowering stage were measured and assessed. In addition, the dry biomass of goldenrods and accompanying species were weighed. The results showed no significant differences between total biomass production of the examined communities, except for *E. graminifolia*, for which species-rich meadow produced more biomass than the commercial grassland and control. Both communities strongly reduced ramet numbers and height and goldenrod biomass production compared to the control. No differences were found between these two vegetation types, except for the flowering stage of *S. canadensis* and *E. graminifolia*, which could not produce seeds in the species-rich meadow community. The results suggest that semi-natural, species-rich meadows are reasonable alternatives to species-poor commercial grasslands to control goldenrod invasion.

Key words: biomass production, biotic resistance, competition, *Euthamia graminifolia*, invasive *Solidago*

Introduction

Under the so-called PAB framework, invasion by a plant species is driven by the level of propagule pressure (P), the suitability of the abiotic conditions (A) for a particular invader, and the biotic interactions (B) that

the invader may face in the resident plant community (Catford et al. 2009). With regard to the biotic interactions, successful invaders must overcome biotic resistance arising from the resident community, which can efficiently reduce the invasion success (Levine et al. 2004; Hui et al. 2016; Beaury et al. 2020). Such resistance can be easily overcome in situations of extreme habitat disturbance that cause vegetation destruction and/or resource fluctuations; therefore, the habitats that are the most vulnerable to invasion are disturbed human-created habitats, especially those dominated by annual plants (Chytrý et al. 2008). However, in the case of undisturbed vegetation or vegetation well adapted to disturbance, the invader must still face habitat resistance due to resident vegetation (Byers and Noonburg 2003; Levine et al. 2004; Beaury et al. 2020).

Habitat resistance has been intensively studied to find general rules that explain the differences between habitats in the number and/or proportion of alien species (e.g. Chytrý et al. 2008; Rejmánek et al. 2005; Levine et al. 2004; Beaury et al. 2020). These differences can be explained by habitat characteristics, such as the availability of resources that resident plant species do not use, competitive ability of native species, allelopathy, presence of herbivores and pathogens, presence of disturbance, or composition of soil microbes (D'Antonio 1993; Lonsdale 1999; Shea and Chesson 2002; Rejmánek et al. 2005; Hierro et al. 2005; Dawson and Schrama 2016). Initially, species-rich habitats were assumed to be more resistant to invasions (Elton 1958; Lonsdale 1999; Mack et al. 2000; Shea and Chesson 2002; Levine et al. 2004; Fridley et al. 2007; Oakley and Knox 2013). The low invasibility of species-rich communities could arise from the diversity of functional traits rather than simply from species richness (Díaz and Cabido 2001; Maron and Marler 2007; Hooper and Dukes 2010). This functional diversity leads to a higher probability that a community representing different traits can fill all available niches, and it correlates with greater complementary use of available resources (Tilman 2004; Pokorný et al. 2005; Frankow-Lindberg 2012; Schittko et al. 2014). In addition, the habitats producing more biomass tend to be more resistant to invasion due to the high use of available resources (Byun et al. 2018). However, the invasion processes are highly context dependent, and the general rules do not necessarily predict whether a habitat may be invaded by a particular invader (Chamberlain et al. 2014). Given a single invader, the vegetation would theoretically be more resistant if the plant community contains species with features close to the invader that enable successful competition with the invader. Additionally, dominant species and their traits may have a positive or negative impact on community resistance to invasion (Smith et al. 2004; Galland et al. 2019).

Goldenrods of North American origin (*Solidago canadensis* L. s.l., *S. gigantea* Aiton, and *Euthamia graminifolia* (L.) Nutt.) have invaded Europe, Asia, and Australia. The *Solidago* species are widespread, whereas *E. graminifolia*

occupies a restricted area, near the site of introduction (CABI 2020). They are fast-growing, highly competitive plants, producing high biomass (Weber 2000; Weber and Jakobs 2005; Szymura and Szymura 2015a, b, 2016; Pal et al. 2020). In Central Europe, they can form dense stands, mostly on abandoned lands and unmaintained grasslands (Fenesi et al. 2015; Czarniecka-Wiera et al. 2019, 2020). Their environmental impact is locally very strong, decreasing biodiversity at different trophic levels (plants, arthropods, birds), altering succession, and disturbing agriculture (Hejda et al. 2009; Moroń et al. 2009; Skórka et al. 2010; Bartha et al. 2014; Fenesi et al. 2015). Consequently, their population should be controlled in compliance with EU law regulations (European Community 2014).

High-value habitat types that are endangered by the goldenrod invasion, particularly if improperly maintained, include semi-natural, species-rich meadows (Bartha et al. 2014; Czarniecka-Wiera et al. 2019). Grasslands serve provisioning ecosystem services, but they also contribute to non-agricultural ecosystem services, such as water flow regulation, carbon storage, erosion control, climate mitigation, pollination, and cultural services (Hönigová et al. 2012; Villoslada et al. 2018; Bengtsson et al. 2019). Unfortunately, a decline of species-rich semi-natural meadows has been observed worldwide (Queiroz et al. 2014; Egoh et al. 2016). In Europe, over 90% of the semi-natural grasslands have been lost since the 1930s (Eriksson et al. 2002; Bullock et al. 2007; Pe'er et al. 2014). The abandonment of maintenance, as well as maintenance intensification, could result into the conversion of semi-natural meadows into highly productive, but species-poor grasslands. Considering the process of preventing goldenrod invasion, vegetation consisting of fast-growing species producing a high biomass could be resistant to goldenrod invasion owing to competitive interactions. This possibility implies that preserving such intensively used meadows is desirable for invasion control. However, given the broad range of ecosystem services provided by semi-natural meadows, their maintenance should be a priority. Additionally, species-rich, low-intensity grasslands are preferred in urban greenery because they increase the resilience of the ecosystem, enhance its ability to accumulate carbon and nitrogen (Onandia et al. 2019; Thompson and Kao-Kniffin 2019), and reduce the public cost for maintenance (Klaus 2013; Hedblom et al. 2017; Norton et al. 2019). Moreover, high plant diversity directly enhances human well-being and brings psychological benefits (Fuller et al. 2007; Hanski et al. 2012; Lachowycz and Jones 2013; Clark et al. 2014; Southon et al. 2018). Unfortunately, it can be assumed that in urban areas, where habitats are usually disturbed and rich in nutrients, plant invasion (e.g., goldenrods) may be facilitated by low-intensity maintenance such as a cutting regime of once or twice per year.

The extent to which the species-rich vegetation desirable for sustainable development is resistant to *Solidago* invasion is unclear in comparison with

highly productive grasslands. Is there a trade-off between biodiversity and biomass production in terms of invasion resistance? We hypothesised that vegetation consisting of fast-growing, high-biomass-producing grass species, which is typical of intensively maintained grasslands, would be more competitive against invasive goldenrods than the species-rich vegetation that is characteristic of semi-natural meadows. In other words, we expected the vegetation typical of intensively maintained grasslands to be more resistant to goldenrod invasion. To test the hypothesis, we established an experiment and grew the plants for three years, and we then compared their biomass production, morphology, and flowering stages.

Materials and methods

The experiment was established in the Research and Teaching Station in Swojczyce belonging to Wrocław University of Environmental and Life Science, Wrocław, Poland (51°6'54"N; 17°7'42"E), at an altitude of 115 m. The average annual precipitation is 583 mm, and the annual temperature is around 9.0 °C (Dubicki et al. 2002). In the station, research on plant and animal production is conducted in an area of 260 ha. The experiment was placed in the teaching garden, where ornamental plants and grasses are grown. Representative photographs of the experiment are presented in the Supplementary material Photos 1–4. The experiment was established by using 70 × 40 cm containers, without bottoms, mounted in the soil (Anthropic Regosol, loamy sand texture, pH in H₂O = 6.90; N = 0.52 g kg⁻¹; P = 155.37 mg kg⁻¹; K = 113.33 mg kg⁻¹; Mg = 46.87 mg kg⁻¹; C = 0.78%). In the containers, three types of habitat were created: a community resembling semi-natural meadow (*meadow*), a commercial grassland (*grasses*), and open soil as a control (*control*). Plant seeds for creating the habitats were introduced in May 2018. Commercial grassland was created using a seed mixture of four highly productive grasses (*Poa pratensis*, *Lolium perenne*, *Festuca pratensis*, *Phleum pratense*) typically used in intensively maintained meadows in Europe. The species-rich habitat (*meadow*) was created using a seed mixture of 37 herb and grass species typical of species-rich, semi-natural meadows in Central Europe. The detailed composition of the seeds is given in Tables S1 and S2. The seeding rate was 4 g m⁻² for both mixtures. In the next year, after the plant communities were successfully established, three goldenrod seedlings were planted in each container. In the control (open soil), weeds were removed before goldenrod planting. In total, 54 containers were used (3 habitat types × 3 goldenrod species × 6 replications). The combination was placed in a completely randomized design (Figure S2, S3, S4). At the end of August in the first and second years of the experiment, all vegetation (created communities and goldenrods) was cut and biomass was removed (Figure S5). If required, the pots were additionally irrigated, but no fertiliser was used.

In the third year of the experiment (2020), the number of goldenrod ramets (ramets number) and the height of the tallest goldenrod ramet were measured on September 1. The flowering stages (0, only vegetative shoots; 1, appearance of generative shoots or flower buds; 2, beginning of flowering (< 50% buds); 3, full flowering (> 50% buds); 4, late flowering (appearance of first seeds) and 5, seed set (> 50% seeds)) were assessed. Then, the plants were removed from the containers, gently washed, divided into above- and below-ground parts, dried, and weighed. Goldenrods and co-occurring plants were analysed separately.

Statistical analyses

Total dry biomass production, including biomass of goldenrods and other species (total biomass), exclusive biomass production of goldenrods (goldenrods biomass), and allocation of goldenrod biomass between above- and below-ground parts (goldenrods A/B ratio) were calculated. The significance of differences amongst habitats for studied traits was tested using the Kruskal–Wallis ANOVA by ranks with the Monte Carlo permutation. The Mann–Whitney test with Bonferroni correction was applied as a post hoc test. The analyses were conducted separately for each goldenrod species. All the analyses were done using R environment using STATS package (Mangiafico 2020).

Results

The total biomass produced in the containers varied widely, ranging from 115.1 to 997.8 g dry weight. The median value was 364.25 g dry weight. No significant differences were found in total biomass between the examined communities except for *E. graminifolia*, where the community resembling semi-natural meadow (*meadow*) produced more biomass than the commercial grassland (*grasses*) and control (Figure 1, Table 1). However, the communities differed significantly in biomass produced exclusively by the goldenrods (goldenrod biomass) for all examined species (Figure 2, Table 1). The goldenrod biomass in mixtures was 20- to 30-fold lower (median value of goldenrod biomass 9.3 g dry weight) than in the control (median value 225.7 g dry weight). No differences were found for goldenrod A/B ratio across all species (Figure 3, Table 1). In addition to the lower biomass production, the goldenrods growing in mixtures also produced fewer ramets (N ramets) than in the control (Figure 4, Table 1). In the case of *E. graminifolia* and *S. gigantea*, the ramet height (height) in the semi-natural meadow treatment was shorter than in the control (Figure 5, Table 1). Moreover, we observed significant differences in flowering phases between communities and control for *E. graminifolia* and *S. canadensis* (Figure 6, Table 1); these species did not produce seeds (reaching only the third stage of flowering) in the meadow community. Total biomass production of species other than *Solidago* in different communities is shown in Figure S1.

Table 1. Results of statistical tests (χ^2 and P) for goldenrod species (columns) grown in different communities, based on the differences in average values of examined traits (rows). Statistically significant results at $p \leq 0.05$ are in bold.

Species	<i>E. graminifolia</i>		<i>S. canadensis</i>		<i>S. gigantea</i>	
	χ^2	P	χ^2	P	χ^2	P
Total biomass	8.78	0.012	3.55	0.169	3.17	0.205
Goldenrod biomass	11.72	0.003	8.77	0.012	11.66	0.003
Goldenrod A/B ratio	1.62	0.443	0.31	0.856	2.00	0.366
Number of ramets	11.37	0.003	8.84	0.011	11.42	0.003
Height	10.16	0.006	4.15	0.125	6.84	0.033
Flowering	10.23	0.004	6.06	0.030	0.88	0.587

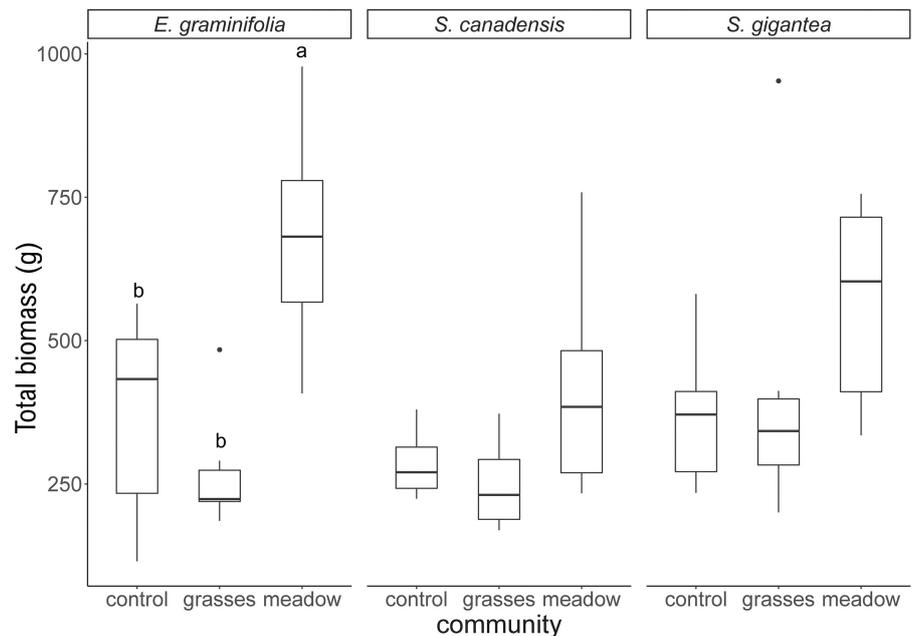


Figure 1. Total biomass production of different communities. Median value (thick line), upper and lower quartiles (box), 1.5 IQR (whiskers) ranges, and outliers (black dots) are shown.

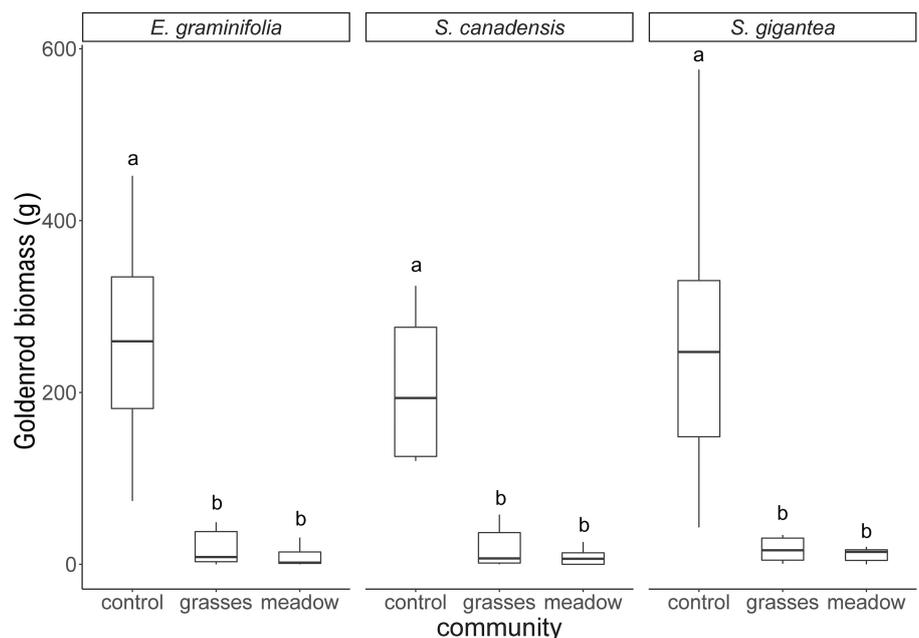


Figure 2. Goldenrod biomass production of different communities. Median value (thick line), upper and lower quartiles (box), and 1.5 IQR (whiskers) ranges are shown.

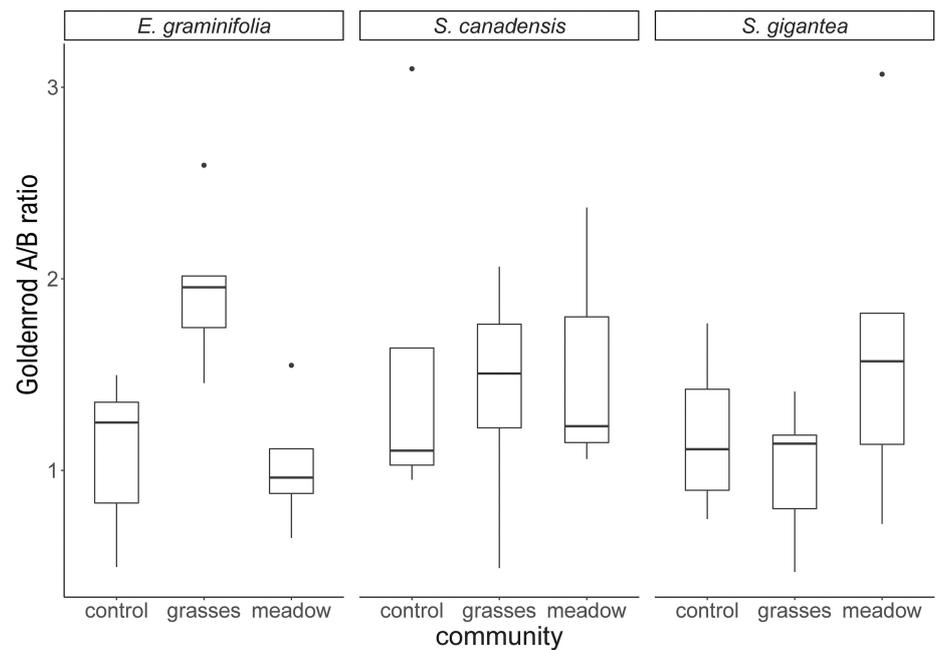


Figure 3. Ratio of above to below-ground biomass of goldenrods in different communities. Median value (thick line), upper and lower quartiles (box), 1.5 IQR (whiskers) ranges, and outliers (black dots) are shown.

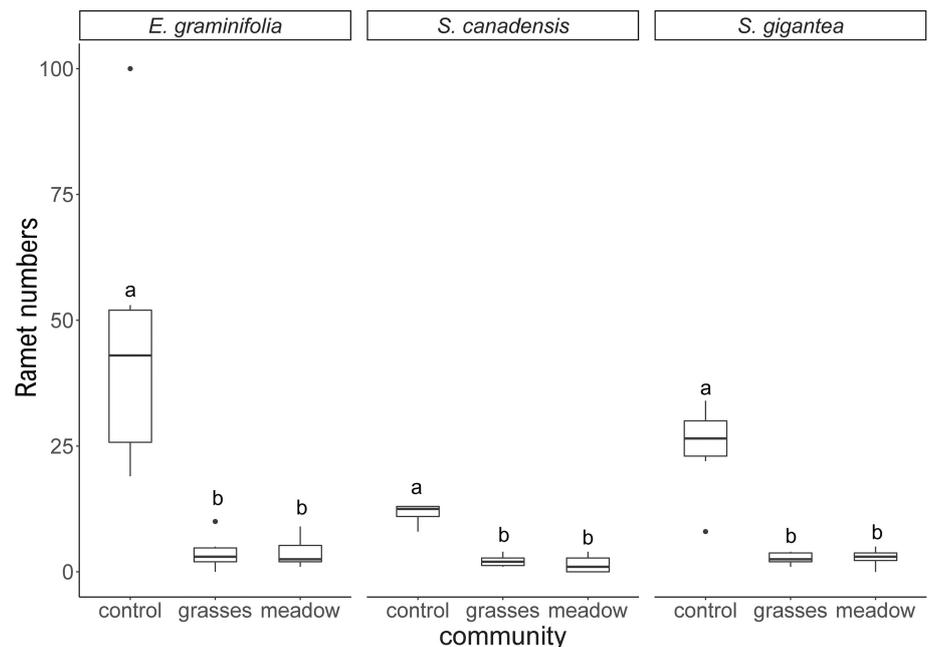


Figure 4. Number of ramets produced by goldenrods in different communities. Median value (thick line), upper and lower quartiles (box), 1.5 IQR (whiskers) ranges, and outliers (black dots) are shown.

Discussion

Our results did not support the hypothesis that a community consisting of fast-growing, highly productive grass species is more resistant to goldenrod invasion than a species-rich community consisting of species typical of semi-natural meadows. No significant differences were found between these two communities in goldenrod biomass production. Similarly, no differences

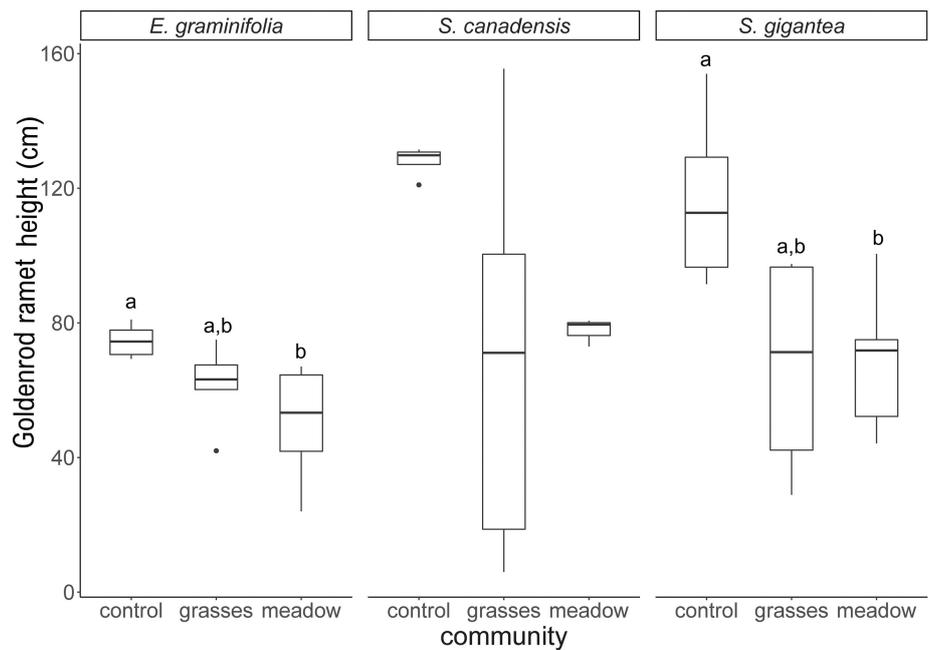


Figure 5. Height of ramets produced by goldenrods in different communities. Median value (thick line), upper and lower quartiles (box), 1.5 IQR (whiskers) ranges, and outliers (black dots) are shown.

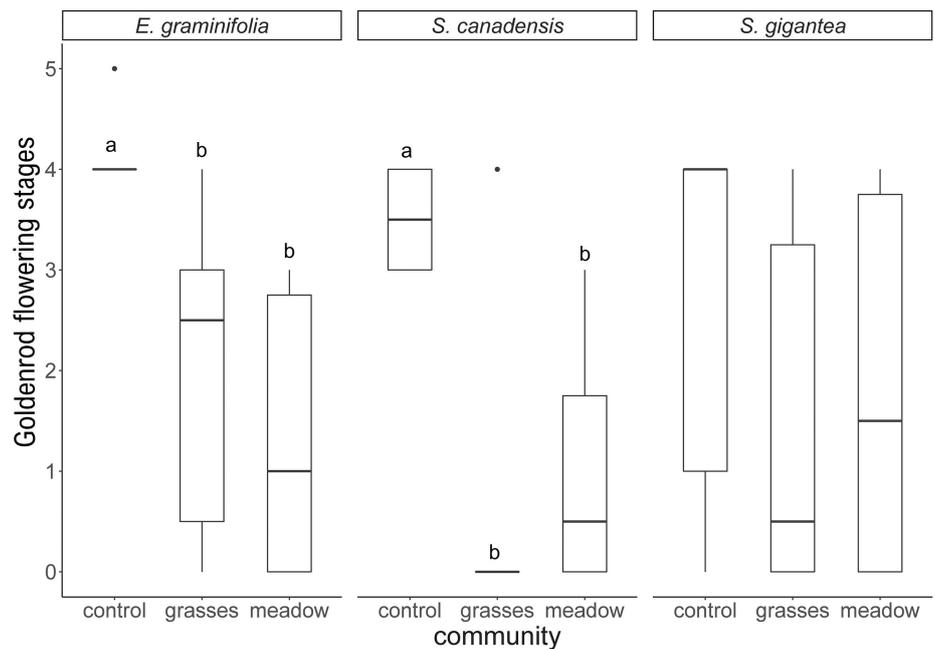


Figure 6. Flowering stages of goldenrods in different communities. Median value (thick line), upper and lower quartiles (box), 1.5 IQR (whiskers) ranges, and outliers (black dots) are shown.

were observed between *grasses* and *meadow* communities in goldenrod biomass distributed into above- and below-ground parts. Nonetheless, the resident plant communities could strongly limit the growth of goldenrods, exhibiting significant habitat resistance against invasion.

Surprisingly, the total biomass productivity of the *grasses* did not exceed the biomass production of the community resembling semi-natural meadow (*meadow*). However, our experiment was conducted under a low-frequency

mowing regime with a relatively late cutting term (August) and without any fertilizer application. Most probably, with typical maintenance of highly productive grasslands (Isselstein et al. 2005), which includes applying fertilizers, mowing the vegetation two to three times per year, and starting the mowing relatively early (May–June), the total productivity of the grass species mixture (*grasses*) would be higher than that of the *meadow* community. However, our study did not focus on a scenario of high biomass productivity, but rather on environment-friendly, low-intensity maintenance.

All the studied invasive goldenrods are known to be strongly competitive species, which reduce the biomass production of native weeds and grasses when grown in a mixture (Szymura and Szymura 2016; Szymura et al. 2018). The results of common garden experiments explained the patterns observed in the field. In particular, the number of vascular plant species is strongly reduced in dense stands of goldenrods (Fenesi et al. 2015; Hejda et al. 2009), and this reduction increases with the proportion of goldenrod in the vegetation (Moroń et al. 2019). The output of competitive interaction can be changed by the presence of disturbances such as mowing, which reduces above-ground biomass, particularly that of dominant species (Szépligeti et al. 2018). Typically, herbaceous plants are less resistant to mowing and grazing than grasses, which usually form a crown node near the ground, making it easier for them to endure frequent disturbances (Chapman 1996). In our experiment, when the goldenrods were introduced into a well-developed, relatively undisturbed vegetation under a low-mowing regime (once a year), the competitive ability of the invaders was reduced. The effect of competitive interactions between resident vegetation involves a wide spectrum of goldenrod growth and development: full biomass production, height, number of ramets, and flowering dynamics. Generally, in our experiment, the goldenrods growing in the control were heavier and taller, producing more ramets than those interacting with resident vegetation. The effect of resident vegetation on flowering dynamics was especially visible for *E. graminifolia* and *S. canadensis*. Successful sexual reproduction is ensured only when the plants reach the fourth and fifth stages of flowering, when the seeds appear. We dug up the plants in September, before the full development of the seeds; however, based on previous observations, if the plants are in the second or third stage of flowering in September, they do not develop mature seeds before the end of the growing season (Szymura and Szymura 2015b). Typically, goldenrod populations in a new range increase their size through vegetative regrowth. The seeds do not germinate in dense *Solidago* stands but instead contribute to long-term dispersal (Bartha et al. 2014; Fenesi et al. 2015). The results suggest that the species-rich community (*meadow*) and the highly productive grassland (*grasses*) in our experiment could not only affect the growth of goldenrods *in situ* but also effectively restrict the long-distance spread of *E. graminifolia* and *S. canadensis* under low-intensity maintenance.

Conclusions

The results show that resident grassland vegetation, under a low-mowing regime, significantly reduced the growth of goldenrods invasive to Europe. We did not find a difference between vegetation formed by fast-growing, highly productive grass species and species-rich communities typical of semi-natural meadows. The results suggest that semi-natural grasslands, which can be used for high-quality hay production as well as species-rich urban grasslands, are as resistant to invasion as highly productive commercial grasslands. In short, there is no trade-off between biodiversity maintenance and goldenrod invasion resistance for extensively used grasslands. Therefore, high-value semi-natural meadows, as well as species-rich urban grasslands with low-intensity maintenance, are reasonable alternatives to intensively maintained species-poor grasslands with regard to control of goldenrod invasion. Moreover, it can be assumed that a species-rich community will be more resistant to the potential invasion of another plant species because of high functional diversity.

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Authorship statements

PCDP: research conceptualization, sample design and methodology, investigation and data collection, data analysis and interpretation, funding provision, writing – original draft; THS: research conceptualization, investigation and data collection, data analysis and interpretation, writing – original draft; LP: investigation and data collection, data analysis and interpretation; TS: investigation and data collection, data analysis and interpretation; MS: research conceptualization, sample design and methodology, investigation and data collection, data analysis and interpretation, funding provision, writing – original draft.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Seed composition of semi-natural meadow (M).

Table S2. Seed composition of productive grasslands (G).

Figure S1. Total biomass production of species other than *Solidago* in different communities and the results of statistical tests.

Figure S2. The experimental site in August 2019.

Figure S3. The experimental site in 2020, before biomass collection.

Figure S4. *Euthamia graminifolia* in the artificially created grassland communities in September 2020, before biomass collection.

Figure S5. Biomass collection and root cleaning.

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