

**Goldenrods invasion in Central Europe
- drivers of invasion and environmental effect**

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PhD thesis

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**Inwazja nawłoci w Europie Środkowej
– czynniki inwazji i wpływ na środowisko**

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SUMMARY

Biological invasions are a worldwide phenomenon negatively altering biodiversity, ecosystem services, the local economy, as well as human health and wellbeing. Because of the substantial environmental impact of the biological invasions, the European Union Member States obligate to prevent introduction and control or eradicate the invasive species.

My PhD dissertation consists of three, thematically coherent, research articles, published in journals listed in the *Journal Citation Reports*. The articles were aimed at drivers of invasion and the environmental effect of alien *Solidago* species, which are the most widespread invasive plants in Central Europe, ordinating in North America.

In the first article (Perera et al. 2021a), I, with co-authors, evaluated the effectiveness of proxies of the PAB framework (propagule pressure (P), abiotic characteristics of the environment (A), and biotic characteristics of both the invader and recipient vegetation (B)) to explain the spatial pattern of *Solidago gigantea* Aiton and *S. canadensis* L. s.l. invasion in regional scale. Study area was Polish part of Carpathian Mountains and their foreground, the analyses were conducted using Species Distribution Models approach. Distributions of both species were limited climatically; however, the *S. canadensis* distribution pattern was mostly correlated with proxies of human pressure, whereas *S. gigantea* distribution was connected with environmental characteristics. Proxies of PAB are helpful in the choice of explanatory variables as well as the ecological interpretation of species distribution models. The results emphasize that human activity can cause variation in the invasion pattern of ecologically similar species (Perera et al. 2021a).

Second part of the research (Perera et al. 2021b) was focused on habitat resistance for plant species invasion. I, with co-authors, verify if community consisting fast-growing, high-biomass-producing grass species, which is typical of intensively maintained grasslands, is more resistant to goldenrods invasion than high-biodiversity, semi-natural grassland. For this purpose, three types of habitats were established: semi-natural meadow, low-biodiversity, high productivity grass community and open soil (control). Then, in next year, three seedlings of alien goldenrods (*S. canadensis*, *S. gigantea*, and *Euthamia graminifolia* (L.) Nutt.) were introduced into the communities, and the experiment was run throughout two years. Results revealed that both created communities strongly reduced ramet numbers and height, as well as goldenrod biomass compared to the control. However, no differences were found between studied communities types, except that *S. canadensis* and *E. graminifolia* did not produce seeds in the community resembling species-rich meadow. It

can be assumed that semi-natural, high-biodiversity meadows are reasonable alternatives to species-poor commercial grasslands to control goldenrod invasion in open landscape, as well as in city greenery (Perera et al. 2021b).

The third article consisting the dissertation (Perera et al. 2022) describe the response of soil invertebrates assemblages on different methods of *Solidago* invaded land restoration. The field experiment, where various seed sources (sowing mixtures: grasses, grasses with legumes, seeds collected from the seminatural meadow, and applying of fresh hay), and the different frequency of mowing (1, 2 and 3 times per year), was established. Next year after experiment establishment, soil samples were taken in four terms, and mesofauna was extracted using the Tullgren funnels method. Results revealed that high mowing intensity negatively influenced soil invertebrates. Mowing twice a season decreased the abundance of mesofauna taxa occurrence, but not their diversity. Considering the seed mixture effects, the plots where grasses with legumes were sown, were the most suitable for the most soil mesofauna taxa. Mowing once per year and sowing grasses with legumes is the most convenient for the soil mesofauna abundance among studied restoration strategies (Perera et al. 2022).

The PhD dissertation answered the raised hypotheses and questions, particularly showing the possibility of applying the PAB framework drivers to explain the pattern of invasive *Solidago* distribution; underlying the role of habitat resistance in control of goldenrod spreading; defining the management methods friendly for soil invertebrates in process of land reclamation.

Perera PCD, Szymura TH, Zając A, Chmolewska D, Szymura M. 2021a. Drivers of *Solidago* species invasion in Central Europe - Case study in the landscape of the Carpathian Mountains and their foreground. *Ecology and Evolution* 11(18), 12429-12444. DOI: 10.1002/ece3.7989

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STRESZCZENIE

Inwazje biologiczne są zjawiskiem ogólnoswiatowym, wpływającym negatywnie na bioróżnorodność, usługi ekosystemowe, lokalną ekonomię oraz zdrowie i samopoczucie ludzi. Ze względu na silny wpływ środowiskowy inwazji biologicznych, państwa członkowskie Unii Europejskiej są zobligowane do zapobiegania introdukcji oraz kontroli lub zwalczania gatunków inwazyjnych.

Moja praca doktorska składa się z trzech, jednolitych tematycznie artykułów naukowych, opublikowanych w czasopismach wymienionych w *Journal Citation Reports*. Artykuły dotyczą czynników warunkujących inwazję oraz wpływ na środowisko obcych gatunków *Solidago*, które są najbardziej rozpowszechnionymi roślinami inwazyjnymi w Europie Środkowej, pochodzącymi z Ameryki Północnej.

W pierwszym artykule (Perera i in. 2021a), wraz ze współautorami oceniłem efektywność grup czynników składających się na koncepcję PAB (presji diaspor (P), czynników abiotycznych środowiska (A) oraz charakterystyki elementów biotycznych, zarówno gatunku inwazyjnego, jak i roślinności miejscowej (B)), w wyjaśnieniu struktury przestrzennej inwazji nawłoci późnej *Solidago gigantea* Aiton i nawłoci kanadyjskiej *S. canadensis* L. s.l. w skali regionalnej. Jako miejsce analiz wybrałem polską część Karpat i ich przedgórze, a jako metodę analiz zastosowałem podejście oparte na modelach rozmieszczenia gatunków. Rozmieszczenie obu gatunków jest ograniczone czynnikami klimatycznymi, lecz zasięg występowania *S. canadensis* jest silniej powiązany z czynnikami wynikającymi z presji człowieka, podczas gdy rozmieszczenie *S. gigantea*, z warunkami siedliskowymi. Wyniki podkreślają, że działalność człowieka może powodować zmienność we wzorcu inwazji podobnych pod względem ekologicznym gatunków (Perera i in. 2021a).

Druga część badań (Perera i in. 2021b) była związana z analizą roli oporu środowiska w inwazji gatunków roślin inwazyjnych. Wraz z współautorami sprawdziliśmy czy zbiorowisko złożone z szybko rosnących, produkujących dużą biomasę gatunków traw, które są typowe dla intensywnie użytkowanych łąk jest bardziej odporne na inwazję nawłoci niż łąka półnatutalna o dużej bioróżnorodności. W tym celu zostały założone trzy typy siedlisk: wielogatunkowa łąka półnaturalna, ubogie gatunkowo, wysokoprodukcyjne zbiorowisko złożone z traw oraz brak zastosowania mieszanki nasion jako kontrola. Następnie, w kolejnym roku, trzy sadzonki obcych gatunków nawłoci (*S. canadensis*, *S. gigantea*, and *Euthamia graminifolia* (L.) Nutt.) zostały posadzone w utworzonych zbiorowiskach i eksperyment był prowadzony przez dwa lata. Wyniki wykazały, że obydwa

utworzone zbiorowiska silnie ograniczyły liczbę i wysokość ramet wytworzonych przez nawłocie, a także ich biomasę w porównaniu z kontrolą. Jednakże nie wykazano różnic pomiędzy dwoma analizowanymi typami zbiorowisk, z wyjątkiem braku wytworzenia nasion przez *S. canadensis* i *E. graminifolia* w zbiorowisku przypominającym bogatą gatunkowo łąkę. W podsumowaniu można stwierdzić, że półnaturalne, bioróżnorodne łąki są odpowiednią alternatywą do ubogich gatunkowo, komercyjnych zbiorowisk trawistych w aspekcie kontroli inwazji w krajobrazie otwartym, a także w zieleni miejskiej (Perera i in. 2021b).

Trzeci artykuł wchodzący w skład rozprawy (Perera et al. 2022) opisuje reakcję zbiorowisk bezkręgowców glebowych na różne metody rekultywacji terenów dotkniętych inwazją *Solidago*. W tym celu został założony eksperyment polowy, w którym zastosowano różne źródła nasion (siew mieszanek: traw, traw z bobowatymi, nasion zebranych z łąki półnaturalnej, a także rozłożenie świeżego pokosu) oraz zróżnicowaną częstość koszenia (1, 2 lub 3 razy w roku). W następnym roku po założeniu eksperymentu, pobrano próby gleby w czterech terminach i dokonano ekstrakcji mezofauny glebowej za pomocą aparatu Tullgrena. Wyniki wskazują, że duża intensywność koszenia negatywnie wpływa na bezkręgowce glebowe. Koszenie dwukrotne w ciągu sezonu wpływa na zmniejszenie liczności występowania mezofauny, lecz nie na zróżnicowanie taksonów. Oceniając efekt zastosowania źródła nasion, poletka na których wysiano mieszankę traw z bobowatymi okazały się najbardziej odpowiednie dla większości taksonów mezofauny glebowej. Koszenie raz w roku i wysiew mieszanki nasion traw z roślinami bobowatymi jest najbardziej odpowiednią strategią rekultywacji pod względem liczności występowania mezofauny glebowej (Perera i in. 2022).

Rozprawa doktorska odpowiada na postawione hipotezy i pytania, szczególnie pokazując możliwość zastosowania koncepcji czynników PAB w wyjaśnieniu wzorca występowania inwazyjnych gatunków z rodzaju *Solidago*; podkreślając rolę oporu środowiska w kontroli rozprzestrzeniania się nawłoci; określając metody użytkowania przyjazne dla bezkręgowców glebowych w procesie odtwarzania siedlisk.

Perera PCD, Szymura TH, Zając A, Chmolewska D, Szymura M. 2021a. Drivers of *Solidago* species invasion in Central Europe - Case study in the landscape of the Carpathian Mountains and their foreground. *Ecology and Evolution* 11(18), 12429-12444. DOI: 10.1002/ece3.7989.

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3. Articles / Artykuły

3.1. Drivers of *Solidago* species invasion in Central Europe—Case study in the landscape of the Carpathian Mountains and their foreground

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Drivers of *Solidago* species invasion in Central Europe—Case study in the landscape of the Carpathian Mountains and their foreground

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Abstract

Aim: The invasion process is a complex, context-dependent phenomenon; nevertheless, it can be described using the PAB framework. This framework encompasses the joint effect of propagule pressure (P), abiotic characteristics of the environment (A), and biotic characteristics of both the invader and recipient vegetation (B). We analyzed the effectiveness of proxies of PAB factors to explain the spatial pattern of *Solidago canadensis* and *S. gigantea* invasion using invasive species distribution models.

Location: Carpathian Mountains and their foreground, Central Europe.

Methods: The data on species presence or absence were from an atlas of neophyte distribution based on a 2 × 2 km grid, covering approximately 31,200 km² (7,752 grid cells). Proxies of PAB factors, along with data on historical distribution of invaders, were used as explanatory variables in Boosted Regression Trees models to explain the distribution of invasive *Solidago*. The areas with potentially lower sampling effort were excluded from analysis based on a target species approach.

Results: Proxies of the PAB factors helped to explain the distribution of both *S. canadensis* and *S. gigantea*. Distributions of both species were limited climatically because a mountain climate is not conducive to their growth; however, the *S. canadensis* distribution pattern was correlated with proxies of human pressure, whereas *S. gigantea* distribution was connected with environmental characteristics. The varied responses of species with regard to distance from their historical distribution sites indicated differences in their invasion drivers.

Main conclusions: Proxies of PAB are helpful in the choice of explanatory variables as well as the ecological interpretation of species distribution models. The results underline that human activity can cause variation in the invasion of ecologically similar species.

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KEYWORDS

alien plants, biological invasion, Boosted Regression Trees, drivers of invasion, PAB framework, *Solidago canadensis*, *Solidago gigantea*

1 | INTRODUCTION

Biodiversity and the function of ecosystems are threatened by global change drivers such as changes in land use and climate, as well as biological invasions (Linders et al., 2019; Sala et al., 2000). Invasive species alter a wide range of ecosystem services, including provisioning, regulation, and cultural and supporting functions, and they are particularly hazardous for biodiversity maintenance, human welfare, and the economy (Charles & Dukes, 2007; Chytrý et al., 2009; Hejda et al., 2009; Pejchar & Mooney, 2009; Vilà & Ibáñez, 2011). Globalization (e.g., international trade and travel) and climate change (e.g., global warming, droughts, and floods) can interact, which can in turn increase the level of biological invasions (Catford et al., 2009; Le Maitre et al., 2004; Pino et al., 2005; Seebens et al., 2015). As the total number of invasive species increases, some sites may host several alien species (Kuebbing & Nuñez, 2015).

The invasion process is a complex phenomenon, driven by numerous interacting processes, and the effect of this interaction is highly contingent on the context (Chamberlain et al., 2014; Frost et al., 2019). Consequently, drivers of plant invasion can vary depending on the specific region and habitat (Taylor et al., 2016). Nevertheless, invasions have a common pattern, which can be summarized as the joint effect of propagule pressure, abiotic characteristics of the environment, and biotic characteristics of both the invader and recipient vegetation (Catford et al., 2009), the so-called PAB framework. Propagule pressure (P) includes dispersal and geographical constraints, while abiotic characteristics (A) comprise environmental and habitat constraints and biotic characteristics (B) describe the internal dynamics of the vegetation and community interactions (Catford et al., 2009). All these factors operate at different spatial scales (Czarnecka-Wiera et al., 2020; Milbau et al., 2009) and are influenced by human activity (Essl et al., 2011). In practice, different indices can be applied as proxies of propagule pressure and abiotic and biotic conditions in modeling plant invasion process (Bazzichetto et al., 2018; Beaury et al., 2020; Chytrý et al., 2008; Szymura et al., 2018).

Related to the propagule pressure, the biological invasion correlates with many anthropogenic factors, such as density of the communication network, percentage of urban areas, gardening, and the fragmentation of natural habitats. Such factors can serve as a proxy of propagule pressure (Foxcroft et al., 2011; Polnac et al., 2012; Štajerová et al., 2017; Szymura et al., 2018; Vilà & Ibáñez, 2011). In addition, economic and demographic variables reflect the intensity of human activities; therefore, socioeconomic factors such as gross domestic production and human population density can be important in predicting the invasion level (Essl et al., 2011; Hulme, 2017; Pino et al., 2005; Pyšek & Richardson, 2010) because they correlate with trade intensity and communication network density

(Hulme, 2009). Among the abiotic interactions with the greatest impact on a large spatial scale (continental, regional), climate is considered the most critical in limiting the geographic distribution of species (Hulme, 2017; Thuiller et al., 2007). In terms of resource availability, invasive species usually prefer productive habitats where they are able to achieve competitive dominance (Czarnecka-Wiera et al., 2020; Peltzer et al., 2016; Perkins et al., 2011). In addition, environments with high variability in resource availability, resulting from periodic external supply (e.g., surface runoff) or destruction of local vegetation that previously used the resources (e.g., human disturbances, abandonment of agricultural crops), are more susceptible to invasions than habitats with stable availability of resources (Davis et al., 2000; Kulmatiski et al., 2006; Rejmánek, 1989). Given the biotic characteristics of the invader and recipient communities, the limiting similarity hypothesis proposes that the invasion by alien species will be successful if the native species of the recipient community differ from the invader in terms of functional traits and resource requirements (MacArthur & Levins, 1967), which decreases competition for resources (Funk et al., 2008). Thus, the functional traits of the invader should not overlap with traits of native plants occurring in the invaded community, which will allow it to occupy an empty niche and successfully invade the community (Funk et al., 2008; Hejda & de Bello, 2013). Because some sites can be invaded by several species simultaneously, determining the interaction between invaders is critical for understanding their distribution (Kuebbing & Nuñez, 2015). For example, the local species assemblage can be driven by a priority effect, and the effect is particularly strong when interacting species have similar use of resources (Vannette & Fukami, 2014). In practice, the abundance and composition of invasive species are also related to landscape characteristics (e.g., habitat fragmentation, patch size, shape, and connections), habitat type, land use, and the composition of the surrounding landscape because these factors correlate with propagule pressure and habitat quality and availability (Basnou et al., 2015; Chytrý et al., 2009; González-Moreno et al., 2013; Štajerová et al., 2017; Szymura et al., 2016).

Because of the complexity of biological invasion, better understanding of the underlying factors and their management is challenging. As tools for obtaining reliable and repeatable information for biological analyses as well as nature conservation and management of the invaders, invasive species distribution models (iSDMs) are considered useful (Lozano et al., 2020; Zurell et al., 2020). Modeling species' environmental requirements and mapping their distributions through space and time help to identify the main introduction pathways and secondary spread and the areas and land use types that are more prone to invasion. These various threads could be woven into a strategy of prevention and elimination of invasive plant species on a regional scale (Lozano et al., 2020). Despite their deficiencies (e.g., problematic species-environment equilibrium; Gallien

et al., 2012; Hattab et al., 2017), iSDMs are still useful in the face of accelerating global changes and data deficiencies, as well as limited research funding (Yates et al., 2018). The PAB approach, despite its obvious advantages for selection of explanatory variables and model results interpretation, has rarely been used within an invasive species distribution modeling framework (but see Bazzichetto et al., 2018; Czarniecka-Wiera et al., 2020; Lozano et al., 2020).

Goldenrod species from North America represent successful invaders in Europe, Asia, Australia, and New Zealand (Gusev, 2015; Szymura & Szymura, 2013; Ye et al., 2019; Zhang & Wan, 2017). In Central Europe, two invasive *Solidago* species occur, *S. gigantea* Aiton (giant goldenrod) and *S. canadensis* L. (Canadian goldenrod). Due to their high environmental impact, wide range of distribution, and locally high abundance, invasive *Solidago* species have to be controlled in Europe (Fenesi et al., 2015; Sheppard et al., 2006; Skórka et al., 2010). They have been proposed for addition to the list of hazardous alien species that threaten ecosystems, habitats, or other species in European Union countries (CABI, 2018; EPPO, 2020; Tokarska-Guzik et al., 2015). Unfortunately, the eradication of widely established invasive plant species, such as *Solidago*, is not feasible. The management strategies need to integrate different options that account for the distribution and abundance of the invader, its environmental niche, and the areas that are likely to experience high impacts (Nagy et al., 2020; Shiferaw et al., 2019; Woodford et al., 2016). Management needs to consider intrinsic factors related to the biology and ecology of the invader, as well as extrinsic environmental factors, such as dispersal vectors and invasion pathways (Shiferaw et al., 2019).

Solidago canadensis and *S. gigantea* differ with regard to ecological niche in their native range (Johnson, 1995; Werner et al., 1980) and the time of introduction into Europe (Tokarska-Guzik, 2005). However, previous studies suggest that these two species do not differ regarding their habitat preferences in Central Europe, and observed differences in their spatial distribution patterns emerge from historical contingency and limitation in long-range dispersal (Szymura & Szymura, 2016). The two *Solidago* species occupy different areas and rarely form mixed-species stands (Szymura & Szymura, 2016). In this study, we aimed to find the main drivers of *Solidago* species' invasion at a regional scale, using a species distribution model and applying the PAB framework for selection of adequate explanatory variables and for ecological interpretation of the models. The distribution models can be used for mapping of invasion probability at a regional level to facilitate invasion control at a macroecological scale.

2 | MATERIALS AND METHODS

2.1 | Studied species

Goldenrod species are hemicryptophytes (shoots are annual and newly sprout each spring) with rhizomes; they are insect pollinated and self-incompatible, with inflorescences forming at the top of each shoot which can produce up to 10,000–20,000 wind-dispersed seeds per one ramet (Bielecka et al., 2017; Guzikowa & Maycock, 1986;

Moran et al., 2017; Schmid et al., 1988). The seeds of *S. canadensis* and *S. gigantea* have a high germination percentage (Weber, 2000; Weber & Jakobs, 2005), but in dense, well-established *Solidago* stands, seed germination and seedling emergence are exceptional. The clone size increases via horizontal rhizomes, and the death of an established genet is a rare event (Meyer & Schmid, 1999a, 1999b).

The native habitats of *S. canadensis* are tall-grass prairies, infrequently grazed pastures, abandoned farmlands, roadsides, and waste areas in North America (Johnson, 1995; Werner et al., 1980). *Solidago gigantea* prefers moist habitats, such as woods, stream edges, and woodland borders (Johnson, 1995). In Europe, *S. gigantea* and *S. canadensis* occupy similar habitats and prefer fallow lands and ruderal habitats on moist to mesic sites, such as abandoned farmlands, scrub, roadsides, forest edges, grasslands, wetlands, and riversides (Szymura & Szymura, 2013, 2016). Invasive goldenrods are highly competitive for nutrients, water, and space, and they release allelopathic compounds that inhibit growth of other plants (Gusev, 2015; Ledger et al., 2015; Werner et al., 1980; Zhang & Wan, 2017). Due to prolific vegetative propagation, they form dense stands and decrease the biodiversity of plants (Chmura et al., 2016; Ye et al., 2019; Zhang & Wan, 2017); arthropods (de Groot et al., 2007), including pollinators (e.g., wild bees, hoverflies, and butterflies) (Lenda et al., 2020; Moroń et al., 2009, 2021) and ants (Kajzer-Bonk et al., 2016; Lenda et al., 2013); and birds (Skórka et al., 2010).

Solidago canadensis was the first alien *Solidago* species recorded in Europe, in 1648, while *S. gigantea* was first recorded in 1758. The species were found in the territory of Poland about 100 years later, *S. gigantea* in 1853 and *S. canadensis* in 1872 (Tokarska-Guzik, 2005). After *S. canadensis* and *S. gigantea* were introduced into botanical gardens, they were distributed among gardeners. The plants were attractive and easy to grow as ornamental plants, and they were useful for beekeepers (Guzikowa & Maycock, 1986; Roháčová & Drozd, 2009; Weber, 1997; Zihare & Blumberga, 2017). Recently, *Solidago* species have become widely distributed throughout Poland. According to the stages of invasion (Blackburn et al., 2011), *S. canadensis* and *S. gigantea* are now fully invasive species, with individuals dispersing, surviving, and reproducing at multiple sites in a wide variation of habitats over an extensive spatial area (E category).

2.2 | Study area and species distribution data

The study area comprises approximately 31,200 km² in the southeast part of Poland, which extends from latitude 50.2° to 49°N and longitude from 19° to 23°E (Figure 1). This area is diversified due to environmental conditions mostly shaped by the altitude ranging from 160 to 2,503 m a.s.l. Additional factors underlying diversity are correlated with climate, land use systems, land relief, and human population density. In the northern part, the lowland areas are used for agriculture and the foothills are dominated by forests, and the southern part has high mountains with alpine vegetation. In addition to the north–south altitudinal gradient, there is also a climatic gradient of continentality, with higher temperature range in the eastern part of the study

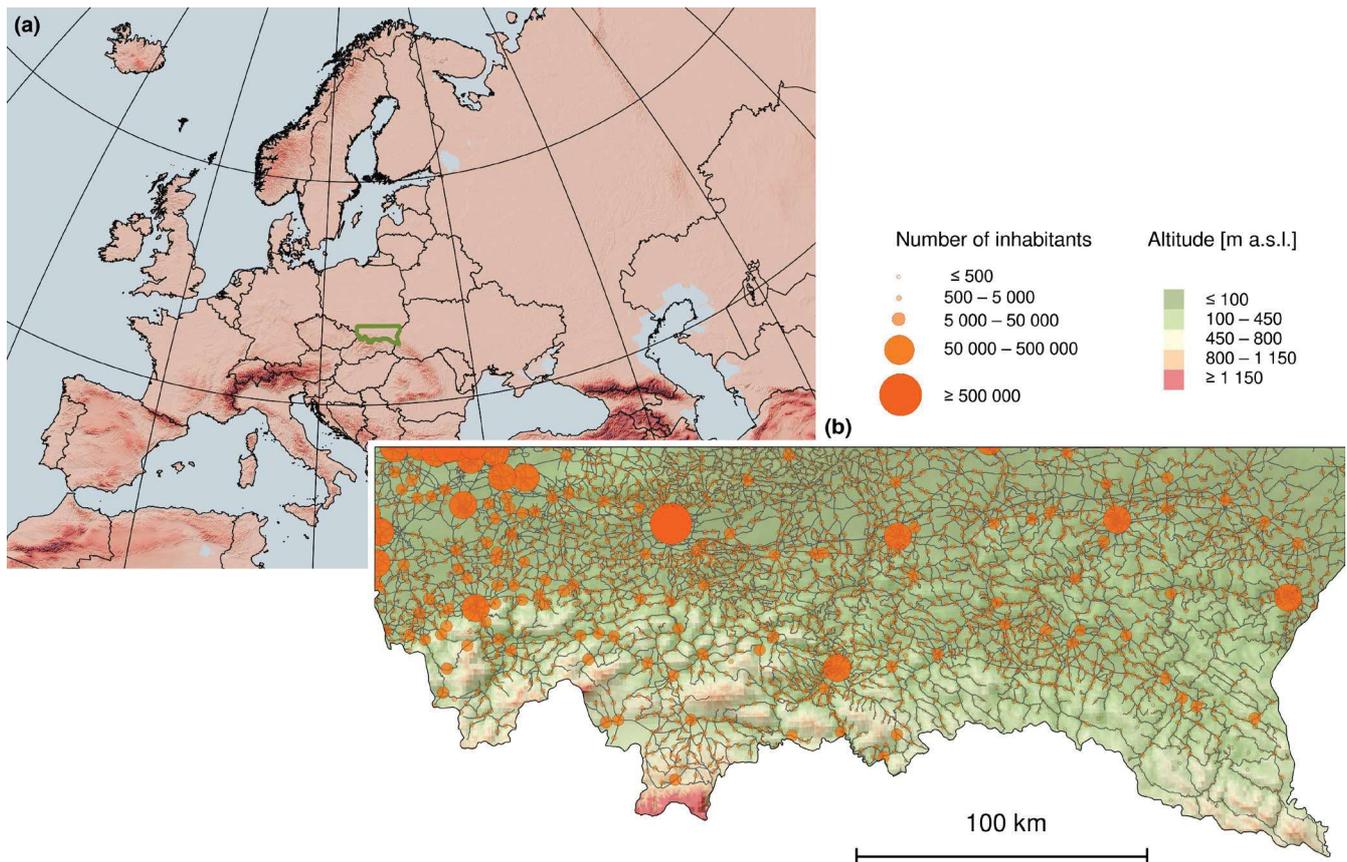


FIGURE 1 The study region location (green) on a background of land relief (a), and distribution of communication network and settlements on the background of altitude within the study region (b)

region (Szabo-Takacs et al., 2015) which, in the studied region, correlated strongly with decreasing eastward precipitation (Appendix S4, Table S3). The study area includes a densely populated industrial landscape (Silesia), urban agglomerations (largest city Kraków), and moderately populated agricultural areas, as well as sparsely populated areas in the mountains. The detailed characteristics of the study area (climate, topography, land use structure, and human population density) were previously described by Szymura et al. (2018).

The data on distribution of the studied *Solidago* species were obtained from the atlas Distribution of Kenophytes in the Polish Carpathians and their Foreland (Zajac & Zajac, 2015), which shows maps of species presence or absence in a 2×2 km grid in the Polish part of the Carpathian Mountains and their foreland, Central Europe. The fieldwork designed for the purpose of compiling the atlas was based on a survey of flora in particular regions (e.g., mountain ranges, particular towns, and surrounding areas) and exploration focused exclusively on neophytes in given regions. These observations were supplemented with additional data from phytosociological relevés, herbarium records, and published materials. The fieldwork was carried out by several dozen professional botanists as well as graduate students, focusing on a predefined 2×2 km grid for sampling (Zajac A., personal information). This work represents a “survey” type of data, according to Elith et al. (2020) nomenclature. Such data, with true absence records, enable species distribution models to be less

biased and to perform better, compared with presence-only records, the “collection” data type (Barbet-Massin et al., 2012; Elith et al., 2020). This distinction is of particular importance for examination of wide-ranging and tolerant species (Brotons et al., 2004). To reduce the possible effect of lower sampling effort in some regions (Bailey et al., 2017; Yang et al., 2013), the potentially undersampled squares were excluded from modeling. For this purpose, we used a “target group approach” (Chapman et al., 2019; Phillips et al., 2009) and a previously established model which explains neophyte richness (the “target group” in this case) as a function of environmental and socioeconomic variables in the studied region (Szymura et al., 2018). We assumed that the squares with the highest negative model residuals (i.e., squares where recorded neophyte richness was much lower than predicted by the model) indicated potentially undersampled regions. After preliminary testing, we decided to exclude from modeling 25% of squares (1950 squares) with the highest negative residual values and simultaneously without any invasive *Solidago* records (for details of this calculation see Appendix S1).

2.3 | Explanatory variables and statistical analysis

We prepared a data set of environmental variables that can be considered as proxies of propagule pressure, abiotic environment,

and biotic characteristics, based on the PAB framework (Catford et al., 2009; Table 1). These proxies were chosen based on the results of previous study on *Solidago* (Szymura et al., 2016) and the most influential drivers of neophytes in the region (Szymura et al., 2018).

The anthropogenic variables were derived from CORINE 2012 database (*urban*), the Central Statistical Office of Poland (*income*), and Statistics Poland (*density*). The income (as an estimator of wealth) is directly correlated with trade intensity and thus reflects the potential to alien species propagule transportation by trade or accidentally (Hulme, 2009; Pyšek et al., 2010). The length of communication routes (*communication*) was obtained from the Polish Geographical Objects Database (BDOO). The other data were calculated from the CORINE 2012 database (*cropland*, *forest*, *SHDI*). A Digital Elevation Model for Europe (EU-DEM) was used to calculate the topographic metrics (*TPI* and *TWI*). Maps prepared by Ballabio et al. (2019) using data from Land Use and Cover Area frame Survey (LUCAS) were used to calculate soil characteristics (content of *N*, *P*, *K*, and soil *pH*). The climate data (*precipitation*, *temperature*) were derived from a climatic model developed by Hijmans et al. (2005). Before the analyses, the Pearson correlations between each pair of explanatory variables were checked. If the coefficient exceeded 0.7, one of the correlated

variables was eliminated to avoid collinearity (Dormann et al., 2013). For details, see Appendix S3 Table S2. The average values of the variables were calculated for each 2 × 2 km grid cell acquired from Zajac and Zajac (2015), and the landscape diversity (*SHDI*) was expressed by Shannon's diversity index.

Maps showing the historical distribution of goldenrods before their spreading phase (Tokarska-Guzik, 2005) were used to calculate the distances from a focal 2 × 2 km square to the nearest site of goldenrod introduction in the 1950s (*distance*, for details see Appendix S3, Map S2). To check whether the presence of one *Solidago* species in a 2 × 2 km square explained the presence of the second species (possible priority effect), the data on distribution of the potential competitor were used as an explanatory variable (*competitor*). All the calculations and map handlings were done using QGIS, SAGA GIS, and FRAGSTAT software.

Goldenrod species spatial pattern of distribution was modeled using a boosted regression trees (BRT) technique (De'Ath, 2007; De'Ath & Fabricius, 2000) employing packages *gbm* (Greenwell et al., 2020), *dismo* (Hijmans et al., 2020), and *Biomod2* (Thuiller et al., 2020) in the R environment. After initial examinations, the BRT settings were applied: tree complexity, 5; bag fraction, 0.5;

TABLE 1 Explanatory variables selected for modeling invasive *Solidago* distribution. Variables in bold type were used in the final model, and the remaining variables were excluded from further analysis due to collinearity

Explanatory variable	Abbreviation	Probable sphere of PAB framework
Communication routes (railways and roads) density	<i>communication</i>	P
Shannon's diversity index of landscape	<i>SHDI</i>	B
<i>Urban area percentage</i>	<i>urban</i>	P
Cropland area percentage	<i>cropland</i>	B
<i>Forest area percentage</i>	<i>forest</i>	B
Human population density	<i>density</i>	P
Income per capita	<i>income</i>	P
<i>Topographic roughness index</i>	<i>TRI</i>	A
Topographic position index	<i>TPI</i>	A
Average annual temperature	<i>temperature</i>	A
Topographic wetness index	<i>TWI</i>	A
Temperature seasonality	<i>Ts</i>	A
<i>Annual sum of precipitation</i>	<i>precipitation</i>	A
CaCO₃ content	<i>Ca</i>	A
K content	<i>K</i>	A
<i>N content</i>	<i>N</i>	A
<i>P content</i>	<i>P</i>	A
pH in H₂O	<i>pH</i>	A
Distance to nearest introduction site <i>S. canadensis</i>	<i>distance_S.can</i>	P
Distance to nearest introduction site <i>S. gigantea</i>	<i>distance_S.gig</i>	P
Presence of competing <i>Solidago</i> species^a	<i>competitor</i>	B

^aPresence of one invasive *Solidago* species in the same 2 × 2 km square was considered as an explanatory variable for the other; that is, in model for *S. canadensis*, its presence explained the presence of *S. gigantea* and vice versa.

learning rate, 0.001; and cross-validation, 10 fold. The optimal number of trees was 3,900 for *S. canadensis* and 3,850 for *S. gigantea*. Models for each species were constructed using all explanatory variables and then simplified to obtain the parsimonious model. The BRT modeling and simplification of models were done based on Elith et al. (2008) suggestions. Then, the modeling, using the tuned model parameters and a minimal set of explanatory variables, was performed in Biomod2 package with spatially blocked cross-validation (Valavi et al., 2019). We applied 5-fold cross-validation, using spatial blocks constructed based on 10 × 10 km squares for *S. canadensis* and 20 × 20 km squares for *S. gigantea*. The sizes of the squares were chosen based on spatial autocorrelation of raw distribution data (Roberts et al., 2017), and the blocks were constructed using BlockCV package within the R environment (Valavi et al., 2019). For details of this approach, see the Appendix S1. The performance of the models was evaluated using area under the receiver operating characteristic curve (AUC). Following qualitative descriptions, an AUC value in the range of 0.7–0.8 can be considered a good prediction, 0.8–0.9 as a very good prediction, and above 0.9 as an excellent prediction (Šimundić, 2009). The ecological interpretation of the model relies on the drawing response curves for each explanatory variable (Elith et al., 2005) and calculation of relative influences of explanatory variables. The relative influence is calculated after model training (calibration) and prediction making. Then, values of one of the variables are randomized, and a new prediction is made. The correlation between this new prediction and the standard prediction is calculated and is considered as an estimation of the variable importance in the model: A high correlation score between the two predictions shows that the randomized variable has little influence on making a prediction and is not considered important for the model in its prediction. In contrast, a low correlation means a significant difference in the prediction making, showing that the variable is important for the model. The variable importance is calculated as 1-correlation, repeated for each variable independently and for each spatially blocked cross-validation run (Thuiller et al., 2012). Eventually, maps of projected *S. canadensis* and *S. gigantea* probability of occurrence were drawn (Figure 5). The probability of species presence in a given 2 × 2 km square was modeled for particular spatially blocked cross-validation runs and averaged, employing the “projection” function in the Biomod2 package. Additionally, maps of squares projected to be suitable for invaders and not colonized yet were produced for conservation purposes (Appendix S7, Map S4).

3 | RESULTS

Goldenrod species were observed in 60.5% of the squares (in 3,544 out of 5,850 finally examined squares). *Solidago gigantea* was the most frequent species (53.1%, 3,107 squares) followed by *S. canadensis* (21.4%, 1,255 squares).

Solidago gigantea localities were widespread throughout almost the entire area, aside from the higher altitudes in the southern part of the study region. The *S. canadensis* was concentrated in the

western part of the study area, while being sporadically dispersed in the eastern part and also avoiding the southern fragment with higher altitudes (Figure 2).

The average value of AUC was 0.836 for *S. canadensis* and 0.786 for *S. gigantea*. Despite some differences in model evaluations of particular spatially blocked folds, the models for *S. canadensis* generally performed better than those for *S. gigantea* (Figure 3a). The parsimonious (simplified) model for *S. canadensis* relied on a higher number of explanatory variables than those for *S. gigantea*.

Both species reacted to climatic conditions, expressed by the annual average temperature (*temperature*) and temperature seasonality (*Ts*), as well as the distance from the initial introduction sites (*distance*) (Figure 3b,c). Moreover, the spatial pattern of distribution of *S. canadensis* was also explained by anthropogenic factors, such as human population density (*density*) as well as the percentage of agricultural lands (*cropland*). The full list of all variables included in the final models, along with their relative influence, is shown in Figure 3b,c.

The modeled response of species on particular variables is shown in Figure 4. The distribution of both species was climatically limited, with the species being unlikely to occur in regions with an average annual temperature below 5.5°C. The probability of *S. canadensis* occurrence increased with human population density (*density*) (Figure 4), as well as distance from its introduction site (*distance_S. can*), with squares placed 100 km distant from the initial sites of introduction having the highest probability. The distribution of *S. gigantea* was also correlated with the pattern of its initial introduction (*distance_S. gig*), and the probability of its occurrence generally decreased with the distance (Figure 4), reaching the lowest value at about 40 km and fluctuating above it.

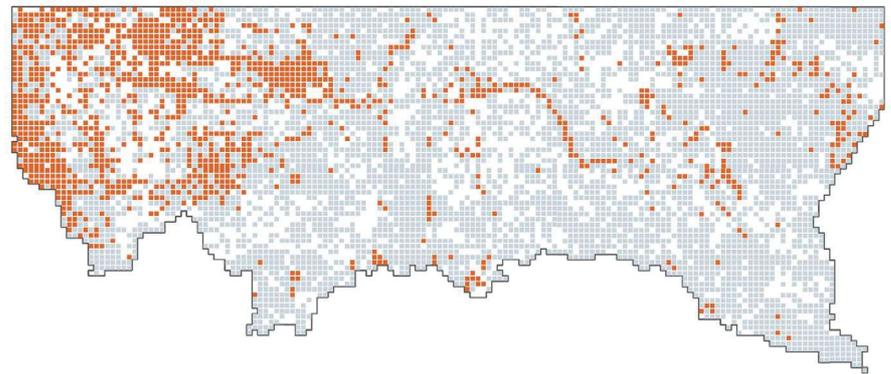
The results of the projections are presented in Figure 5. The average cutoff values, calculated based on the AUC values, were 0.205 for *S. canadensis* and 0.539 for *S. gigantea*. In a comparison of the observed distribution with the model's prediction, the number of squares suitable for the invaders and not colonized yet (including the undersampled squares excluded from the analyses) increased by 45% (1,255 squares with presence versus 2,293 predicted) for *S. canadensis* and 36% (3,107 squares with presence vs. 4,897 predicted) in the case of *S. gigantea*. For detailed maps see Appendix S7, Map S4.

4 | DISCUSSION

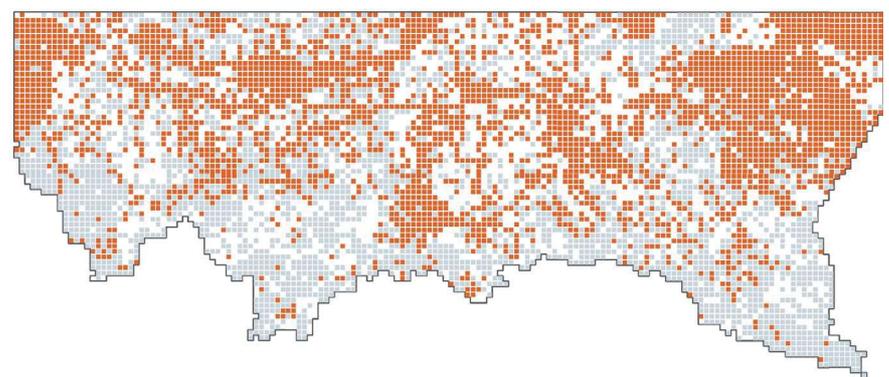
The model's performance in interpreting the AUC values (Šimundić, 2009) should be considered as good for *S. gigantea* and very good for *S. canadensis*, despite the relatively limited number of explanatory variables retained after the model's simplification. Moreover, in the case of species with broad environmental tolerance, such as the studied *Solidago*, the model's performance is usually lower than it is in comparing with specialist species, both plants and animals (Guisan et al., 2007; Regos et al., 2019). The model's performance is improved by variables that can be interpreted as proxies of P, A,

FIGURE 2 Distribution of invasive *Solidago* species (orange color) in studied region. The light gray color show distribution of squares with confirmed *Solidago* absence. Squares excluded from analysis, are not shown (left blank)

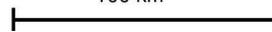
S. canadensis



S. gigantea



100 km



and B factors (see discussion below); however, the importance of the variables differed considerably between particular P, A, and B factors, as well as species studied.

4.1 | Ecological interpretation of the models

4.1.1 | Propagule pressure

The recent distributions of examined species were correlated with initial patterns of their introductions in the 1950s. Quite surprisingly, the two species revealed an opposite relationship to these historical patterns. In the case of *S. gigantea*, the pattern was rather simple and intuitive: The probability was highest in squares closer to the sites of initial distribution. However, *S. canadensis* quite surprisingly was the most likely to occur in squares 100 km from the initial sites of introduction. These results suggest different mechanisms of long-range dispersals, not related to biological issues, since their seeds, dispersal mechanism, and flowering time are similar (Weber, 2000; Weber & Jakobs, 2005).

Recently, *S. canadensis* was considered to have a higher ornamental value (because of larger size, bigger inflorescences, and clump occurrence) than *S. gigantea*. As a result, it is offered by garden shops, but *S. gigantea* is not (Szymura M. personal

observations, data from internet shops offering ornamental plants). A similar pattern of trade has been described in Estonia, Central Europe, where only *S. canadensis* is offered in markets (Õöpik et al., 2013). Moreover, the honey from *S. canadensis* has recently been promoted on social media, without supporting scientific data, as a “superfood” with healing properties. This claim could encourage beekeepers to produce goldenrod honey, which would lead to further spread of *S. canadensis* and exacerbate its existing negative environmental impact (Lenda et al., 2020). Thus, it could be assumed that the long-range dispersal of *S. canadensis* is recently enhanced by humans.

The distribution of *S. canadensis* is positively correlated with human population density. This straightforward correlation breaks if the population density exceeds 5,000 ind km⁻². This happened in a few of the most densely inhabited squares, representing strict city centers. It was generally found that the plant species richness in areas with moderate levels of urbanization (e.g., suburban areas) exceeded the richness recorded in nonurbanized areas as well as in central, urban core areas (McKinney, 2008). The lack of a further increase in alien species richness in strict city centers, despite the high propagule pressure, was explained by the loss of suitable areas for plants (McKinney, 2008). Such generally limited neophytes' richness caused by population density has previously been shown for this region (Szymura et al., 2018).

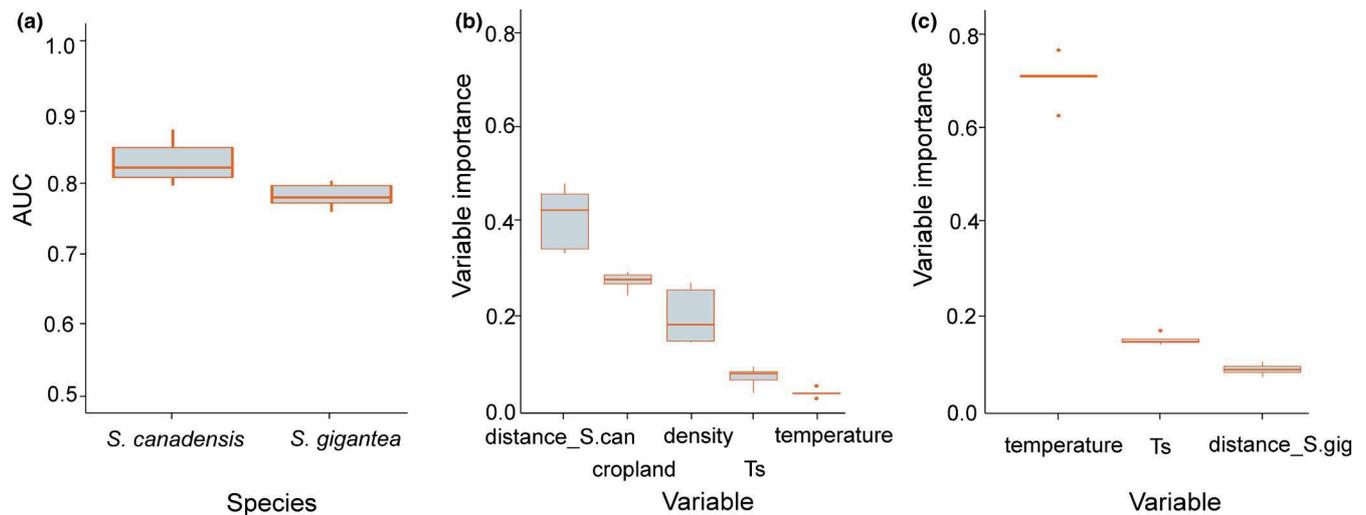


FIGURE 3 The values of area under curve (AUC) for simplified models of *S. canadensis* and *S. gigantea* distributions (a), and variable importance for each variable involved in the simplified models of (b) *S. canadensis* and (c) *S. gigantea*. The boxplot shows the results of runs in the spatially blocked, 5-fold cross-validation. The values of variable importance close to 1 indicate high variable importance to the model, while those close to 0 have low importance. Abbreviations: *cropland*, cropland area percentage; *density*, human population density; *temperature*, average annual temperature; *Ts*, temperature seasonality; *distance_S.can*, distance to nearest introduction site *S. canadensis*; *distance_S.gig*, distance to nearest introduction site *S. gigantea*

The results of the modeling support the assumption that recent *S. gigantea* dispersal has occurred mostly spontaneously without any human aid, while *S. canadensis* dispersal is still related to human presence and, additionally, intentional transport over longer distances via, for example, Internet commerce (Lenda et al., 2014). This pattern is partially related to longer invasion history of *S. gigantea* comparing to *S. canadensis*, with caused that the studied region is exposed to *S. gigantea* seed for a longer time.

4.1.2 | Abiotic factors

The variables representing abiotic environment (A) are the most important for model performance for both species; however, the impact of these variables was more pronounced in the case of *S. gigantea*, compared with *S. canadensis*.

The distribution of both species was restricted climatically, and their presence was unlikely in areas with an average yearly temperature below approximately 5.5°C. The temperature corresponds with the altitudinal zonation of vegetation in the studied region and relates to a lower limit of the montane zone, starting from an altitude of approximately 600–850 m a.s.l. in the studied region. The negative effect of cold climate on the distribution of both *Solidago* species studied is in accordance with studies examining their potential distribution in Europe, which indicated that northern Europe as a region is outside their climatic requirements (Weber, 2001). Although both species can be observed sporadically at higher altitudes, their typical upper limit is 1,200 m a.s.l. (Moran et al., 2017; Weber & Jakobs, 2005). In the case of *S. gigantea*, positive correlations have been found between the mean temperature and growth parameters, and high spring temperatures (above 24°C) are advantageous

for germination (for review, see Weber & Jakobs, 2005). *Solidago canadensis* plants are taller at lower altitudes, and at higher altitudes, they are not able to develop seeds because of the limited length of the vegetation period (Moran et al., 2017). It should be noted that the data referred to here regarding altitude come from the central Alps, while the climate in the Carpathian Mountains is more severe; therefore, the upper limits of the vegetation zones are at lower altitudes in the Carpathian Mountains compared with the Alps (Ellenberg, 1988; Pawłowski, 1972).

The species distributions were also correlated with temperature seasonality, which in the studied region is also related to the precipitation pattern (Appendix S4, Table S3). *Solidago canadensis* is more abundant in the western part of the study region, which has lower temperature seasonality and higher precipitation, while *S. gigantea* avoids the southern part of the region with higher precipitation and also lower temperature seasonality. Previous studies examining the potential range of this species in Europe (Weber, 2001) suggested that these aspects (continentality gradient and precipitation) did not restrict their distribution in this part of Europe. Therefore, the extent to which the observed relation is causal is not clear, and the possibility exists that it reflects a peculiarity of the distribution in the studied region.

The models did not indicate that soil properties and land relief features are among the crucial factors explaining the distributions of the invaders. Both species are known to have rather broad tolerance to soils (Szymura & Szymura, 2016; Weber & Jakobs, 2005; Werner et al., 1980), which could explain why soil properties were not relevant in studied region. Observations from early phase of invasion on studied region, up to 1989s, underlined the role of river valleys, as a main route of invasion (Tokarska-Guzik, 2005). The results obtained here show that the species are broadly widespread and their invasion is no longer related to watercourses.

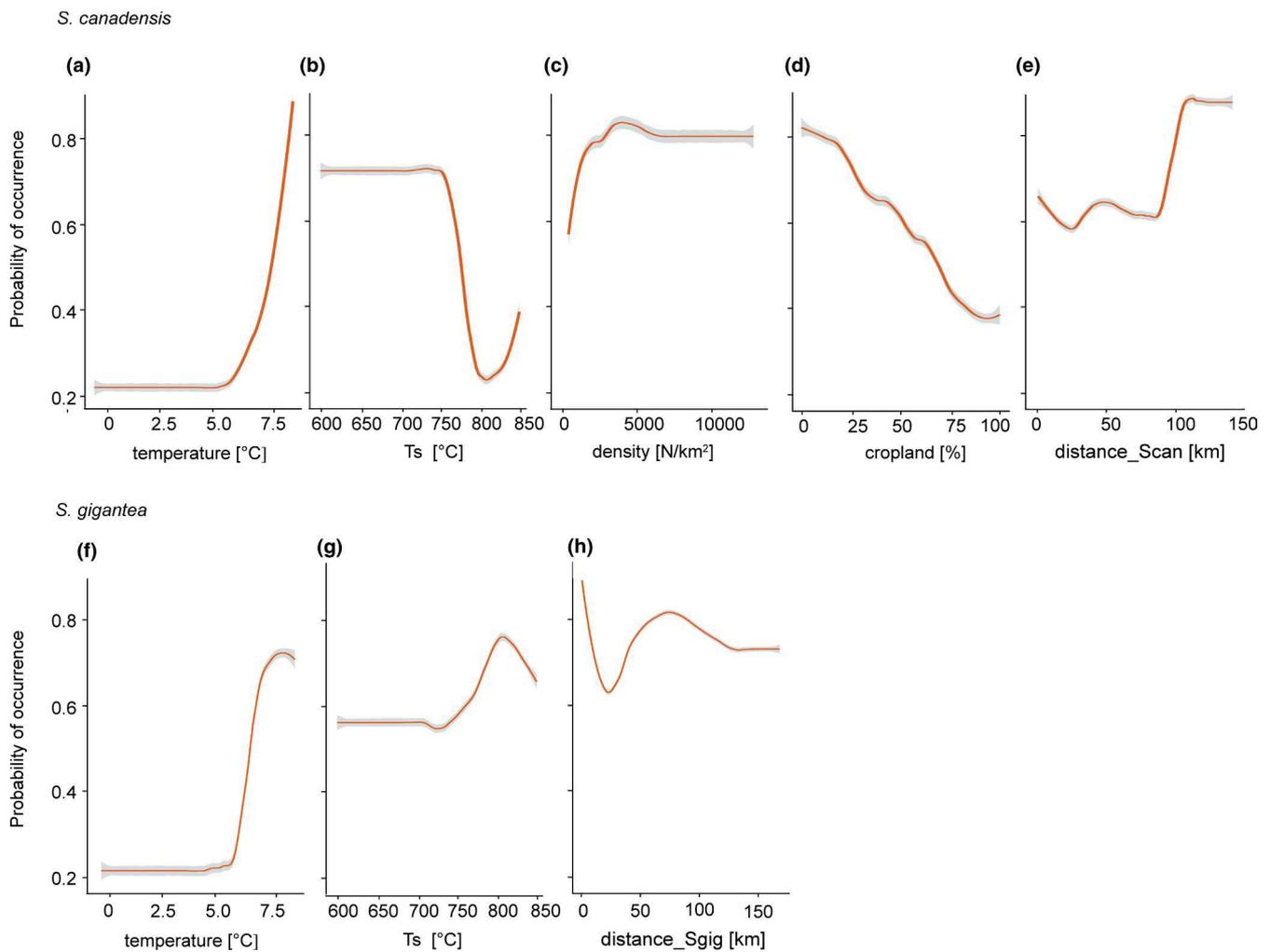


FIGURE 4 The modeled responses of *Solidago* species for particular environmental variables. The shape of the response was modeled using the evaluation strips method (Elith et al., 2005), with spatially blocked, 5-fold cross-validation. The graphs are sorted according to decreasing value of variables' importance, upper panel for *S. canadensis*, lower for *S. gigantea*. Abbreviations: *cropland*, cropland area percentage; *density*, human population density; *temperature*, average annual temperature; *Ts*, temperature seasonality; *distance_S.can*, distance to nearest introduction site *S. canadensis*; *distance_S.gig*, distance to nearest introduction site *S. gigantea*

4.1.3 | Biotic factors

Because of the character of the data (observation for 2×2 km grid), we had no detailed information regarding invaded habitats. However, the data still allowed testing the hypothesis regarding species co-occurrence at landscape scale and the effect of dominant land cover/land use forms. Results from other region of Central Europe revealed existence of large areas dominated by a single invasive *Solidago* species, where the presence of another was unlikely. This spatial pattern results, most likely, from priority effect (Szymura & Szymura, 2016). In the studied region, we had no evidences for such phenomenon: The presence of one species did not explain the absence of the other. The species rarely formed mixed stands (Szymura & Szymura, 2016), but considering grain size used in this examination (square 2×2 km) it can be assumed that they could co-occur in the same landscape. We also found that the presence of *S. canadensis* is rather unlikely in a landscape dominated by agricultural areas. It could be linked to high use of herbicides and a small amount

of available area for invasive goldenrod habitats (e.g., abandoned fields, meadow, pastures) in lands with intense, large-scale agriculture (Szymura & Szymura, 2016; Szymura, Szymura, & Wolski, 2016).

The relatively low importance of variables that can be related to biotic interactions does not necessarily mean that biotic interactions did not shape invasion pattern. It is more likely related to the grid size in this study (2×2 km), while the biotic interactions occur mostly in the closest vicinity of the studied individuals. Such data can potentially be derived from other sources of information, namely phytosociological relevés, which document species composition and abundance in small plots (~ 25 m² for herbal vegetation).

4.2 | Conservation implications

The two species differed regarding prominent constraints: both were limited climatically, avoiding cold, mountain climate, but *S. canadensis* with a still limited range was also related to proxies of

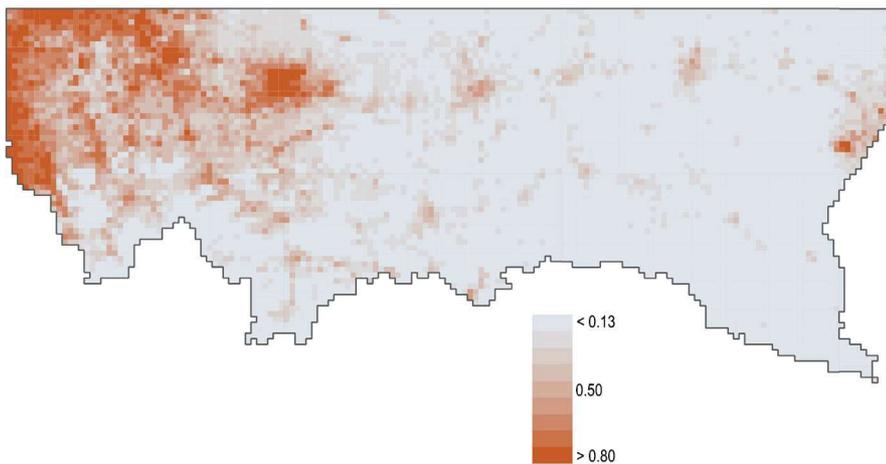
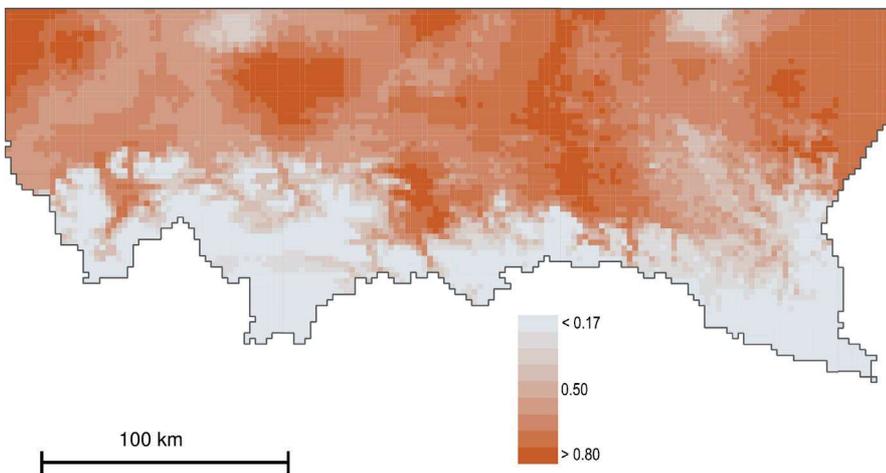
S. canadensis*S. gigantea*

FIGURE 5 The projected probability of presence of the invasive *Solidago* species. The optimal cutoff value was 0.205 for *S. canadensis* and 0.539 for *S. gigantea*

human pressure. Based on the results, it can be hypothesized that recent dispersal of *S. gigantea* in the studied region has happened mostly spontaneously, while the spread of *S. canadensis* could be related to trade and intentional introductions. Given the wide range of distribution of both species, their successful eradication in the region seems unlikely. The eradication of *Solidago* is not easy and must include the establishment of native vegetation to prevent re-invasion of the *Solidago* on the site. It needs a long time and financial effort (Szymura et al., 2019; Szymura, Szymura, & Wolski, 2016). However, local eradication in mountains, above 600–850 m a.s.l. where the species occur infrequently may still be feasible and could be considered as a management option. In the case of *S. canadensis*, proscription of its sale could restrict its further spread. Assuming the successful restriction of the trade, eradication in the eastern and central parts of the region, where the species is still uncommon, will be achievable. Similarly, the control of invasive plant species populations in human settlements and their surrounding area seems to be a reasonable method. In contrast, the management of *S. gigantea* should focus on areas with a high value for nature conservation that are close to already existing populations of this species. Among management of invasive *Solidago* stands, the mowing, grazing, flooding,

and combination of these methods are considered (Nagy et al., 2020, 2021). Herbicide use should be banned because of its environmental impact, including the effect on native vegetation (Schulz et al., 2021; Weidlich et al., 2020); moreover, its long-term effect is not better than mechanic methods (Szymura et al., 2019). Nonetheless, the model's prediction suggests a considerable increase of invaded areas by both species. The location of suitable squares that are not yet colonized suggests that the expansion of the invaders will take place by range filing rather than increasing the range (Appendix S7, Map S4). In Central Europe especially prone to invasion are abandoned agricultural lands (Bartha et al., 2014; Fenesi et al., 2015), therefore a policy preventing agricultural land abandonment is desirable to counteract the further increase of goldenrods invasion level. The model outputs seem to be transferable into other areas with similar climate, land use history, economy, and invasion history, including the Carpathian Mountains and the surrounding regions in Slovakia, Ukraine, Hungary, and Romania. However, we did not have enough data to directly test the possible model application, using the limited number of explanatory variables, to maximize the iSDM transferability (Petitpierre et al., 2017). In this context, the procedure of model simplification (Elith et al., 2008), which reduced the number

of explanatory variables, seems to be a great advantage of the BRT modeling technique.

4.3 | Model limitations, and methodological problems

Recently, numerous iSDMs have been based on presence-only data and employ so-called background points (pseudo-absences). Nonetheless, data not only on species presence but also their true (i.e., confirmed) absence are considered more relevant for modeling (Barbet-Massin et al., 2012; Brotons et al., 2004; Elith et al., 2020). Unfortunately, confirmed absence data are problematic because they need a high sampling effort (Barbet-Massin et al., 2012; MacKenzie & Royle, 2005) to be realistic. Our results show that exclusion of squares with low sampling effort improves the model's performance. This suggests an issue of sampling bias, which can be ameliorated by appropriate procedures. Our approach seems to be promising, but it needs further study in order to better understand its operation. The typical assumption, such as higher sampling effort in densely populated areas and near roads, is not adequate for invasive species because they typically occur in urban areas and along communication routes (Niinemets & Peñuelas, 2008; Szymura, Szymura, & Wolski, 2016).

Another problem consists of causality in our model: The approach applied represents a correlative type of model that is unable to directly capture the underlying processes driving the observed patterns of distribution. Contrary to the correlative approach, the mechanistic (or process-based) models, which are built using explicit descriptions of biological mechanisms, are free from this disadvantage (Yates et al., 2018). In result, mechanistic and hybrid models have recently been recommended for modeling species distribution (Zurell et al., 2016). Studies in simulated systems reveal great potential of mechanistic models as BioGEEM in examination of ecological questions (Cabral et al., 2019). However, they still meet a numerous obstacles in practical implementation, especially in macroecological and biogeographical applications (Cabral et al., 2017), since simulation of large, species-rich ecosystems is challenging (Cabral et al., 2019). They need appropriate formulation including detailed data on species response to environment, preferably coming from experiments, which are typically unavailable (Yates et al., 2018; Zurell et al., 2016). In practice, the models rely to a considerable degree on parametrization based on observational data, and as a result, the difference between correlative and mechanistic models is often fuzzy (Yates et al., 2018). Similarly, there is a problem with incorporating the effect of long-range seed dispersal by wind. It needs detailed data regarding wind direction and velocity, seed dispersal kernel, and local population demography (Neubert & Caswell, 2000). As result, models are developed for restricted areas (e.g., Baker, 2017; Williams et al., 2008), which caused particularly useful for modeling dispersal of newly established populations (Gallien et al., 2010). To conclude, the recent state of knowledge regarding processes driving *Solidago* invasion restricts application of

mechanistic or hybrid models of their invasion to a regional spatial extent.

5 | CONCLUSIONS

The PAB framework enhanced the iSDM by helping in the selection of explanatory variables, as well as the ecological interpretation of the models. Nonetheless, in practice it needs high-quality data that are typically unavailable to fulfill this approach, especially regarding biotic interactions. In case of plant invasion, adequate data on the biotic component could be delivered by phytosociological relevés. The employment of maps showing the historical distribution of invasive species enhanced the modeling by revealing differences in patterns of species spread into a region. In result, the model reveals that two alien species with similar ecology and biology can vary considerably in their invasion pattern due to direct human interference. Therefore, the conservation options, derived from iSDM, should be focused on a particular species, not groups of species, even if they have similar ecology and are closely related taxonomically.

The presence/absence data, in addition to their pre-eminence compared with opportunistic, presence-only data for species distribution modeling purposes, are still prone to some bias. Results of this study suggest that the bias is correlated with mistakenly reported species absence. Exclusion of the potentially undersampled plots increased the model performance; however, additional data are needed (e.g., richness of target species group).

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CONFLICT OF INTEREST

The authors declare no competing interest.

AUTHOR CONTRIBUTIONS

Peliyagodage Chathura Dineth Perera: Conceptualization (supporting); Formal analysis (supporting); Funding acquisition (equal); Investigation (supporting); Methodology (equal); Visualization (supporting); Writing-original draft (lead); Writing-review & editing (lead). **Tomasz H. Szymura:** Conceptualization (equal); Data curation

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DATA AVAILABILITY STATEMENT

All data used are available publicly from the sources given in the manuscript and appendices.

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REFERENCES

- Bailey, J. J., Boyd, D. S., Hjort, J., Lavers, C. P., & Field, R. (2017). Modelling native and alien vascular plant species richness: At which scales is geodiversity most relevant? *Global Ecology and Biogeography*, 26(7), 763–776. <https://doi.org/10.1111/geb.12574>
- Baker, C. M. (2017). Target the source: Optimal spatiotemporal resource allocation for invasive species control. *Conservation Letters*, 10(1), 41–48. <https://doi.org/10.1111/conl.12236>
- Ballabio, C., Lugato, E., Fernández-Ugalde, O., Orgiazzi, A., Jones, A., Borrelli, P., Montanarella, L., & Panagos, P. (2019). Mapping LUCAS topsoil chemical properties at European scale using Gaussian process regression. *Geoderma*, 355, 113912. <https://doi.org/10.1016/j.geoderma.2019.113912>
- Barbet-Massin, M., Jiguet, F., Albert, C. H., & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: How, where and how many? *Methods in Ecology and Evolution*, 3(2), 327–338. <https://doi.org/10.1111/j.2041-210X.2011.00172.x>
- Bartha, S., Szentes, S., Horváth, A., Házi, J., Zimmermann, Z., Molnár, C., Dancza, I., Margóczy, K., Pál, R. W., Purger, D., Schmidt, D., Óvári, M., Komoly, C., Sutyinszki, Z., Szabó, G., Csathó, A. I., Juhász, M., Pensza, K., & Molnár, Z. (2014). Impact of mid-successional dominant species on the diversity and progress of succession in regenerating temperate grasslands. *Applied Vegetation Science*, 17, 201–213. <https://doi.org/10.1111/avsc.12066>
- Basnou, C., Iguzquiza, J., & Pino, J. (2015). Examining the role of landscape structure and dynamics in alien plant invasion from urban Mediterranean coastal habitats. *Landscape and Urban Planning*, 136, 156–164. <https://doi.org/10.1016/j.landurbplan.2014.12.001>
- Bazzichetto, M., Malavasi, M., Barták, V., Acosta, A. T. R., Moudry, V., & Carranza, M. L. (2018). Modeling plant invasion on Mediterranean coastal landscapes: An integrative approach using remotely sensed data. *Landscape and Urban Planning*, 171, 98–106. <https://doi.org/10.1016/j.landurbplan.2017.11.006>
- Beaury, E. M., Finn, J. T., Corbin, J. D., Barr, V., & Bradley, B. A. (2020). Biotic resistance to invasion is ubiquitous across ecosystems of the United States. *Ecology Letters*, 23(3), 476–482. <https://doi.org/10.1111/ele.13446>
- Bielecka, A., Królak, E., & Biardzka, E. (2017). Habitat conditions of Canadian goldenrod in a selected region of eastern Poland. *Journal of Ecological Engineering*, 18(4), 76–81. <https://doi.org/10.12911/22998993/74284>
- Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., Wilson, J. R. U., & Richardson, D. M. (2011). A proposed unified framework for biological invasions. *Trends in Ecology and Evolution*, 26(7), 333–339. <https://doi.org/10.1016/j.tree.2011.03.023>
- Brotons, L., Thuiller, W., Araújo, M. B., & Hirzel, A. H. (2004). Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography*, 27(4), 437–448. <https://doi.org/10.1111/j.0906-7590.2004.03764.x>
- CABI. (2018). *Solidago canadensis* L. Retrieved from <https://www.cabi.org/isc/datasheet/50599>
- Cabral, J. S., Valente, L., & Hartig, F. (2017). Mechanistic simulation models in macroecology and biogeography: State-of-art and prospects. *Ecography*, 40(2), 267–280. <https://doi.org/10.1111/ecog.02480>
- Cabral, J. S., Wiegand, K., & Kreft, H. (2019). Interactions between ecological, evolutionary and environmental processes unveil complex dynamics of insular plant diversity. *Journal of Biogeography*, 46(7), 1582–1597. <https://doi.org/10.1111/jbi.13606>
- Catford, J. A., Jansson, R., & Nilsson, C. (2009). Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions*, 15(1), 22–40. <https://doi.org/10.1111/j.1472-4642.2008.00521.x>
- Chamberlain, S. A., Bronstein, J. L., & Rudgers, J. A. (2014). How context dependent are species interactions? *Ecology Letters*, 17(7), 881–890. <https://doi.org/10.1111/ele.12279>
- Chapman, D., Pescott, O. L., Roy, H. E., & Tanner, R. (2019). Improving species distribution models for invasive non-native species with biologically informed pseudo-absence selection. *Journal of Biogeography*, 46(5), 1029–1040. <https://doi.org/10.1111/jbi.13555>
- Charles, H., & Dukes, J. S. (2007). Impacts of invasive species on ecosystem services. *Biological Invasions*, 193, 217–237. https://doi.org/10.1007/978-3-540-36920-2_13
- Chmura, D., Dyba, P., Kraj, P., Peplińska, N., Pilorz, A., & Roman, M. (2016). Invasion of alien *Solidago* taxa into urban habitats: A study of selected towns in Southern Poland. *Chemistry-Didactics-Ecology-Metrology*, 20(1–2), 97–104. <https://doi.org/10.1515/cdem-2015-0010>
- Chytrý, M., Jarošík, V., Pyšek, P., Hájek, O., Knollová, I., Tichý, L., & Danihelka, J. (2008). Separating habitat invasibility by alien plants from the actual level of invasion. *Ecology*, 89(6), 1541–1553. <https://doi.org/10.1890/07-0682.1>
- Chytrý, M., Pyšek, P., Wild, J., Pino, J., Maskell, L. C., & Vilà, M. (2009). European map of alien plant invasions based on the quantitative assessment across habitats. *Diversity and Distributions*, 15(1), 98–107. <https://doi.org/10.1111/j.1472-4642.2008.00515.x>
- Czarnecka-Wiera, M., Szymura, T. H., & Kački, Z. (2020). Understanding the importance of spatial scale in the patterns of grassland invasions. *Science of the Total Environment*, 727, 138669. <https://doi.org/10.1016/j.scitotenv.2020.138669>
- Davis, M. A., Grime, J. P., & Thompson, K. (2000). Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology*, 88(3), 528–534. <https://doi.org/10.1046/j.1365-2745.2000.00473.x>
- de Groot, M., Kleijn, D., & Jogan, N. (2007). Species groups occupying different trophic levels respond differently to the invasion of semi-natural vegetation by *Solidago canadensis*. *Biological Conservation*, 136(4), 612–617. <https://doi.org/10.1016/j.biocon.2007.01.005>
- De'Ath, G. (2007). Boosted trees for ecological modeling and prediction. *Ecology*, 88(1), 243–251.
- De'Ath, G., & Fabricius, K. E. (2000). Classification and regression trees: A powerful yet simple technique for ecological data analysis. *Ecology*, 81(11), 3178–3192.
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation

- study evaluating their performance. *Ecography*, 36(1), 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>
- Elith, J., Ferrier, S., Huettmann, F., & Leathwick, J. (2005). The evaluation strip: A new and robust method for plotting predicted responses from species distribution models. *Ecological Modelling*, 186(3), 280–289. <https://doi.org/10.1016/j.ecolmodel.2004.12.007>
- Elith, J., Graham, C., Valavi, R., Abegg, M., Bruce, C., Ford, A., Guisan, A., Hijmans, R. J., Huettmann, F., Lohmann, L., Loiselle, B., Moritz, C., Overton, J., Peterson, A. T., Phillips, S., Richardson, K., Williams, S., Wiser, S. K., Wohlgemuth, T., & Zimmermann, N. E. (2020). Presence-only and presence-absence data for comparing species distribution modeling methods. *Biodiversity Informatics*, 15(2), 69–80. <https://doi.org/10.17161/bi.v15i2.13384>
- Elith, J., Leathwick, J. R., & Hastie, T. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology*, 77(4), 802–813. <https://doi.org/10.1111/j.1365-2656.2008.01390.x>
- Ellenberg, H. H. (1988). *Vegetation ecology of central Europe*. Cambridge University Press.
- EPPO. (2020). *European and Mediterranean plant protection organisation invasive species alert list*. Retrieved from https://www.eppo.int/ACTIVITIES/plant_quarantine/alert_list
- Essl, F., Dullinger, S., Rabitsch, W., Hulme, P. E., Hülber, K., Jarošík, V., Kleinbauer, I., Krausmann, F., Kühn, I., Nentwig, W., Vilà, M., Genovesi, P., Gherardi, F., Desprez-Loustau, M.-L., Roques, A., & Pyšek, P. (2011). Socioeconomic legacy yields an invasion debt. *Proceedings of the National Academy of Sciences of the United States of America*, 108(1), 203–207. <https://doi.org/10.1073/pnas.1011728108>
- Fenesi, A., Vágási, C. I., Beldean, M., Földesi, R., Kolcsár, L. P., Shapiro, J. T., Török, E., & Kovács-Hostyánszki, A. (2015). *Solidago canadensis* impacts on native plant and pollinator communities in different-aged old fields. *Basic and Applied Ecology*, 16(4), 335–346. <https://doi.org/10.1016/j.baae.2015.03.003>
- Foxcroft, L. C., Pickett, S. T. A., & Cadenasso, M. L. (2011). Expanding the conceptual frameworks of plant invasion ecology. *Perspectives in Plant Ecology, Evolution and Systematics*, 13(2), 89–100. <https://doi.org/10.1016/j.ppees.2011.03.004>
- Frost, C. M., Allen, W. J., Courchamp, F., Jeschke, J. M., Saul, W. C., & Wardle, D. A. (2019). Using network theory to understand and predict biological invasions. *Trends in Ecology & Evolution*, 34(9), 831–843. <https://doi.org/10.1016/j.tree.2019.04.012>
- Funk, J. L., Cleland, E. E., Suding, K. N., & Zavaleta, E. S. (2008). Restoration through reassembly: Plant traits and invasion resistance. *Trends in Ecology and Evolution*, 23, 695–703. <https://doi.org/10.1016/j.tree.2008.07.013>
- Gallien, L., Douzet, R., Pratte, S., Zimmermann, N. E., & Thuiller, W. (2012). Invasive species distribution models—how violating the equilibrium assumption can create new insights. *Global Ecology and Biogeography*, 21(11), 1126–1136. <https://doi.org/10.1111/j.1466-8238.2012.00768.x>
- Gallien, L., Münkemüller, T., Albert, C. H., Boulangeat, I., & Thuiller, W. (2010). Predicting potential distributions of invasive species: Where to go from here? *Diversity and Distributions*, 16(3), 331–342. <https://doi.org/10.1111/j.1472-4642.2010.00652.x>
- González-Moreno, P., Pino, J., Carreras, D., Basnou, C., Fernández-Rebollar, I., & Vilà, M. (2013). Quantifying the landscape influence on plant invasions in Mediterranean coastal habitats. *Landscape Ecology*, 28(5), 891–903. <https://doi.org/10.1007/s10980-013-9857-1>
- Greenwell, B., Boehmke, B., Cunningham, J., & GBM Developers. (2020). *gbm: Generalized boosted regression models. R package version 2.1.8*. Retrieved from <https://CRAN.R-project.org/package=gbm>
- Guisan, A., Zimmermann, N. E., Elith, J., Graham, C. H., Phillips, S., & Peterson, A. T. (2007). What matters for predicting the occurrences of trees: Techniques, data, or species' characteristics? *Ecological Monographs*, 77(4), 615–630. <https://doi.org/10.1890/06-1060.1>
- Gusev, A. P. (2015). The impact of invasive Canadian goldenrod (*Solidago canadensis* L.) on regenerative succession in old fields (the Southeast of Belarus). *Russian Journal of Biological Invasions*, 6(2), 74–77. <https://doi.org/10.1134/S2075111715020034>
- Guzikowa, M., & Maycock, P. F. (1986). The invasion and expansion of three North American species of goldenrod (*Solidago canadensis* L. sensu lato. *S. gigantea* Ait. and *S. graminifolia* (L) Salisb) in Poland. *Acta Societatis Botanicorum Poloniae*, 55(3), 367–384. <https://doi.org/10.5586/asbp.1986.034>
- Hattab, T., Garzón-López, C. X., Ewald, M., Skowronek, S., Aerts, R., Horen, H., Brasseur, B., Gallet-Moron, E., Spicher, F., Decocq, G., Feilhauer, H., Honnay, O., Kempeneers, P., Schmidlein, S., Somers, B., Van De Kerchove, R., Rocchini, D., & Lenoir, J. (2017). A unified framework to model the potential and realized distributions of invasive species within the invaded range. *Diversity and Distributions*, 23(7), 806–819. <https://doi.org/10.1111/ddi.12566>
- Hejda, M., & de Bello, F. (2013). Impact of plant invasions on functional diversity in the vegetation of Central Europe. *Journal of Vegetation Science*, 24(5), 890–897. <https://doi.org/10.1111/jvs.12026>
- Hejda, M., Pyšek, P., & Jarošík, V. (2009). Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology*, 97(3), 393–403. <https://doi.org/10.1111/j.1365-2745.2009.01480.x>
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology: A Journal of the Royal Meteorological Society*, 25(15), 1965–1978. <https://doi.org/10.1002/joc.1276>
- Hijmans, R. J., Phillips, S., Leathwick, J., & Elith, J. (2020). *dismo: Species distribution modeling. R package version 1.3-3*. Retrieved from <https://CRAN.R-project.org/package=dismo>
- Hulme, P. E. (2009). Trade, transport and trouble: Managing invasive species pathways in an era of globalization. *Journal of Applied Ecology*, 46(1), 10–18. <https://doi.org/10.1111/j.1365-2664.2008.01600.x>
- Hulme, P. E. (2017). Climate change and biological invasions: Evidence, expectations, and response options. *Biological Reviews*, 3, 1297–1313. <https://doi.org/10.1111/brv.12282>
- Johnson, M. F. (1995). Goldenrods in Virginia: *Euthamia* (Nutt.) Nutt. and *Solidago* L. *Castanea*, 60(2), 114–140.
- Kajzer-Bonk, J., Szpiłtyk, D., & Woyciechowski, M. (2016). Invasive goldenrods affect abundance and diversity of grassland ant communities (Hymenoptera: Formicidae). *Journal of Insect Conservation*, 20(1), 99–105. <https://doi.org/10.1007/s10841-016-9843-4>
- Kuebbing, S. E., & Nuñez, M. A. (2015). Negative, neutral, and positive interactions among nonnative plants: Patterns, processes, and management implications. *Global Change Biology*, 21(2), 926–934. <https://doi.org/10.1111/gcb.12711>
- Kulmatiski, A., Beard, K. H., & Stark, J. M. (2006). Soil history as a primary control on plant invasion in abandoned agricultural fields. *Journal of Applied Ecology*, 43(5), 868–876. <https://doi.org/10.1111/j.1365-2664.2006.01192.x>
- Le Maitre, D. C., Richardson, D. M., & Chapman, R. A. (2004). Alien plant invasions in South Africa: Driving forces and the human dimension: Working for water. *South African Journal of Science*, 100(1–2), 103–112.
- Ledger, K. J., Pal, R. W., Murphy, P., Nagy, D. U., Filep, R., & Callaway, R. M. (2015). Impact of an invader on species diversity is stronger in the non-native range than in the native range. *Plant Ecology*, 216(9), 1285–1295. <https://doi.org/10.1007/s11258-015-0508-2>
- Lenda, M., Skórka, P., Knops, J. M., Moroń, D., Sutherland, W. J., Kuszewska, K., & Woyciechowski, M. (2014). Effect of the internet commerce on dispersal modes of invasive alien species. *PLoS One*, 9(6), e99786. <https://doi.org/10.1371/journal.pone.0099786>
- Lenda, M., Skórka, P., Kuszewska, K., Moroń, D., Betcik, M., Baczek Kwinta, R., Janowiak, F., Duncan, D. H., Veski, P. A., Possingham, H.

- P., & Knops, J. M. (2020). Misinformation, internet honey trading and beekeepers drive a plant invasion. *Ecology Letters*, 24(2), 165–169. <https://doi.org/10.1111/ele.13645>
- Lenda, M., Witek, M., Skórka, P., Moroń, D., & Woyciechowski, M. (2013). Invasive alien plants affect grassland ant communities, colony size and foraging behaviour. *Biological Invasions*, 15(11), 2403–2414. <https://doi.org/10.1007/s10530-013-0461-8>
- Linders, T. E. W., Schaffner, U., Eschen, R., Abebe, A., Choge, S. K., Nigatu, L., Mbaabu, P. R., Shiferaw, H., & Allan, E. (2019). Direct and indirect effects of invasive species: Biodiversity loss is a major mechanism by which an invasive tree affects ecosystem functioning. *Journal of Ecology*, 107(6), 2660–2672. <https://doi.org/10.1111/1365-2745.13268>
- Lozano, V., Marzalletti, F., Carranza, M. L., Chapman, D., Branquart, E., Dološ, K., Große-Stoltenberg, A., Fiori, M., Capece, P., & Brundu, G. (2020). Modelling *Acacia saligna* invasion in a large Mediterranean island using PAB factors: A tool for implementing the European legislation on invasive species. *Ecological Indicators*, 116, 106516. <https://doi.org/10.1016/j.ecolind.2020.106516>
- MacArthur, R., & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, 101(921), 377–385. <https://doi.org/10.2307/2459090>
- Mackenzie, D. I., & Royle, J. A. (2005). Designing occupancy studies: General advice and allocating survey effort. *Journal of Applied Ecology*, 42(6), 1105–1114. <https://doi.org/10.1111/j.1365-2664.2005.01098.x>
- McKinney, M. L. (2008). Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems*, 11(2), 161–176. <https://doi.org/10.1007/s11252-007-0045-4>
- Meyer, A. H., & Schmid, B. (1999a). Seed dynamics and seedling establishment in the invading perennial *Solidago altissima* under different experimental treatments. *Journal of Ecology*, 87(1), 28–41. <https://doi.org/10.1046/j.1365-2745.1999.00316.x>
- Meyer, A. H., & Schmid, B. (1999b). Experimental demography of the old-field perennial *Solidago altissima*: The dynamics of the shoot population. *Journal of Ecology*, 87(1), 17–27. <https://doi.org/10.1046/j.1365-2745.1999.00315.x>
- Milbau, A., Stout, J. C., Graae, B. J., & Nijs, I. (2009). A hierarchical framework for integrating invasibility experiments incorporating different factors and spatial scales. *Biological Invasions*, 11(4), 941–950. <https://doi.org/10.1007/s10530-008-9306-2>
- Moran, E. V., Reid, A., & Levine, J. M. (2017). Population genetics and adaptation to climate along elevation gradients in invasive *Solidago canadensis*. *PLoS One*, 12(9), e0185539. <https://doi.org/10.1371/journal.pone.0185539>
- Moroń, D., Lenda, M., Skórka, P., Szentgyörgyi, H., Settele, J., & Woyciechowski, M. (2009). Wild pollinator communities are negatively affected by invasion of alien goldenrods in grassland landscapes. *Biological Conservation*, 142(7), 1322–1332. <https://doi.org/10.1016/j.biocon.2008.12.036>
- Moroń, D., Marjańska, E., Skórka, P., Lenda, M., & Woyciechowski, M. (2021). Invader–pollinator paradox: Invasive goldenrods benefit from large size pollinators. *Diversity and Distributions*, 27(4), 632–641. <https://doi.org/10.1111/ddi.13221>
- Nagy, D. U., Rauschert, E. S., Callaway, R. M., Henn, T., Filep, R., & Pal, R. W. (2021). Intense mowing management suppresses invader, but shifts competitive resistance by a native to facilitation. *Restoration Ecology*, e13483. <https://doi.org/10.1111/rec.13483>
- Nagy, D. U., Rauschert, E. S., Henn, T., Cianfaglione, K., Stranczinger, S., & Pal, R. W. (2020). The more we do, the less we gain? Balancing effort and efficacy in managing the *Solidago gigantea* invasion. *Weed Research*, 60(3), 232–240. <https://doi.org/10.1111/wre.12417>
- Neubert, M. G., & Caswell, H. (2000). Demography and dispersal: Calculation and sensitivity analysis of invasion speed for structured populations. *Ecology*, 81(6), 1613–1628.
- Niinemets, Ü., & Peñuelas, J. (2008). Gardening and urban landscaping: Significant players in global change. *Trends in Plant Science*, 13(2), 60–65. <https://doi.org/10.1016/j.tplants.2007.11.009>
- Õöpik, M., Bunce, R. G. B., & Tischler, M. (2013). Horticultural markets promote alien species invasions: An Estonian case study of herbaceous perennials. *NeoBiota*, 17, 19. <https://doi.org/10.3897/neobiota.17.4217>
- Pawłowski, B. (1972). Szata roślinna gór polskich. In W. Szafer, & K. Zarzycki (Eds.), *Szata roślinna Polski* (pp. 189–253). PWN.
- Pejchar, L., & Mooney, H. A. (2009). Invasive species, ecosystem services and human well-being. *Trends in Ecology & Evolution*, 24(9), 497–504. <https://doi.org/10.1016/j.tree.2009.03.016>
- Peltzer, D. A., Kurokawa, H., & Wardle, D. A. (2016). Soil fertility and disturbance interact to drive contrasting responses of co-occurring native and nonnative species. *Ecology*, 97(2), 515–529. <https://doi.org/10.1890/15-0298.1>
- Perkins, L. B., Leger, E. A., & Nowak, R. S. (2011). Invasion triangle: An organizational framework for species invasion. *Ecology and Evolution*, 1(4), 610–625. <https://doi.org/10.1002/ece3.47>
- Petitpierre, B., Broennimann, O., Kueffer, C., Daehler, C., & Guisan, A. (2017). Selecting predictors to maximize the transferability of species distribution models: Lessons from cross-continental plant invasions. *Global Ecology and Biogeography*, 26(3), 275–287. <https://doi.org/10.1111/geb.12530>
- Phillips, S. J., Dudík, M., Elith, J., Graham, C. H., Lehmann, A., Leathwick, J., & Ferrier, S. (2009). Sample selection bias and presence-only distribution models: Implications for background and pseudo-absence data. *Ecological Applications*, 19(1), 181–197. <https://doi.org/10.1890/07-2153.1>
- Pino, J., Font, X., Carbo, J., Jové, M., & Pallares, L. (2005). Large-scale correlates of alien plant invasion in Catalonia (NE of Spain). *Biological Conservation*, 122(2), 339–350. <https://doi.org/10.1016/j.biocon.2004.08.006>
- Pollnac, F., Seipel, T., Repath, C., & Rew, L. J. (2012). Plant invasion at landscape and local scales along roadways in the mountainous region of the Greater Yellowstone Ecosystem. *Biological Invasions*, 14(8), 1753–1763. <https://doi.org/10.1007/s10530-012-0188-y>
- Pyšek, P., Jarosik, V., Hulme, P. E., Kuhn, I., Wild, J., Arianoutsou, M., Bacher, S., Chiron, F., Didžiulis, V., Essl, F., Genovesi, P., Gherardi, F., Hejda, M., Kark, S., Lambdon, P. W., Desprez-Loustau, M.-L., Nentwig, W., Pergl, J., Poboljsaj, K., ... Winter, M. (2010). Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proceedings of the National Academy of Sciences of the United States of America*, 107(27), 12157–12162. <https://doi.org/10.1073/pnas.1002314107>
- Pyšek, P., & Richardson, D. M. (2010). Invasive species, environmental change and management, and health. *Annual Review of Environment and Resources*, 35, 25–55. <https://doi.org/10.1146/annurev-environ-033009-095548>
- Regos, A., Gagne, L., Alcaraz-Segura, D., Honrado, J. P., & Domínguez, J. (2019). Effects of species traits and environmental predictors on performance and transferability of ecological niche models. *Scientific Reports*, 9(1), 1–14. <https://doi.org/10.1038/s41598-019-40766-5>
- Rejmánek, M. (1989). Invasibility of plant communities. In J. A. Drake, F. Di Castri, R. H. Groves, F. J. Kruger, H. A. Mooney, M. Rejmanek, & M. H. Williamson (Eds.), *Ecology of biological invasion: A global perspective* (pp. 369–388). Wiley and Sons.
- Roberts, D. R., Bahn, V., Ciuti, S., Boyce, M. S., Elith, J., Guillera-Aroita, G., Hauenstein, S., Lahoz-Monfort, J. J., Schröder, B., Thuiller, W., Warton, D. I., Wintle, B. A., Hartig, F., & Dormann, C. F. (2017). Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. *Ecography*, 40(8), 913–929. <https://doi.org/10.1111/ecog.02881>
- Roháčová, M., & Drozd, P. (2009). How many heteropteran species can live on alien goldenrods *Solidago canadensis* and *S. gigantea* in

- Europe? *Biologia*, 64(5), 981–993. <https://doi.org/10.2478/s11756-009-0151-2>
- Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., & Leemans, R. (2000). Global biodiversity scenarios for the year 2100. *Science*, 287(5459), 1770–1774. <https://doi.org/10.1126/science.287.5459.1770>
- Schmid, B., Puttick, G. M., Burgess, K. H., & Bazzaz, F. A. (1988). Correlations between genet architecture and some life history features in three species of *Solidago*. *Oecologia*, 75(3), 459–464. <https://doi.org/10.1007/BF00376952>
- Schulz, R., Bub, S., Petschick, L. L., Stehle, S., & Wolfram, J. (2021). Applied pesticide toxicity shifts toward plants and invertebrates, even in GM crops. *Science*, 372(6537), 81–84. <https://doi.org/10.1126/science.abe1148>
- Seebens, H., Essl, F., Dawson, W., Fuentes, N., Moser, D., Pergl, J., Pyšek, P., van Kleunen, M., Weber, E., Winter, M., & Blasius, B. (2015). Global trade will accelerate plant invasions in emerging economies under climate change. *Global Change Biology*, 21(11), 4128–4140. <https://doi.org/10.1111/gcb.13021>
- Sheppard, A. W., Shaw, R. H., & Sforza, R. (2006). Top 20 environmental weeds for classical biological control in Europe: A review of opportunities, regulations and other barriers to adoption. *Weed Research*, 46(2), 93–117. <https://doi.org/10.1111/j.1365-3180.2006.00497.x>
- Shiferaw, H., Schaffner, U., Bewket, W., Alamirew, T., Zeleke, G., Teketay, D., & Eckert, S. (2019). Modelling the current fractional cover of an invasive alien plant and drivers of its invasion in a dryland ecosystem. *Scientific Reports*, 9(1), 1–12. <https://doi.org/10.1038/s41598-018-36587-7>
- Šimundić, A. M. (2009). Measures of diagnostic accuracy: Basic definitions. *EJIFCC*, 19(4), 203.
- Skórka, P., Lenda, M., & Tryjanowski, P. (2010). Invasive alien goldenrods negatively affect grassland bird communities in Eastern Europe. *Biological Conservation*, 143(4), 856–861. <https://doi.org/10.1016/j.biocon.2009.12.030>
- Štajerová, K., Šmilauer, P., Brůna, J., & Pyšek, P. (2017). Distribution of invasive plants in urban environment is strongly spatially structured. *Landscape Ecology*, 32(3), 681–692. <https://doi.org/10.1007/s10980-016-0480-9>
- Szabo-Takacs, B., Farda, A., Zahradníček, P., & Štěpánek, P. (2015). Continentality in Europe according to various resolution regional climate models with A1B scenario in the 21st century. *Quarterly Journal of the Hungarian Meteorological Service*, 119(4), 515–535.
- Szymura, M., Świercz, S., Szymura, T. H., & Jarczak, D. (2019). How to establish grassland on sites invaded by *Solidago*: results of a five-year experiment. In P. Pyšek, J. Pergl, & D. Moodley (Eds.), *15th Ecology and Management of Alien Plant Invasions (EMAPI) book of abstracts: Integrating research, management and policy* (p. 82). Institute of Botany, Czech Academy of Sciences.
- Szymura, M., & Szymura, T. H. (2013). Soil preferences and morphological diversity of goldenrods (*Solidago* L.) from south-western Poland. *Acta Societatis Botanicorum Poloniae*, 82(2), 107–115. <https://doi.org/10.5586/asbp.2013.005>
- Szymura, M., & Szymura, T. H. (2016). Historical contingency and spatial processes rather than ecological niche differentiation explain the distribution of invasive goldenrods (*Solidago* and *Euthamia*). *Plant Ecology*, 217(5), 565–582. <https://doi.org/10.1007/s11258-016-0601-1>
- Szymura, M., Szymura, T. H., & Świercz, S. (2016). Do landscape structure and socio-economic variables explain the *Solidago* invasion? *Folia Geobotanica*, 51(1), 13–25. <https://doi.org/10.1007/s12224-016-9241-4>
- Szymura, M., Szymura, T. H., & Wolski, K. (2016). Invasive *Solidago* species: How large area do they occupy and what would be the cost of their removal? *Polish Journal of Ecology*, 64(1), 25–34. <https://doi.org/10.3161/15052249PJE2016.64.1.003>
- Szymura, T. H., Szymura, M., Zając, M., & Zając, A. (2018). Effect of anthropogenic factors, landscape structure, land relief, soil and climate on risk of alien plant invasion at regional scale. *Science of the Total Environment*, 626, 1373–1381. <https://doi.org/10.1016/j.scitotenv.2018.01.131>
- Taylor, K. T., Maxwell, B. D., Pauchard, A., Nuñez, M. A., Peltzer, D. A., Terwei, A., & Rew, L. J. (2016). Drivers of plant invasion vary globally: Evidence from pine invasions within six ecoregions. *Global Ecology and Biogeography*, 25(1), 96–106. <https://doi.org/10.1111/geb.12391>
- Thuiller, W., Georges, D., Engler, R., & Lafourcade, B. (2012). *Biomod: Tutorial*. Retrieved from <http://www.will.chez-alice.fr/pdf/BiomodTutorial.pdf>
- Thuiller, W., Georges, D., Gueguen, M., Engler, R., & Breiner, F. (2020). *biomod2: Ensemble platform for species distribution modeling*. R package version 3.4.13.
- Thuiller, W., Richardson, D. M., & Midgley, G. F. (2007). Will climate change promote alien plant invasions? *Biological Invasions*, 193, 197–211. https://doi.org/10.1007/978-3-540-36920-2_12
- Tokarska-Guzik, B. (2005). *The establishment and spread of alien plant species (kenophytes) in the flora of Poland*. Wydawnictwo Uniwersytetu Śląskiego.
- Tokarska-Guzik, B., Bzdęga, K., Nowak, T., Urbisz, A., Węgrzynek, B., & Dajdok, Z. (2015). *Propozycja listy roślin gatunków obcych, które mogą stanowić zagrożenie dla przyrody Polski i Unii Europejskiej – Uniwersytet Śląski w Katowicach, Katowice*. (The proposal lists of plants alien species that may endanger to Polish and European Union nature).
- Valavi, R., Elith, J., Lahoz-Monfort, J. J., & Guillera-Aroita, G. (2019). Block CV: An R package for generating spatially or environmentally separated folds for k-fold cross-validation of species distribution models. *Methods in Ecology and Evolution*, 10(2), 225–232. <https://doi.org/10.1111/2041-210X.13107>
- Vannette, R. L., & Fukami, T. (2014). Historical contingency in species interactions: Towards niche-based predictions. *Ecology Letters*, 17(1), 115–124. <https://doi.org/10.1111/ele.12204>
- Vilà, M., & Ibáñez, I. (2011). Plant invasions in the landscape. *Landscape Ecology*, 26(4), 461–472. <https://doi.org/10.1007/s10980-011-9585-3>
- Weber, E. (1997). Morphological variation of the introduced perennial *Solidago canadensis* L. sensu lato (Asteraceae) in Europe. *Botanical Journal of Linnean Society*, 123(3), 197–210. <https://doi.org/10.1111/j.1095-8339.1997.tb01413.x>
- Weber, E. (2000). Biological flora of Central Europe: *Solidago altissima* L. *Flora*, 195(2), 123–134. [https://doi.org/10.1016/S0367-2530\(17\)30960-X](https://doi.org/10.1016/S0367-2530(17)30960-X)
- Weber, E. (2001). Current and potential ranges of three exotic goldenrods (*Solidago*) in Europe. *Conservation Biology*, 15(1), 122–128. <https://doi.org/10.1111/j.1523-1739.2001.99424.x>
- Weber, E., & Jakobs, G. (2005). Biological flora of central Europe: *Solidago gigantea* Aiton. *Flora-Morphology, Distribution, Functional Ecology of Plants*, 200(2), 109–118. <https://doi.org/10.1016/j.flora.2004.09.001>
- Weidlich, E. W., Flórido, F. G., Sorcini, T. B., & Brancalion, P. H. (2020). Controlling invasive plant species in ecological restoration: A global review. *Journal of Applied Ecology*, 57(9), 1806–1817. <https://doi.org/10.1111/1365-2664.13656>
- Werner, P. A., Bradbury, I. A. N. K., & Grossi, R. S. (1980). The biology of Canadian weeds. 45 *Solidago canadensis* L. *Canadian Journal of Plant Science*, 60, 1393–1409. <https://doi.org/10.4141/cjps80-194>
- Williams, N. S., Hahs, A. K., & Morgan, J. W. (2008). A dispersal-constrained habitat suitability model for predicting invasion of alpine vegetation. *Ecological Applications*, 18(2), 347–359. <https://doi.org/10.1890/07-0868.1>
- Woodford, D. J., Richardson, D. M., MacIsaac, H. J., Mandrak, N. E., Van Wilgen, B. W., Wilson, J. R., & Weyl, O. L. (2016). Confronting the wicked problem of managing biological invasions. *NeoBiota*, 31, 63. <https://doi.org/10.3897/neobiota.31.10038>

- Yang, W., Ma, K., & Kreft, H. (2013). Geographical sampling bias in a large distributional database and its effects on species richness–environment models. *Journal of Biogeography*, 40(8), 1415–1426. <https://doi.org/10.1111/jbi.12108>
- Yates, K. L., Bouchet, P. J., Caley, M. J., Mengersen, K., Randin, C. F., Parnell, S., Fielding, A. H., Bamford, A. J., Ban, S., Barbosa, A. M., Dormann, C. F., Elith, J., Embling, C. B., Ervin, G. N., Fisher, R., Gould, S., Graf, R. F., Gregr, E. J., Halpin, P. N., ... Sequeira, A. M. M. (2018). Outstanding challenges in the transferability of ecological models. *Trends in Ecology & Evolution*, 33(10), 790–802. <https://doi.org/10.1016/j.tree.2018.08.001>
- Ye, X. Q., Yan, Y. N., Wu, M., & Yu, F. H. (2019). High capacity of nutrient accumulation by invasive *Solidago canadensis* in a coastal grassland. *Frontiers in Plant Science*, 10, 575. <https://doi.org/10.3389/fpls.2019.00575>
- Zajac, A., & Zajac, M. (2015). *Distribution of Kenophytes in the Polish Carpathians and their Foreland* (p. 304). Instytut Botaniki Uniwersytetu Jagiellońskiego.
- Zhang, F., & Wan, F. (2017). Canada Goldenrod *Solidago canadensis* L. In F. Wan, M. Jiang, & A. Zhan (Eds.), *Biological Invasions and Its Management in China. Invading Nature - Springer Series in Invasion Ecology*, 13, 143–15. Singapore: Springer. https://doi.org/10.1007/978-981-10-3427-5_10
- Zihare, L., & Blumberg, D. (2017). Insight into bioeconomy. *Solidago canadensis* as a valid resource. *Energy Procedia*, 128, 275–280. <https://doi.org/10.1016/j.egypro.2017.09.074>
- Zurell, D., Franklin, J., König, C., Bouchet, P. J., Dormann, C. F., Elith, J., Fandos, G., Feng, X., Guillerá-Arroita, G., Guisan, A., Lahoz-Monfort,

- J. J., Leitão, P. J., Park, D. S., Peterson, A. T., Rapacciuolo, G., Schmatz, D. R., Schröder, B., Serra-Diaz, J. M., Thuiller, W., ... Merow, C. (2020). A standard protocol for reporting species distribution models. *Ecography*, 43(9), 1261–1277. <https://doi.org/10.1111/ecog.04960>
- Zurell, D., Thuiller, W., Pagel, J., Cabral, J. S., Münkemüller, T., Gravel, D., Dullinger, S., Normand, S., Schiffers, K. H., Moore, K. A., & Zimmermann, N. E. (2016). Benchmarking novel approaches for modelling species range dynamics. *Global Change Biology*, 22(8), 2651–2664. <https://doi.org/10.1111/gcb.13251>

SUPPORTING INFORMATION

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

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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; Morón 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

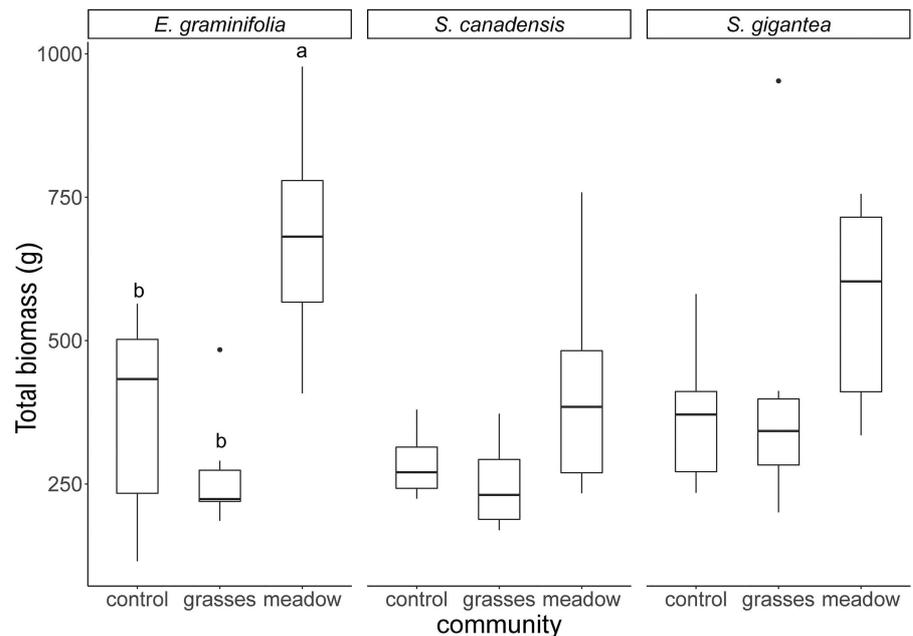


Figure 1. Total biomass production of different communities. Median value (thick line), upper and lower quartiles (box), 1.5 IQR (whiskers) ranges, and outliers (black dots) are shown.

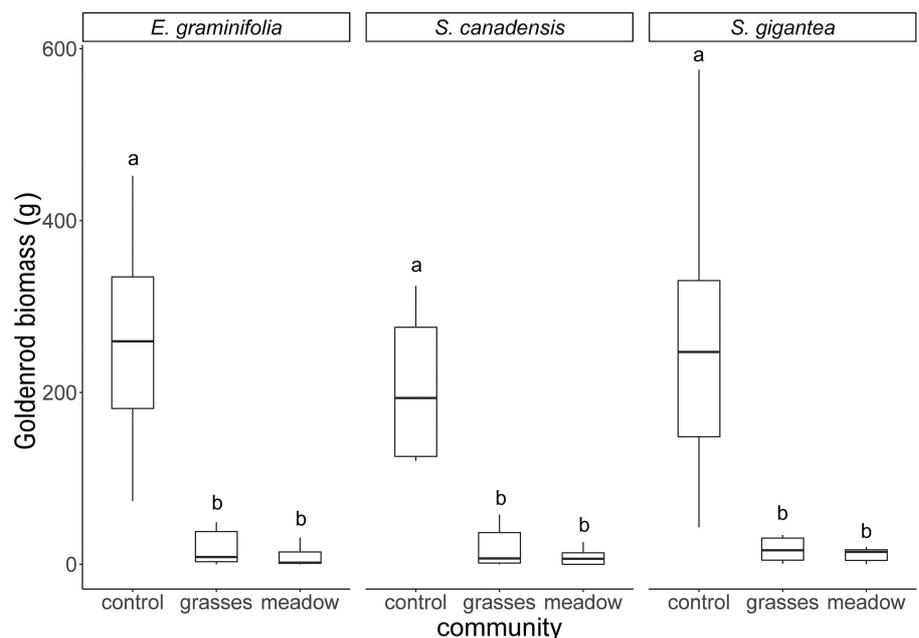


Figure 2. Goldenrod biomass production of different communities. Median value (thick line), upper and lower quartiles (box), and 1.5 IQR (whiskers) ranges are shown.

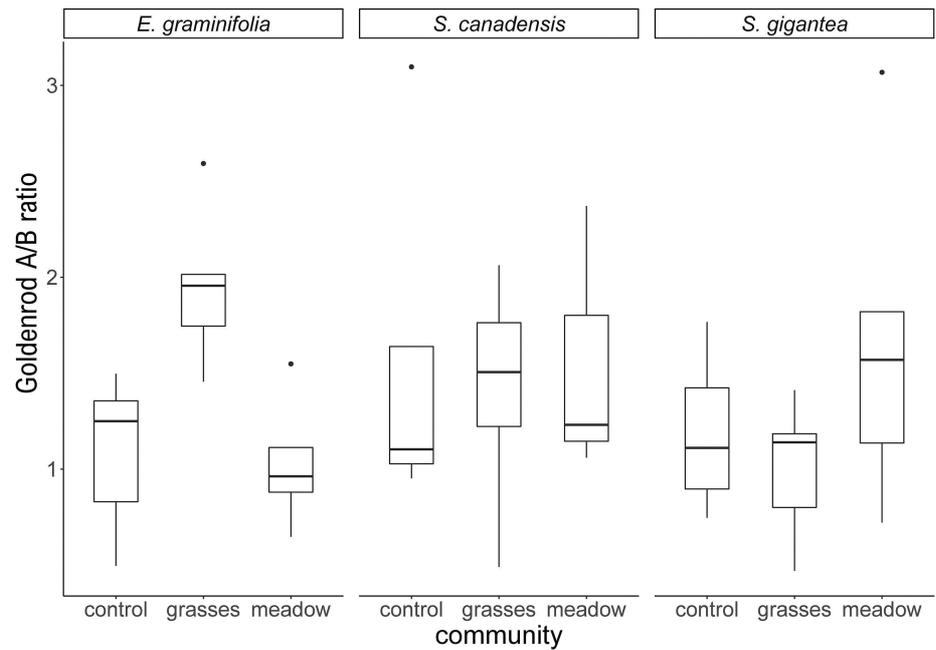


Figure 3. Ratio of above to below-ground biomass of goldenrods in different communities. Median value (thick line), upper and lower quartiles (box), 1.5 IQR (whiskers) ranges, and outliers (black dots) are shown.

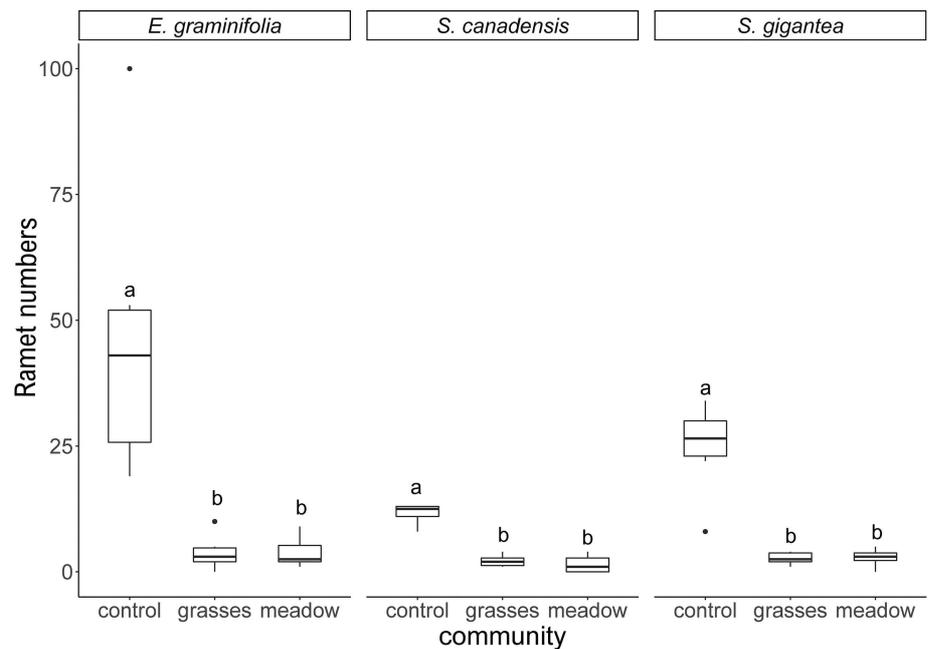


Figure 4. Number of ramets produced by goldenrods in different communities. Median value (thick line), upper and lower quartiles (box), 1.5 IQR (whiskers) ranges, and outliers (black dots) are shown.

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

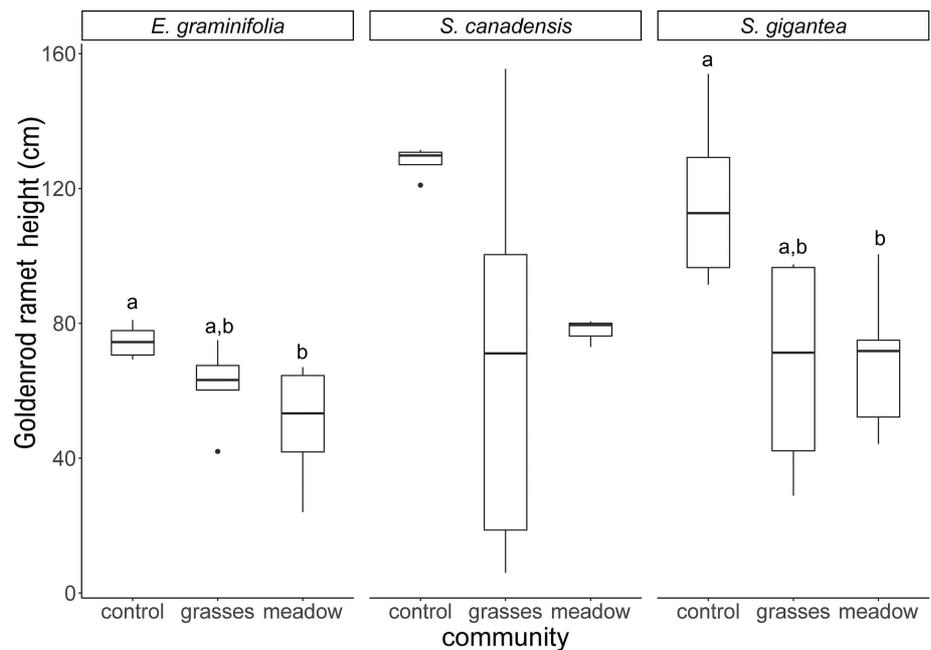


Figure 5. Height of ramets produced by goldenrods in different communities. Median value (thick line), upper and lower quartiles (box), 1.5 IQR (whiskers) ranges, and outliers (black dots) are shown.

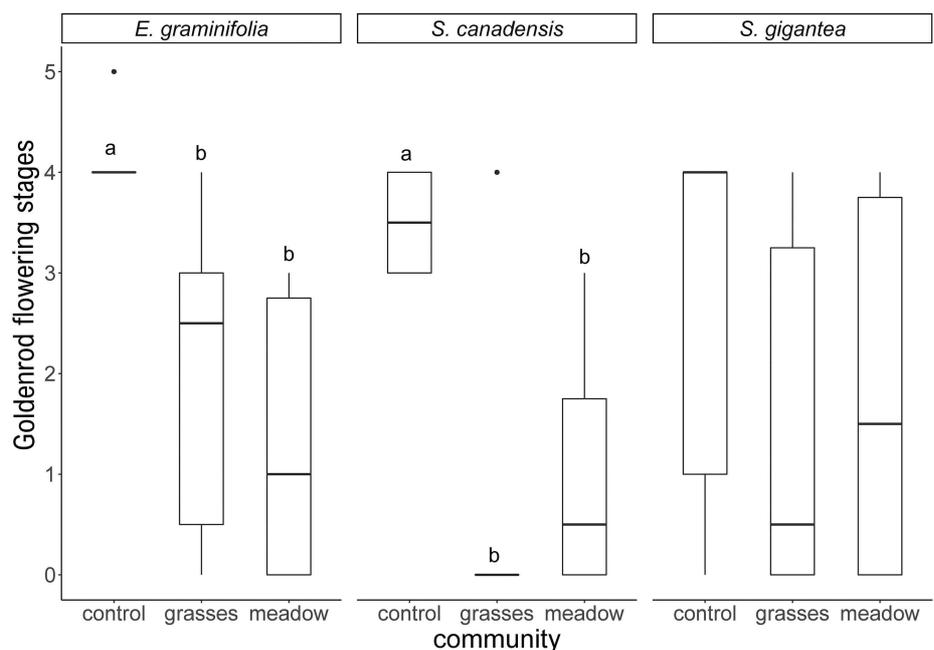


Figure 6. Flowering stages of goldenrods in different communities. Median value (thick line), upper and lower quartiles (box), 1.5 IQR (whiskers) ranges, and outliers (black dots) are shown.

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.

References

- Bartha S, Szentes S, Horváth A, Házi J, Zimmermann Z, Molnár C, Dancza I, Margoczi K, Pal RW, Purger D, Schmidt D, Óvari M, Komoly C, Sutyinszki Z, Szabo G, Csatho AI, Juhasz M, Penksza K, Molnár Z (2014) Impact of mid-successional dominant species on the diversity and progress of succession in regenerating temperate grasslands. *Applied Vegetation Science* 17: 201–213, <https://doi.org/10.1111/avsc.12066>
- Beaury EM, Finn JT, Corbin JD, Barr V, Bradley BA (2020) Biotic resistance to invasion is ubiquitous across ecosystems of the United States. *Ecology Letters* 23: 476–482, <https://doi.org/10.1111/ele.13446>

- Bengtsson J, Bullock JM, Egoh B, Everson C, Everson T, O'Connor T, O'Farrell PJ, Smith HG, Lindborg R (2019) Grasslands-more important for ecosystem services than you might think. *Ecosphere* 10: e02582, <https://doi.org/10.1002/ecs2.2582>
- Bullock JM, Pywell RF, Walker KJ (2007) Long-term enhancement of agricultural production by restoration of biodiversity. *Journal of Applied Ecology* 44: 6–12, <https://doi.org/10.1111/j.1365-2664.2006.01252.x>
- Byers JE, Noonburg EG (2003) Scale dependent effects of biotic resistance to biological invasion. *Ecology* 84: 1428–1433, <https://doi.org/10.1890/02-3131>
- Byun C, de Blois S, Brisson J (2018) Management of invasive plants through ecological resistance. *Biological Invasions* 20: 13–27, <https://doi.org/10.1007/s10530-017-1529-7>
- CABI (2020) Invasive Species Compendium. www.cabi.org/isc/ (accessed 24 September 2020)
- Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions* 15: 22–40, <https://doi.org/10.1111/j.1472-4642.2008.00521.x>
- Chamberlain SA, Bronstein JL, Rudgers JA (2014) How context dependent are species interactions? *Ecology Letters* 17: 881–890, <https://doi.org/10.1111/ele.12279>
- Chapman GP (1996) The biology of grasses. Cab International, Wallingford, UK, 273 pp
- Chytrý M, Jarosik V, Pyšek P, Hájek O, Knollová I, Tichý L, Danihelka J (2008) Separating habitat invasibility by alien plants from the actual level of invasion. *Ecology* 89: 1541–1553, <https://doi.org/10.1890/07-0682.1>
- Clark NE, Lovell R, Wheeler BW, Higgins SL, Depledge MH, Norris K (2014) Biodiversity, cultural pathways, and human health: a framework. *Trends in Ecology & Evolution* 29: 198–204, <https://doi.org/10.1016/j.tree.2014.01.009>
- Czarniecka-Wiera M, Kački Z, Chytrý M, Palpurina S (2019) Diversity loss in grasslands due to the increasing dominance of alien and native competitive herbs. *Biodiversity and Conservation* 28: 2781–2796, <https://doi.org/10.1007/s10531-019-01794-9>
- Czarniecka-Wiera M, Szymura TH, Kački Z (2020) Understanding the importance of spatial scale in the patterns of grassland invasions. *Science of The Total Environment* 138669, <https://doi.org/10.1016/j.scitotenv.2020.138669>
- Dawson W, Schrama M (2016) Identifying the role of soil microbes in plant invasions. *Journal of Ecology* 104: 1211–1218, <https://doi.org/10.1111/1365-2745.12619>
- D'Antonio CM (1993) Mechanisms controlling invasions of coastal plant communities by the alien succulent, *Carpobrotus edulis*. *Ecology* 74: 83–95, <https://doi.org/10.2307/1939503>
- Díaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution* 16: 646–655, [https://doi.org/10.1016/S0169-5347\(01\)02283-2](https://doi.org/10.1016/S0169-5347(01)02283-2)
- Dubicki A, Dubicka M, Szymanowski M (2002) Klimat Wrocławia. [Climat of Wrocław] In: Smolnicki K, Szykasiuk M (eds), Środowisko Wrocławia [Environment of Wrocław] Dolnośląska Fundacja Ekorozwoju, Wrocław, Poland, pp 9–20
- Elton CS (1958) The ecology of invasions by animals and plants. Methuen, London, England, 181 pp, <https://doi.org/10.1007/978-1-4899-7214-9>
- Egoh BN, Bengtsson J, Lindborg R, Bullock JM, Dixon AP, Rouget M (2016) The importance of grasslands in providing ecosystem services: opportunities for poverty alleviation. In: Potschin M, Haines-Young R, Fish R, Turner RK (eds), Routledge handbook of ecosystem services. Routledge, New York, USA, pp 421–441, <https://doi.org/10.4324/9781315775302-37>
- Eriksson O, Cousins SAO, Bruun H-H (2002) Land-use history and fragmentation of traditionally managed grasslands in Scandinavia. *Journal of Vegetation Science* 13: 743–748, <https://doi.org/10.1111/j.1654-1103.2002.tb02102.x>
- European Community (2014) Regulation of the European Parliament and of the Council on the prevention and management of the introduction and spread of invasive alien species. Regulation EU No. 1143/2014 Brussels. Belgium, <http://data.europa.eu/eli/reg/2014/1143/oj>
- Fenesi A, Geréd J, Meiners SJ, Tóthmérész B, Török P, Ruprecht E (2015) Does disturbance enhance the competitive effect of the invasive *Solidago canadensis* on the performance of two native grasses? *Biological Invasions* 17: 3303–3315, <https://doi.org/10.1007/s10530-015-0954-8>
- Frankow-Lindberg BE (2012) Grassland plant species diversity decreases invasion by increasing resource use. *Oecologia* 169: 793–802, <https://doi.org/10.1007/s00442-011-2230-7>
- Fridley JD, Stachowicz JJ, Naeem S, Sax, DF, Seabloom EW, Smith MD, Stohlgren TJ, Tilman D, Von Holle B (2007) The invasion paradox: reconciling pattern and process in species invasions. *Ecology* 88: 3–17, [https://doi.org/10.1890/0012-9658\(2007\)88\[3:TIPRPA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88[3:TIPRPA]2.0.CO;2)
- Fuller RA, Irvine KN, Devine-Wright P, Warren PH, Gaston KJ (2007) Psychological benefits of greenspace increase with biodiversity. *Biology Letters* 3: 390–394, <https://doi.org/10.1098/rsbl.2007.0149>
- Galland T, Adeux G, Dvořáková H, E-Vojtkó A, Orbán I, Lussu M Puy J, Blažek P, Lanta V, Lepš J, dr Bello F, Carmona CP, Valencia E, Götzenberger L (2019) Colonization resistance and establishment success along gradients of functional and phylogenetic diversity in experimental plant communities. *Journal of Ecology* 107: 2090–2104, <https://doi.org/10.1111/1365-2745.13246>

- Hanski I, von Herten L, Fyhrquist N, Koskinen K, Torppa K, Laatikainen T, Karisola P, Auvinen P, Paulin L, Mäkelä MJ, Vartiainen E, Kosunen TU, Alenius H, Hahtela T (2012) Environmental biodiversity, human microbiota, and allergy are interrelated. *PNAS* 109: 8334–8339, <https://doi.org/10.1073/pnas>
- Hedblom M, Lindberg F, Vogel E, Wissman J, Ahrné K (2017) Estimating urban lawn cover in space and time: Case studies in three Swedish cities. *Urban Ecosystems* 20: 1109–1119, <https://doi.org/10.1007/s11252-017-0658-1>
- Hejda M, Pyšek P, Jarošík V (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology* 97: 393–403, <https://doi.org/10.1111/j.1365-2745.2009.01480.x>
- Hierro JL, Maron JL, Callaway RM (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *Journal of Ecology* 93: 5–15, <https://doi.org/10.1111/j.0022-0477.2004.00953.x>
- Hooper DU, Dukes JS (2010) Functional composition controls invasion success in a California serpentine grassland. *Journal of Ecology* 98: 764–777, <https://doi.org/10.1111/j.1365-2745.2010.01673.x>
- Hönigová I, Vačkář D, Lorencová E, Melichar J, Götzl M, Sonderegger G, Oušková V, Hošek M, Chobot K (2012) Survey on grassland ecosystem services. Report to the EEA-European Topic Centre on Biological Diversity. Nature Conservation Agency of the Czech Republic, Prague, Czech Republic, 78 pp
- Hui C, Richardson DM, Landi P, Minoarivelo HO, Garnas J, Roy HE (2016) Defining invasiveness and invasibility in ecological networks. *Biological Invasions* 18: 971–983, <https://doi.org/10.1007/s10530-016-1076-7>
- Isselstein J, Jeangros B, Pavlu V (2005) Agronomic aspects of biodiversity targeted management of temperate grasslands in Europe - a review. *Agronomy Research* 3(2): 139–151
- Klaus VH (2013) Urban grassland restoration: a neglected opportunity for biodiversity conservation. *Restoration Ecology* 21: 665–669, <https://doi.org/10.1111/rec.12051>
- Lachowycz K, Jones AP (2013) Towards a better understanding of the relationship between greenspace and health: Development of a theoretical framework. *Landscape and Urban Planning* 118: 62–69, <https://doi.org/10.1016/j.landurbplan.2012.10.012>
- Levine JM, Adler PB, Yelenik SG (2004) A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters* 7: 975–989, <https://doi.org/10.1111/j.1461-0248.2004.00657.x>
- Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology* 80: 1522–1536, [https://doi.org/10.1890/0012-9658\(1999\)080\[1522:GPOPIA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[1522:GPOPIA]2.0.CO;2)
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10: 689–710, [https://doi.org/10.1890/1051-0761\(2000\)010\[0689:BICEGC\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2)
- Mangiafico S (2020) rcompanion: Functions to Support Extension Education Program Evaluation. R package version 2.3.26. <https://CRAN.R-project.org/package=rcompanion>
- Maron J, Marler M (2007) Native plant diversity resists invasion at both low and high resource levels. *Ecology* 88: 2651–2661, <https://doi.org/10.1890/06-1993.1>
- Moroń D, Lenda M, Skórka P, Szentgyörgyi H, Settele J, Woyciechowski M (2009) Wild pollinator communities are negatively affected by invasion of alien goldenrods in grassland landscapes. *Biological Conservation* 142: 1322–1332, <https://doi.org/10.1016/j.biocon.2008.12.036>
- Moroń D, Skórka P, Lenda M, Kajzer-Bonk J, Mielczarek Ł, Rożej-Pabijan E, Wantuch M (2019) Linear and non-linear effects of goldenrod invasions on native pollinator and plant populations. *Biological Invasions* 21: 947–960, <https://doi.org/10.1007/s10530-018-1874-1>
- Norton BA, Bending GD, Clark R, Corstanje R, Dunnett N, Evans KL, Grafius DR, Gravestock E, Grice SM, Harris JA, Hilton S, Hoyle H, Lim E, Mercer TG, Pawlett M, Pescott OL, Richards JP, Southon GE, Warren PH (2019) Urban meadows as an alternative to short mown grassland: effects of composition and height on biodiversity. *Ecological Applications* 29: e01946, <https://doi.org/10.1002/eap.1946>
- Oakley CA, Knox JS (2013) Plant species richness increases resistance to invasion by non-resident plant species during grassland restoration. *Applied Vegetation Science* 16: 21–28, <https://doi.org/10.1111/j.1654-109X.2012.01202.x>
- Onandia G, Schittko C, Ryo M, Bernard-Verdier M, Heger T, Joshi J, Kowarik I, Gessler A (2019) Ecosystem functioning in urban grasslands: The role of biodiversity, plant invasions and urbanization. *PLoS ONE* 14: e0225438, <https://doi.org/10.1371/journal.pone.0225438>
- Queiroz C, Beilin R, Folke C, Lindborg R (2014) Farmland abandonment: Threat or opportunity for biodiversity conservation? *Frontiers in Ecology and the Environment* 12: 288–296, <https://doi.org/10.1890/120348>
- Pal RW, Maron JL, Nagy DU, Waller LP, Tosto A, Liao H, Callaway RM (2020) What happens in Europe stays in Europe: apparent evolution by an invader does not help at home. *Ecology* 101: e03072, <https://doi.org/10.1002/ecy.3072>
- Pe'er G, Dicks LV, Visconti P, Arlettaz R, Baldi A, Benton TG, Collins S, Dieterich M, Gregory RD, Hartig F, Henle K, Hobson PR, Kleijn D, Neumann RK, Robijns T, Schmidt J, Schwartz A, Sutherland WJ, Turbé A, Wulf F, Scott AV (2014) EU agricultural reform fails on biodiversity. *Science* 344: 1090–1092, <https://doi.org/10.1126/science.1253425>

- Pokorny ML, Sheley RL, Zabinski CA, Engel RE, Svejcar TJ, Borkowski JJ (2005) Plant functional group diversity as a mechanism for invasion resistance. *Restoration Ecology* 13: 448–459, <https://doi.org/10.1111/j.1526-100X.2005.00056.x>
- Rejmánek M, Richardson DM, Pyšek P (2005) Plant invasions and invasibility of plant communities. *Vegetation Ecology* 20: 332–355
- Schittko C, Hawa M, Wurst S (2014) Using a multi-trait approach to manipulate plant functional diversity in a biodiversity-ecosystem function experiment. *PLoS ONE* 9: e99065, <https://doi.org/10.1371/journal.pone.0099065>
- Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution* 17: 170–176, [https://doi.org/10.1016/S0169-5347\(02\)02495-3](https://doi.org/10.1016/S0169-5347(02)02495-3)
- Skórka P, Lenda M, Tryjanowski P (2010) Invasive alien goldenrods negatively affect grassland bird communities in Eastern Europe. *Biological Conservation* 143: 856–861, <https://doi.org/10.1016/j.biocon.2009.12.030>
- Smith MD, Wilcox JC, Kelly T, Knapp AK (2004) Dominance not richness determines invasibility of tallgrass prairie. *Oikos* 106: 253–262, <https://doi.org/10.1111/j.0030-1299.2004.13057.x>
- Southon GE, Jorgensen A, Dunnett N, Hoyle H, Evans KL (2018) Perceived species-richness in urban green spaces: Cues, accuracy and well-being impacts. *Landscape and Urban Planning* 172: 1–10, <https://doi.org/10.1016/j.landurbplan.2017.12.002>
- Szépligeti M, Körösi Á, Szentirmai I, Házi J, Bartha D, Bartha S (2018) Evaluating alternative mowing regimes for conservation management of Central European mesic hay meadows: a field experiment. *Plant Biosystems* 152: 90–97, <https://doi.org/10.1080/11263504.2016.1255268>
- Szymura M, Szymura TH (2015a) Growth, phenology, and biomass allocation of alien *Solidago* species in central Europe. *Plant Species Biology* 30: 245–256, <https://doi.org/10.1111/1442-1984.12059>
- Szymura M, Szymura TH (2015b) The dynamics of growth and flowering of invasive *Solidago* species. *Steciana* 19: 143–152, <https://doi.org/10.12657/steciana.019.016>
- Szymura M, Szymura TH (2016) Interactions between alien goldenrods (*Solidago* and *Euthamia* species) and comparison with native species in Central Europe. *Flora* 218: 51–61, <https://doi.org/10.1016/j.flora.2015.11.009>
- Szymura M, Szymura TH, Wolski K, Świercz S (2018) Can native grass species outcompete invasive goldenrods? Results of a replacement series experiment. *Weed Research* 58: 304–317, <https://doi.org/10.1111/wre.12306>
- Thompson GL, Kao-Kniffin J (2019) Urban Grassland Management Implications for Soil C and N Dynamics: A Microbial Perspective. *Frontiers in Ecology and Evolution* 7: 315, <https://doi.org/10.3389/fevo.2019.00315>
- Tilman D (2004) Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences* 101: 10854–10861, <https://doi.org/10.1073/pnas.0403458101>
- Villoslada M, Vinogradovs I, Ruskule A, Veidemane K, Nikodemus O, Kasparinskis R, Sepp K, Gulbinas J (2018) A multitiered approach for grassland ecosystem services mapping and assessment: The Viva Grass tool. *One Ecosystem* 3: e25380, <https://doi.org/10.3897/oneeco.3.e25380>
- Weber E (2000) Biological flora of Central Europe: *Solidago altissima* L. *Flora* 195: 123–134, [https://doi.org/10.1016/S0367-2530\(17\)30960-X](https://doi.org/10.1016/S0367-2530(17)30960-X)
- Weber E, Jakobs G (2005) Biological flora of central Europe: *Solidago gigantea* Aiton. *Flora* 200: 109–118, <https://doi.org/10.1016/j.flora.2004.09.001>

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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3.3. The impact of restoration methods for Solidago-invaded land on soil invertebrates

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OPEN

The impact of restoration methods for *Solidago*-invaded land on soil invertebrates

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The belowground community structure of soil biota depends on plant composition and may be affected by invasive plant species. We hypothesized that the type of land restoration method applied affects the abundance and composition of soil invertebrates. Our field experiment centred on *Solidago* species control using different seed mixtures and methods of seed introduction (sowing mixtures: grasses, grasses with legumes, seeds from a seminatural meadow, and application of fresh hay) and different frequencies of mowing (one, two, or three times per year). Soil invertebrates were identified to the taxa, using light microscopes. Richness and diversity indices were calculated, and a redundancy analysis was conducted. Generally, mowing intensity negatively influenced soil organisms, although increased mowing frequency positively affected the abundance of some taxa (Symphyla, Hemiptera). Mowing twice per year decreased the abundance of soil invertebrates, but not their diversity. Soil invertebrate taxa had the greatest abundance in the plots sown with a seed mixture containing grasses with legumes. Among the restoration methods studied, mowing once a year and introducing grasses with legumes represented the least harmful strategy with regard to soil invertebrate abundance. Further studies are needed to investigate the dynamics of soil mesofauna exposed to long-term mowing and changes in vegetation characteristics.

Plant invasions have serious negative effects on ecosystems and species diversity^{1,2} and can disrupt the linkages between the above- and belowground communities^{3,4}. Goldenrods (*Solidago canadensis* L. and *Solidago gigantea* Aiton.) are among the most widespread invasive alien plants in Central Europe⁵. Invasive *Solidago* species can alter soil physicochemical properties (e.g., soil moisture, water holding capacity, organic carbon, total nitrogen content, available phosphorus, exchangeable cations) and cause biological changes in the soil (e.g., microbial biomass, respiration rate, nitrogen mineralization, soil enzyme activities)^{2,6–8}. Moreover, *Solidago* invasion has had negative consequences in communities of springtails⁷, nematodes⁹, coleopterans^{10,11}, ants^{12–14}, and pollinators¹⁵.

The ecological restoration of lands invaded by alien plants may use herbicides, mowing, burning, and labour-intensive practices such as slashing or hand-felling and harrowing^{16–18}. However, herbicides negatively affect non-target species and the belowground community^{18,19}. In addition, during restoration activities, seeding methods, seeding rates, and the use of a cover crop with native grasses respectively influence the disturbance, colonization, and nitrogen content of the soil^{16,20}. Either individually or in combination, multiple forms of control strategies, such as manual removal, periodic flooding, grazing, scalping, mowing, rototilling, different seeding methods, turf stripping, and the use of herbicides have been investigated in recent studies on the ecological restoration of *Solidago*-invaded land^{20–22}. Świercz et al. showed that herbicide (containing glyphosate) was beneficial for short-term eradication of invasive *Solidago* spp. and subsequent restoration of a meadow²¹. However, a 6-year experiment by Szymura et al. showed that herbicides were not effective for long-term removal of *Solidago* spp.²⁰. In their study, adding fresh hay and mowing twice per year represented the best practice for restoring old fields invaded by *Solidago* spp.

Soil invertebrates inhabit the upper layer of soil and include medium-sized organisms (0.2–2 mm), such as most of the Collembola, Acari, Protura, and Nematoda, among others²³. Soil invertebrates function as a community that supports major soil functions, such as the decomposition of organic matter and nutrient cycling²⁴.

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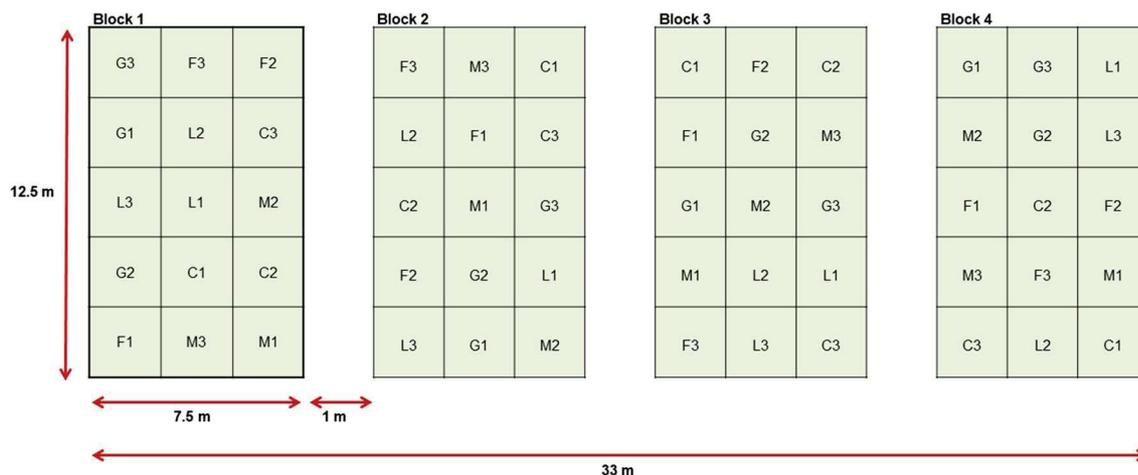


Figure 1. Experimental design based on sowing mixtures [grasses (G), grasses with legumes (L), seeds from the seminatural meadow (M), application of fresh hay (H), and control (C)] and mowing regimes [once (1), twice (2), and three times (3)].

Thus, changes in soil fauna, directly or indirectly, have impacts on soil functioning. Soil fauna communities and certain taxa or species serve as important indicators of soil health²⁵.

Plant species composition can alter soil ecosystems by changing the structure of the habitat and its abiotic properties²⁷. In addition, plant species composition can cause changes in soil invertebrate abundance and diversity. For example, both grasses and legumes have a beneficial effect on the density and diversity of *Collembola*²⁶, while invasive plants reduce their density⁷.

Many restoration practices mainly focus on the aboveground components of ecosystems²⁷. However, restoration ecology involves the integration of aboveground–belowground linkages, or plant–soil interactions, as well as the identification of effective intervention practices and the prediction of ecosystem recovery^{3,27,28}. Although the impact of *Solidago* spp. on belowground soil components such as soil invertebrates has not been well documented⁷, it is known that soil microarthropods are sensitive to land management practices. For example, frequent mowing negatively affects soil organisms such as nematodes²⁹, earthworms³⁰, and bacteria³¹. Therefore, soil invertebrates can be used as bioindicators of biological soil quality through assessment of their rapid response to any changes in the soil environment^{32–34}.

The current study aimed to evaluate how *Solidago* control methods and the use of different seed mixtures affected soil invertebrates in *Solidago*-invaded stands undergoing land restoration. We hypothesized that the abundance and composition of different soil invertebrates collected from these stands would vary according to the type of restoration method. From a practical point of view, we aimed to identify a method that effectively removes *Solidago*, while maintaining high biodiversity and abundance of soil invertebrates.

Materials and methods

Study site. The experiment was conducted on abandoned former agricultural land dominated by invasive North American *Solidago* spp. (*S. gigantea* and *S. canadensis*), at an altitude of 118 m a.s.l. The land is in a small river valley and is surrounded by suburban buildings and extensively used meadows in Wrocław, Poland (51°09'42.57"N, 17°06'43.97"E; elevation 116.4 m). The soil type is Anthropric Regosol, loamy sand texture. The mean annual temperature in the region is 9 °C, and the mean annual precipitation is 578.2 mm. Meteorological data for the period of 1968–2019 were obtained from the Agro- and Hydrometeorology Observatory in Swójczyce, Wrocław (51°06'56.6"N, 17°08'29.4"E).

Field experimental design. The field experiment on *Solidago* species removal and land reclamation was established in April 2020. The experiment used a 5 × 3 factorial arrangement in a completely randomized design with four replications, as shown in Fig. 1. The four blocks, each containing 15 plots (2.5 × 2.5 m), were established with a separation of 1 m from each other. The entire experimental area was mowed, and the soil was then prepared for seeding, using a rototiller followed by a power harrow. After the area was seeded, it was compacted with a roller. Two experimental factors were used: (1) various methods of seed introduction and seed composition (sowing mixtures: grasses, grasses with legumes, seeds collected from the seminatural meadow, application of fresh hay and without seed application) (Table 1), and (2) different frequencies of mowing (one, two, or three times per year). The species composition of seed mixtures and fresh hay are presented in Supplementary Table S1. In both 2020 and 2021, the plots were mown according to the planned scheme: once (June), twice (June and August), or three times (June, August, and September).

Material collection and preparation. A single sample of soil was collected from the centre of each plot with the use of a 10-cm-diameter circular sampler, at a depth of 10 cm in autumn (September 2020 and August 2021), spring (April 2021), and summer (June 2021), respectively. The samples were collected within 2 × 2 m

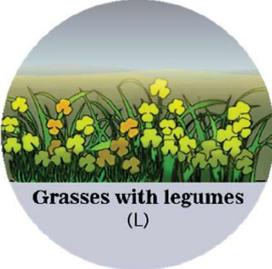
Sowed mixtures	Description
 <p>Grasses (G)</p>	Conventional mixture of four grass species used for grassland establishment
 <p>Grasses with legumes (L)</p>	Four grass species (the same used in the G mixture), along with two clover species
 <p>Semi-natural meadow (M)</p>	A mixture of 37 plant species typically occurring in seminatural grasslands. Rieger-Hofmann GmbH distributes the specialized seed mixture, which is produced using seed mixtures of native species with a controlled geographical origin
 <p>Fresh hay (F)</p>	Fresh hay was collected at the Experimental Station of Wrocław University of Environmental and Life Sciences in Radomierz (50°54'15.1"N, 15°53'58.8"E), Silesia, Poland, Central Europe. The station is located in the sub-mountain area, Kaczawskie Mountains. The pastures are grazed for the entire growing season, and rotation pasturage is used, with sporadic mowing. During the field observation in June 2020, 47 species were observed. The fresh hay was collected and spread in July 2020
 <p>Control (C)</p>	No seed application

Table 1. Various methods of seed introduction and composition (The species composition of seed mixtures and fresh hay are presented in Supplementary Table S1).

areas inside each experimental plot. The soil samples were illuminated in Tullgren funnels (25 W light bulb) for 24 h. Soil organisms extracted from the soil were kept in 75% alcohol until their identification according to taxa. The soil organisms were identified according to the Soil Invertebrate Key of the Ecological Society of America³⁵.

Data analysis. The richness and diversity indices of the total fauna communities were calculated. The Shannon–Weaver index (H') was calculated according to the following formula³⁶:

df	Seed		Mowing		Season		Seed × Mowing		Seed × Season		Mowing × Season	
	4		2		3		8		12		6	
	F	p	F	p	F	p	F	p	F	p	F	p
Abundance	0.35	0.84	3.84	0.02	29.28	< 0.001	1.70	0.10	0.77	0.68	0.58	0.75
Number of taxa	3.45	0.01	2.95	0.06	57.43	< 0.001	0.94	0.49	1.04	0.42	1.99	0.07
Shannon–Weaver	2.73	0.03	0.13	0.87	9.24	< 0.001	0.82	0.59	1.35	0.19	0.41	0.87
Pielou	0.68	0.60	1.03	0.35	57.00	< 0.001	0.65	0.74	1.33	0.20	0.36	0.90
Margalef	2.88	0.02	0.72	0.49	8.08	< 0.001	0.86	0.55	0.32	0.34	1.75	0.11

Table 2. The statistical summary of the effects of experimental treatments on the community indices of soil invertebrates. Bold values indicate significant effects.

$$H' = - \sum_{i=1}^R p_i \ln p_i$$

where p_i is the proportion of individuals belonging to the i th taxa and R is the total number of species. The Pielou index (J) was calculated according to the formula³⁷:

$$J = \frac{H'}{\ln(S)}$$

where H' is the Shannon–Weaver index and S is the total number of species in a sample.

The Margalef species richness index (D) was calculated according to the following formula³⁸:

$$D = \frac{S - 1}{\ln(N)}$$

where S is the total number of species in a sample and N is the total number of individuals in the sample.

Statistical analysis was done with SAS University Edition (version 9.0), using the generalized linear mixed model (GLMM) with repeated measurements. The explanatory variables were mowing, seed introduction method, season, and their interactions. The repeated factor was the season, and the random factor was the block. Significant differences between treatments were revealed using the Tukey HSD test ($p \leq 0.05$). The invertebrate taxa were correlated with the environmental factors by using redundancy analysis (RDA) performed in Canoco 5.0. The data were log-transformed before analysis. Only taxa that occurred in at least three samples were included in the analysis.

Ethics approval. The experimental research and field studies on plants, including the collection of plant material, complied with the relevant institutional, national, and international guidelines and legislation.

Results

Community responses. Both experimental factors, the seed composition and introduction method and the mowing regimes, significantly affected the soil invertebrates (Table 2). The average number of all organisms was significantly higher in plots mowed once compared with plots mowed twice (Fig. 2A), and the diversity indices differed significantly between seed introduction methods (Table 2). The number of taxa was higher in plots where the mixture of grass with legumes was sown (L), in comparison with control (C) and grass mixture (G) plots (Fig. 2B). In addition, two diversity indices (Shannon Weaver and Margalef) showed that higher diversity was associated with legumes (L) relative to other treatments, particularly the use of grass species (G) (Fig. 2C,D). The interactions of seed × mowing, seed × season, and mowing × season did not yield significant differences, while season significantly affected abundance, number of taxa, and both diversity indices (Table 2).

Taxa responses. Among all factors, mowing had the greatest impact on the abundance of all soil invertebrate taxa (Table 3). Mowing once positively affected Isopoda, Chilopoda, Oribatida, Gamasida, and adult Coleoptera abundance (Fig. 3A,B,C,D,H). Seed introduction methods significantly affected Diptera larvae and Coleoptera adults (Table 3). In both cases, the mean number of organisms was higher in plots where grasses with legumes (L) were sown compared with other seed mixtures (Fig. 3E,F), and there were no differences between other seed composition and introduction methods. The differences in Nematoda abundance were significant for seed composition and introduction method, as well as season (Fig. 3G). Season was significant for all taxa except Diptera larvae (Table 3).

Redundancy analysis (Fig. 4) was used to compare the relative effects of mowing and the seed composition and introduction method on different taxa simultaneously (see the results of redundancy analysis in Supplementary Table S2). The abundance of most of the soil invertebrate taxa had positive correlations with the grass with legumes mixture and mowing once per season. The abundance of a few taxa (Symphyta, Hemiptera) was positively associated with greater mowing frequency. The effects of the seed introduction method were less distinct. Most

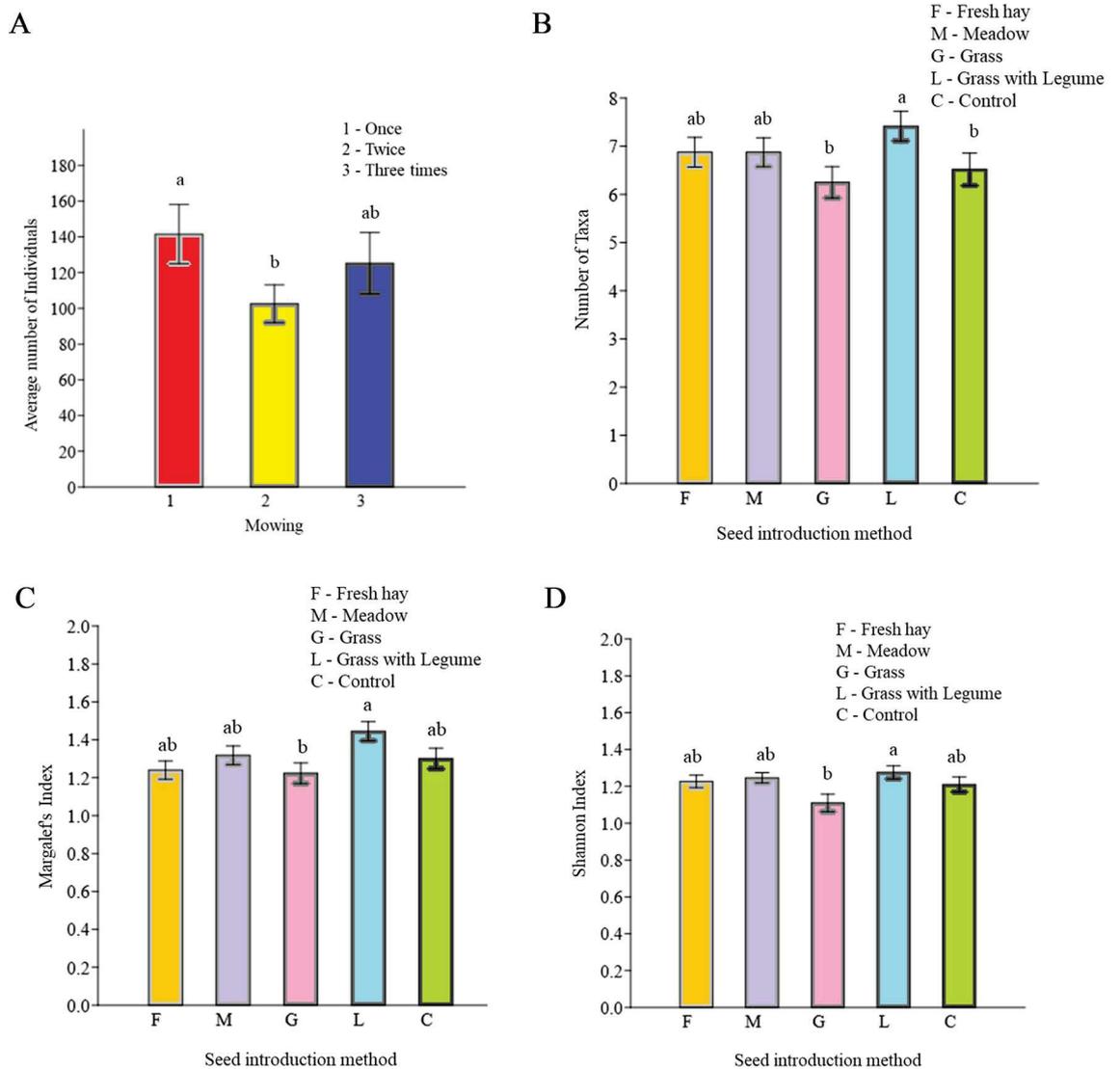


Figure 2. The effects of mowing and seed introduction methods on the community indices of soil invertebrates and their demographic responses. The different lowercase letters indicate significant differences between treatments, $p \leq 0.05$.

of the taxa (e.g., Isopoda, Collembola, Chilopoda) were positively oriented to the grass with legumes mixture (L), particularly in comparison with grass and the control.

Discussion

Land restoration methods are often applied to large areas, and they should not only be effective but also safe for the environment³⁹. It is important to assess the risk related to the application of land restoration methods with regard to both the aboveground impacts and the belowground effects. A useful tool for assessing changes in the soil environment is the analysis of soil fauna occurrence and diversity. The indicators based on soil fauna are related to soil functionality and further plant growth⁴⁰. Soil fauna mainly supports the decomposition of soil organic matter and affects the turnover of nutrients⁴¹. The presence of these organisms is closely related to the soil structure and the chemical properties of the soil, and any changes in soil conditions could have an impact on this group of organisms⁴².

We found that high mowing frequency negatively affected soil fauna abundance. This study tested three mowing regimes (one, two, and three times a year) and revealed that mowing once per year positively affected soil fauna. This finding is in line with the study of Zhao et al., in which nematode abundance decreased under more frequent mowing, from once per year (high intensity) to once every 6–12 years (low frequency)²⁹. In addition, unmown meadows were more beneficial for earthworms relative to meadows mown once a year³⁰.

Van Eekeren et al. concluded that mowing without tillage is one of the best practices for restoring the soil micro-arthropods and ecosystem services in permanent grasslands⁴³. Mowing techniques (e.g., the type of mowing heads and mower) can also have a considerable impact arthropod fauna^{44,45}. However, Hyvönen et al. found

Soil Invertebrates	Seed		Mowing		Season		Seed × Mowing		Seed × Season		Mowing × Season	
	4		2		3		8		12		6	
df	F	p	F	p	F	p	F	p	F	p	F	p
Astigmata	1.15	0.33	0.24	0.79	6.22	<0.001	0.84	0.57	1.33	0.20	0.70	0.65
Chilopoda	0.77	0.54	4.07	0.02	15.04	<0.001	1.90	0.06	0.80	0.65	1.24	0.29
Collembola	0.60	0.66	2.12	0.12	31.02	<0.001	1.66	0.11	1.03	0.43	0.68	0.66
Gamasida	1.06	0.38	0.81	0.45	45.31	<0.001	2.58	0.01	0.71	0.74	1.05	0.39
Isopoda	1.23	0.30	3.36	0.04	10.32	<0.001	0.77	0.63	1.01	0.44	2.05	0.06
Oribatida	0.79	0.53	3.47	0.03	18.84	<0.001	0.35	0.94	0.63	0.82	1.95	0.07
Nematoda	1.71	0.15	0.17	0.85	14.11	<0.001	1.10	0.37	2.60	0.00	0.67	0.68
Symphyla	1.63	0.17	0.05	0.95	15.18	<0.001	1.56	0.14	0.65	0.80	1.73	0.12
Arachnida	0.40	0.81	0.33	0.72	8.74	<0.001	0.95	0.48	0.54	0.89	0.80	0.57
Diptera larvae	4.02	0.00	0.16	0.85	4.33	0.055	0.57	0.80	1.05	0.40	1.68	0.13
Coleoptera adult	2.91	0.02	3.44	0.03	11.76	<0.001	0.37	0.94	0.72	0.73	0.90	0.49
Coleoptera larvae	1.27	0.28	0.43	0.65	8.82	<0.001	0.71	0.68	0.43	0.95	0.25	0.96

Table 3. The statistical summary of the effects of experimental treatments and their interactions on abundance of the soil invertebrates. Bold values indicate significant effects.

that mown meadows had higher abundances of pollinators such as bumblebees and honeybees³⁰. The effect of mowing on the belowground ecosystem is generally unknown and needs further study. We suggest that mowing indirectly affects soil fauna through changes in soil conditions. Soil fauna is closely related to soil functions and microbial activity⁴⁶, and mowing negatively affects soil conditions, such as temperature, moisture, and carbon sequestration⁴⁷, as well as microbial activity³¹. In a study in Mongolia, the mowing of grasslands had an extreme effect on the upper soil layer, as shown by a 4 °C increase in the soil temperature and a 47% decrease in the soil moisture⁴⁷. Such negative effects on soil conditions can further affect soil fauna. Although mowing is beneficial for maintaining grassland vegetation, we recommend limiting this treatment to avoid disrupting the belowground ecosystem.

In our study, we removed the aboveground biomass during mowing, which may have reduced soil invertebrate abundance. Grass harvesting is the traditional way of grasslands management all over the world, which consequently causes biomass removal and reduction of the resources for decomposers^{31,47}. However, leaving the cuttings did not mitigate the negative effect of mowing on earthworms in comparison with non-mown areas³⁰. In addition, the thickness and origin of the litter can have an impact on the abundance of soil invertebrates such as springtails, nematodes, and mites^{48,49}. For instance, knotweed litter negatively affected Collembola, because of its extended decomposition time and slower nutrient release compared with native species⁴⁸.

The current study also described a direct influence between seasons and soil invertebrates, and seasonal reliance on plant community characteristics was associated with the soil invertebrate community. In particular, Collembola abundance changed during the season, which may have been related to the sensitivity of those organisms to soil moisture and temperature⁵⁰. The seasonal changes in earthworm communities in grassland ecosystem were previously explained by the availability and quality of organic resources during each season, which is the probable explanation for similar observations in our study⁵¹.

According to Eisenhauer et al. and Hyvönen et al., the presence of various plant functional groups differentially affects the densities of particular soil invertebrates and their consistency over time^{30,51,52}. Moreover, ample evidence indicates that legumes have positive effects on ecosystem functioning^{53,54}. The cultivation of legumes improves the soil nitrogen level and primary productivity, as well as carbon sequestration⁵³. In addition, legumes increase the bacterial activity in the soil⁵⁵ and enhance the complexity of the trophic links in the soil food web⁵⁶. Legumes' ability to create specific root systems can also change the diversity of soil fauna⁵⁷. Furthermore, the introduction of legumes can increase ecosystem resistance to plant invasion⁵⁸. In the present study, the introduction of legumes with grass seeds positively affected soil invertebrates' abundance and diversity, which accorded with the findings of previous research^{59–62}. The results also showed that the introduction of grass only or no introduction of seeds (control) was not beneficial for soil fauna.

Study findings indicated that both mowing and aboveground plant diversity significantly affected soil fauna. These effects have several possible explanations, and further research is needed to test them. The most probable explanation is that changes in soil conditions had an indirect effect on soil fauna. Nevertheless, the soil fauna is an effective indicator of grassland management and restoration success.

Conclusions

Our results demonstrate that a greater intensity of mowing has a negative impact on soil organisms. Mowing twice a season decreased the abundance of invertebrate taxa. The application of a seed mixture of grass with legumes increased the diversity of soil invertebrates compared with other seed composition and introduction methods. The mixture of legumes and grass seeds was also beneficial for the abundance of most invertebrate taxa. Mowing once a season and the introduction of a mixture of grasses with legumes constitute the most suitable method for restoring *Solidago*-invaded stands, while also maintaining soil invertebrate abundance.

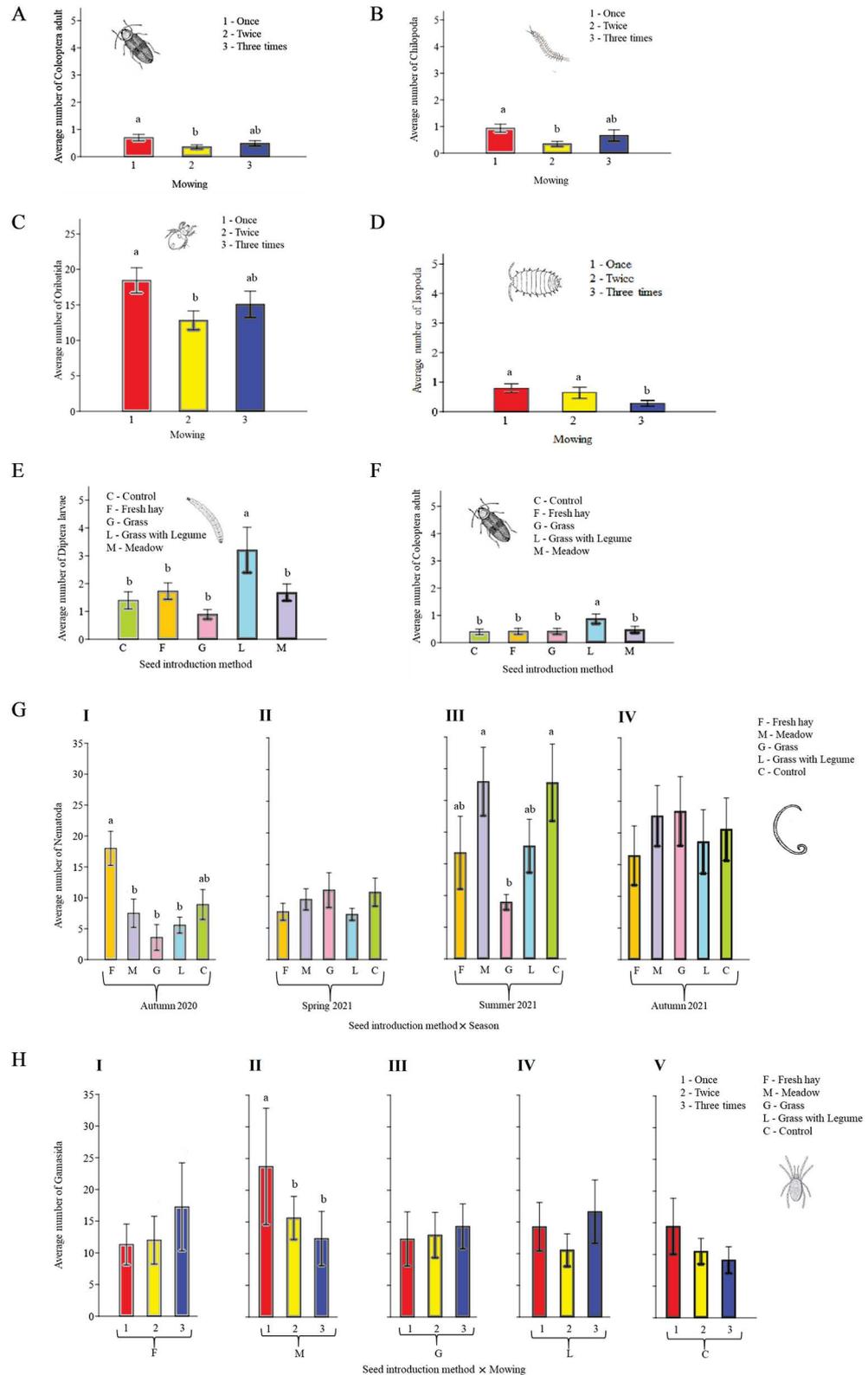


Figure 3. The effects of mowing and seed introduction methods, as well as their interactions, on the abundance of taxa. The different lowercase letters indicate significant differences between treatments; mowing regimes (A–D) and seed introduction method (E,F), $p \leq 0.05$. The significance of differences is shown within the particular groups: (G) season and (H) seed introduction method, $p \leq 0.05$.

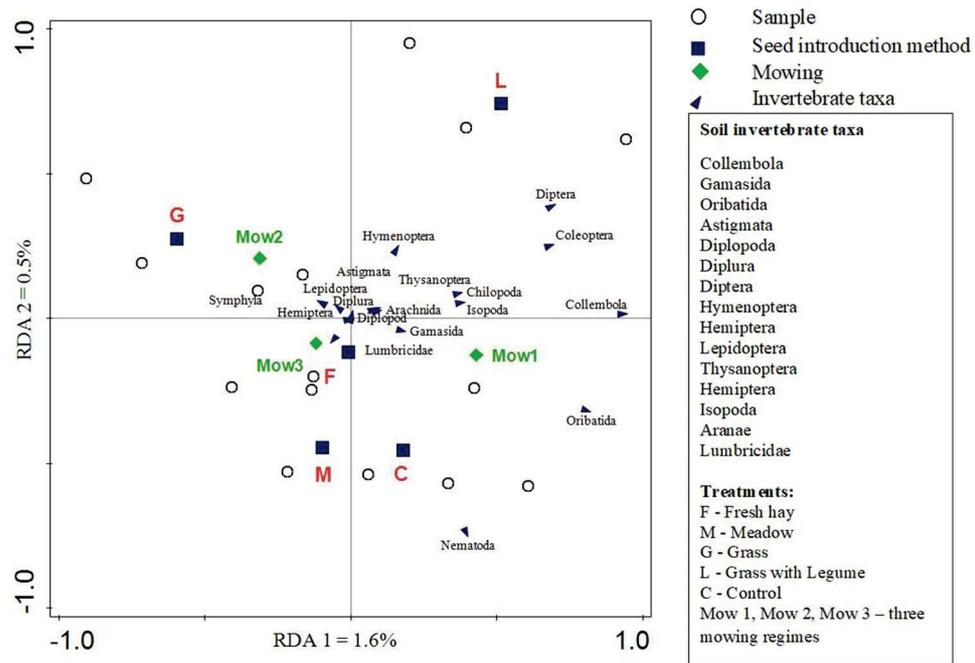


Figure 4. The redundancy analysis biplot of soil invertebrate community in association with mowing, seed introduction methods, and season.

Data availability

The data that support the findings of this study are available from the corresponding author upon request.

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References

- Bauer, T., Bäte, D. A., Kempfer, F. & Schirmel, J. Differing impacts of two major plant invaders on urban plant-dwelling spiders (Araneae) during flowering season. *Biol. Invasions* **23**(5), 1473–1485. <https://doi.org/10.1007/s10530-020-02452-w> (2021).
- Ustinova, E. N., Schepetov, D. M., Lysenkov, S. N. & Tiunov, A. V. Soil arthropod communities are not affected by invasive *Solidago gigantea* Aiton (Asteraceae), based on morphology and metabarcoding analyses. *Soil Biol. Biochem.* **159**, 108288. <https://doi.org/10.1016/j.soilbio.2021.108288> (2021).
- Tanner, R. A. *et al.* Impacts of an Invasive Non-Native Annual Weed, *Impatiens glandulifera*, on Above- and Below-Ground Invertebrate Communities in the United Kingdom. *PLoS ONE* **8**(6), e67271. <https://doi.org/10.1371/journal.pone.0067271> (2013).
- Wei, Q. *et al.* The diversity of soil mesofauna decline after bamboo invasion in subtropical China. *Sci. Total Environ.* **789**, 147982. <https://doi.org/10.1016/j.scitotenv.2021.147982> (2021).
- Szymura, M. & Szymura, T. H. Growth, phenology, and biomass allocation of alien *Solidago* species in central Europe. *Plant Species Biol.* **30**(4), 245–256. <https://doi.org/10.1111/1442-1984.12059> (2015).
- Bobulská, L., Demková, L., Čerevková, A. & Renčo, M. Invasive goldenrod (*Solidago gigantea*) influences soil microbial activities in forest and grassland ecosystems in central Europe. *Diversity* **11**(8), 134. <https://doi.org/10.3390/d11080134> (2019).
- Sterzyńska, M., Shrubovych, J. & Nicia, P. Impact of plant invasion (*Solidago gigantea* L.) on soil mesofauna in a riparian wet meadows. *Pedobiologia* **64**, 1–7. <https://doi.org/10.1016/j.pedobi.2017.07.004> (2017).
- Zubek, S. *et al.* *Solidago canadensis* invasion in abandoned arable fields induces minor changes in soil properties and does not affect the performance of subsequent crops. *Land Degrad. Dev.* **31**(3), 1–12. <https://doi.org/10.1002/ldr.3452> (2019).
- Čerevková, A., Miklisová, D., Bobulská, L. & Renčo, M. Impact of the invasive plant *Solidago gigantea* on soil nematodes in a semi-natural grassland and a temperate broadleaved mixed forest. *J. Helminthol.* **94**, 1–14. <https://doi.org/10.1017/S0022149X19000324> (2020).
- de Groot, M., Kleijn, D. & Jogan, N. Species groups occupying different trophic levels respond differently to the invasion of semi-natural vegetation by *Solidago canadensis*. *Biol. Conserv.* **136**(4), 612–617. <https://doi.org/10.1016/j.biocon.2007.01.005> (2007).
- Baranová, B., Manko, P. & Jászay, T. Differences in surface-dwelling beetles of grasslands invaded and non-invaded by goldenrods (*Solidago canadensis*, *S. gigantea*) with special reference to Carabidae. *J. Insect. Conserv.* **18**(4), 623–635. <https://doi.org/10.1007/s10841-014-9666-0> (2014).
- Lenda, M., Witek, M., Skórka, P., Moroň, D. & Woyciechowski, M. Invasive alien plants affect grassland ant communities, colony size and foraging behaviour. *Biol. Invasions* **15**(11), 2403–2414. <https://doi.org/10.1007/s10530-013-0461-8> (2013).
- Kajzer-Bonk, J., Szpiłtyk, D. & Woyciechowski, M. Invasive goldenrods affect abundance and diversity of grassland ant communities (Hymenoptera: Formicidae). *J. Insect Conserv.* **20**(1), 99–105. <https://doi.org/10.1007/s10841-016-9843-4> (2016).
- Trigos-Peral, G. *et al.* Ant communities and *Solidago* plant invasion: Environmental properties and food sources. *Entomol. Sci.* **21**(3), 270–278. <https://doi.org/10.1111/ens.12304> (2018).
- Fenesi, A. *et al.* *Solidago canadensis* impacts on native plant and pollinator communities in different-aged old fields. *Basic Appl. Ecol.* **16**(4), 335–346. <https://doi.org/10.1016/j.baae.2015.03.003> (2015).
- Sheley, R. L., Mangold, J. M. & Anderson, J. L. Potential for successional theory to guide restoration of invasive-plant-dominated rangeland. *Ecol. Monogr.* **76**(3), 365–379. [https://doi.org/10.1890/0012-9615\(2006\)076\[0365:PFSTTG\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2006)076[0365:PFSTTG]2.0.CO;2) (2006).

17. Byun, C., de Blois, S. & Brisson, J. Management of invasive plants through ecological resistance. *Biol. Invasions* **20**(1), 13–27. <https://doi.org/10.1007/s10530-017-1529-7> (2018).
18. Weidlich, E. W. A., Flórido, F. G., Sorriani, T. B. & Brancalion, P. H. S. Controlling invasive plant species in ecological restoration: A global review. *J. Appl. Ecol.* **57**(9), 1806–1817. <https://doi.org/10.1111/1365-2664.13656> (2020).
19. Zaller, J. G. *et al.* Effects of glyphosate-based herbicides and their active ingredients on earthworms, water infiltration and glyphosate leaching are influenced by soil properties. *Environ. Sci. Eur.* **33**(1), 1–16. <https://doi.org/10.1186/s12302-021-00492-0> (2021).
20. Szymura, M., Świerszcz, S. & Szymura, T. H. Restoration of ecologically valuable grassland on sites degraded by invasive *Solidago*: Lessons from a six year experiment. *Land Degrad. Dev.* <https://doi.org/10.1002/ldr.4278> (2022).
21. Świerszcz, S., Szymura, M., Wolski, K. & Szymura, T. H. Comparison of methods for restoring meadows invaded by *Solidago* species. *Pol. J. Environ. Stud.* **26**(3), 1251–1258. <https://doi.org/10.15244/pjoes/67338> (2017).
22. Nagy, D. U. *et al.* The more we do, the less we gain? Balancing effort and efficacy in managing the *Solidago gigantea* invasion. *Weed Res.* **60**(3), 232–240. <https://doi.org/10.1111/wre.12417> (2020).
23. Bardgett, R. D. & van der Putten, W. H. Belowground biodiversity and ecosystem functioning. *Nature* **515**, 505–511. <https://doi.org/10.1038/nature13855> (2014).
24. Bardgett, R. D. & Wardle, D. A. *Aboveground-Belowground Linkages: Biotic Interactions, Ecosystem Processes, and Global Change* (Oxford University Press, Oxford, 2010).
25. Gruss, I. *et al.* Microarthropods and vegetation as biological indicators of soil quality studied in poor sandy sites at former military facilities. *Land Degrad. Dev.* **33**(2), 358–367. <https://doi.org/10.1002/ldr.4157> (2022).
26. Sabais, A. C. W., Scheu, S. & Eisenhauer, N. Plant species richness drives the density and diversity of Collembola in temperate grassland. *Acta Oecol.* **37**(3), 195–202. <https://doi.org/10.1016/j.actao.2011.02.002> (2011).
27. Kardol, P. & Wardle, D. A. How understanding aboveground-belowground linkages can assist restoration ecology. *Trends Ecol. Evol.* **25**(11), 670–679. <https://doi.org/10.1016/j.tree.2010.09.001> (2010).
28. Eviner, V. T. & Hawkes, C. V. Embracing variability in the application of plant-soil interactions to the restoration of communities and ecosystems. *Restor. Ecol.* **16**(4), 713–729. <https://doi.org/10.1111/j.1526-100X.2008.00482.x> (2008).
29. Zhao, J., Chen, J., Wu, H., Li, L. & Pan, F. Effects of mowing frequency on soil nematode diversity and community structure in a Chinese meadow steppe. *Sustainability* **13**, 5555. <https://doi.org/10.3390/su13105555> (2021).
30. Hyvönen, T. *et al.* Aboveground and belowground biodiversity responses to seed mixtures and mowing in a long-term set-aside experiment. *Agric. Ecosyst. Environ.* <https://doi.org/10.1016/j.agee.2021.107656> (2021).
31. Gilmullina, A., Rumpel, C., Blagodatskaya, E. & Chabbi, A. Management of grasslands by mowing versus grazing – impacts on soil organic matter quality and microbial functioning. *Appl. Soil Ecol.* <https://doi.org/10.1016/j.apsoil.2020.103701> (2020).
32. Kládívková, E. J. Tillage systems and soil ecology. *Soil Tillage Res.* **61**(1–2), 61–76. [https://doi.org/10.1016/S0167-1987\(01\)00179-9](https://doi.org/10.1016/S0167-1987(01)00179-9) (2001).
33. Bispo, A. *et al.* Indicators for monitoring soil biodiversity. *Integr. Environ. Assess. Manag.* **5**(4), 717–719 (2009).
34. Santorufó, L., van Gestel, C. A. M., Rocco, A. & Maisto, G. Soil invertebrates as bioindicators of urban soil quality. *Environ. Pollut.* **161**, 57–63. <https://doi.org/10.1016/j.envpol.2011.09.042> (2012).
35. Boyce R. L. Life Under Your Feet: Measuring soil invertebrate diversity. Teaching Issues and Experiments in Ecology, Ecological Society of America, 3: Experiment #1. <https://tiee.esa.org/vol/v3/experiments/soil/downloads.html> (2005).
36. Shannon, C. E. A mathematical theory of communication. *Bell Syst. Tech. J.* **27**, 379–656 (1948).
37. Pielou, E. C. The measurement of diversity in different types of biological collections. *J. Theor. Biol.* **13**, 131–144. [https://doi.org/10.1016/0022-5193\(66\)90013-0](https://doi.org/10.1016/0022-5193(66)90013-0) (1966).
38. Margalef, R. Information theory in ecology. *Gen. Syst.* **3**, 36–71 (1958).
39. Jones, H. P. Impact of ecological restoration on ecosystem services. In *Encyclopedia of Biodiversity* (ed. Levin, S. A.) 199–208 (Academic Press, New York, 2013).
40. Menta, C. Soil fauna diversity - function, soil degradation, biological indices, soil restoration. In *Biodiversity Conservation and Utilization in a Diverse World* (ed. Lameed, G. A.) (IntechOpen, London, 2012).
41. Hoffland, E., Kuypers, T. W., Comans, R. N. & Creamer, R. E. Eco-functionality of organic matter in soils. *Plant Soil* **455**(1), 1–22. <https://doi.org/10.1007/s11104-020-04651-9> (2020).
42. Huera-Lucero, T., Labrador-Moreno, J., Blanco-Salas, J. & Ruiz-Téllez, T. A framework to incorporate biological soil quality indicators into assessing the sustainability of territories in the Ecuadorian Amazon. *Sustainability* **12**(7), 3007. <https://doi.org/10.3390/su12073007> (2020).
43. van Eekeren, N. *et al.* Microarthropod communities and their ecosystem services restore when permanent grassland with mowing or low-intensity grazing is installed. *Agric. Ecosyst. Environ.* **323**, 107682. <https://doi.org/10.1016/j.agee.2021.107682> (2022).
44. Humbert, J. Y., Ghazoul, J., Sauter, G. J. & Walter, T. Impact of different meadow mowing techniques on field invertebrates. *J. Appl. Entomol.* **134**(7), 592–599. <https://doi.org/10.1111/j.1439-0418.2009.01503.x> (2010).
45. Steidle, J. L. M., Kimmich, T., Csader, M. & Betz, O. Negative impact of roadside mowing on arthropod fauna and its reduction with ‘arthropod-friendly’ mowing technique. *J. Appl. Entomol.* <https://doi.org/10.1111/jen.12976> (2022).
46. Briones, M. J. Soil fauna and soil functions: a jigsaw puzzle. *Front. Environ. Sci.* **2**, 7. <https://doi.org/10.3389/fenvs.2014.00007> (2014).
47. Shao, C., Chen, J., Li, L. & Zhang, L. Ecosystem responses to mowing manipulations in an arid Inner Mongolia steppe: An energy perspective. *J. Arid Environ.* **82**, 1–10. <https://doi.org/10.1016/j.jaridenv.2012.02.019> (2012).
48. de Almeida, T., Forey, E. & Chauvat, M. Alien invasive plant effect on soil fauna is habitat dependent. *Diversity* **14**(2), 61. <https://doi.org/10.3390/d14020061> (2022).
49. Wissuwa, J., Salamon, J. A. & Frank, T. Effects of habitat age and plant species on predatory mites (Acari, Mesostigmata) in grassy arable fallows in Eastern Austria. *Soil Biol. Biochem.* **50**, 96–107. <https://doi.org/10.1016/j.soilbio.2012.02.025> (2012).
50. Petersen, H. Collembolan communities in shrublands along climatic gradients in Europe and the effects of experimental warming and drought on population density, biomass and diversity. *Soil Org.* **83**(3), 463–488 (2011).
51. Eisenhauer, N. *et al.* Plant community impacts on the structure of earthworm communities depend on season and change with time. *Soil Biol. Biochem.* **41**(12), 2430–2443. <https://doi.org/10.1016/j.soilbio.2009.09.001> (2009).
52. Eisenhauer, N. *et al.* Plant diversity surpasses plant functional groups and plant productivity as driver of soil biota in the long term. *PLoS ONE* **6**(1), 15–18. <https://doi.org/10.1371/journal.pone.0016055> (2011).
53. Gao, D., Wang, X., Fu, S. & Zhao, J. Legume plants enhance the resistance of soil to ecosystem disturbance. *Front. Plant Sci.* **8**, 1295. <https://doi.org/10.3389/fpls.2017.01295> (2017).
54. Yang, G., Roy, J., Veresoglou, S. D. & Rillig, M. C. Soil biodiversity enhances the persistence of legumes under climate change. *New Phytol.* **229**(5), 2945–2956. <https://doi.org/10.1111/nph.17065> (2021).
55. Zhao, J., Zeng, Z., He, X., Chen, H. & Wang, K. Effects of monoculture and mixed culture of grass and legume forage species on soil microbial community structure under different levels of nitrogen fertilization. *Eur. J. Soil Biol.* **68**, 61–68. <https://doi.org/10.1016/j.ejsobi.2015.03.008> (2015).
56. Zhao, J., Wang, X., Wang, X. & Fu, S. Legume-soil interactions: legume addition enhances the complexity of the soil food web. *Plant Soil* **385**(1), 273–286. <https://doi.org/10.1007/s11104-014-2234-2> (2014).
57. Bonkowski, M., Villenave, C. & Griffiths, B. Rhizosphere fauna: the functional and structural diversity of intimate interactions of soil fauna with plant roots. *Plant Soil* **321**, 213–233. <https://doi.org/10.1007/s11104-009-0013-2> (2009).

58. Hector, A., Dobson, K., Minns, A., Bazeley-White, E. & Hartley Lawton, J. Community diversity and invasion resistance: an experimental test in a grassland ecosystem and a review of comparable studies. *Ecol. Res.* **16**(5), 819–83. <https://doi.org/10.1046/j.1440-1703.2001.00443.x> (2001).
59. Gastine, A., Scherer-Lorenzen, M. & Leadley, P. W. No consistent effects of plant diversity on root biomass, soil biota and soil abiotic conditions in temperate grassland communities. *Appl. Ecol.* **24**, 101–111. [https://doi.org/10.1016/S0929-1393\(02\)00137-3](https://doi.org/10.1016/S0929-1393(02)00137-3) (2003).
60. Scherber, C. *et al.* Effects of plant diversity on invertebrate herbivory in experimental grassland. *Oecologia* **147**(3), 489–500. <https://doi.org/10.1007/s00442-005-0281-3> (2006).
61. Viketoft, M., Palmberg, C., Sohlenius, B., Huss-Danell, K. & Bengtsson, J. Plant species effects on soil nematode communities in experimental grasslands. *Appl. Soil Ecol.* **30**(2), 90–103. <https://doi.org/10.1016/j.apsoil.2005.02.007> (2005).
62. Viketoft, M. *et al.* Long-term effects of plant diversity and composition on soil nematode communities in model grasslands. *Ecology* **90**(1), 90–99. <https://doi.org/10.1890/08-0382.1> (2009).

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P.C.D.P., I.G., J.T., and M.S. conceived the idea. P.C.D.P. and M.S. secured the funds. P.C.D.P. and I.G. analysed the data and prepared figures. P.C.D.P., I.G., C.C., J.T., M.S., and T.H.S. collected the data. P.C.D.P., M.S. and T.H.S. maintained the experiment field. P.C.D.P., I.G., J.T., C.C., M.S. and T.H.S. drafted the original manuscript. All authors participated in manuscript writing.

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Competing interests

The authors declare no competing interests.

Additional information

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4. Author contribution statements / Oświadczenia współautorów

4.1. Drivers of *Solidago* species invasion in Central Europe—Case study in the landscape of the Carpathian Mountains and their foreground

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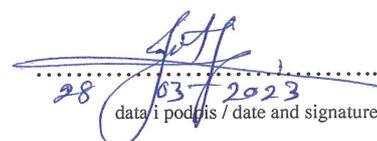
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PCD Perera, Tomasz H. Szymura, Louis de Patoul, Tetiana Sladkovska and Magdalena Szymura, (2021) A community resembling semi-natural meadow is as resistant to goldenrod invasion as highly productive commercial grassland. Management of Biological Invasions, 12(4): 873-885p. <https://doi.org/10.3391/mbi.2021.12.4.07>

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Udział w badaniach i zbiorze danych, a także w analizie danych i ich interpretacji.

Participation in investigation and data collection, as well as data analysis and interpretation.

04.04.2023 Sladkovska

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Magdalena Szymura

4.04.2023, Wrocław

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STATEMENT

Oświadczam, że w pracy / I declare that at article:

PCD Perera, Tomasz H. Szymura, Louis de Patoul, Tetiana Sladkovska and Magdalena Szymura, (2021) A community resembling semi-natural meadow is as resistant to goldenrod invasion as highly productive commercial grassland. *Management of Biological Invasions*, 12(4): 873-885p. <https://doi.org/10.3391/mbi.2021.12.4.07>

mój udział polegał na / my contribution was:

Udział w tworzeniu koncepcji badań, planowaniu doświadczenia i metodologii, udział w badaniach i zbiorze danych, analizie danych i ich interpretacji, udział w zapewnieniu finansowania i pisaniu oryginalnego manuskryptu.

Participation in research conceptualization, sample design and methodology, investigation and data collection, data analysis and interpretation, funding provision, and writing original draft.

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4.3. The impact of restoration methods for *Solidago*-invaded land on soil invertebrates

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STATEMENT

Oświadczam, że w pracy / I declare that at article:

Perera, P. C. D., Gruss, I., Twardowski, J., Chmielowiec, C., Szymura, M., & Szymura, T. H.
(2022). The impact of restoration methods for Solidago-invaded land on soil invertebrates.
Scientific Reports, 12(1), 1-10. <https://doi.org/10.1038/s41598-022-20812-5>

mój udział polegał na / my contribution was:

Udział w tworzeniu koncepcji badań, pozyskaniu finansowania, zbiorze i analizie danych oraz
przygotowaniu ilustracji, utrzymaniu eksperymentu, a także w redagowaniu oryginalnego
manuskryptu.

Conceived the idea, secured the funds, collected the data, analysed the data and prepared
figures, maintained the experiment field and drafted the original manuscript.


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Iwona Gruss
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Afiliacja / Affiliation

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STATEMENT

Oświadczam, że w pracy / I declare that at article:

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mój udział polegał na / my contribution was:

Udział w tworzeniu koncepcji badań, zbiorze i analizie danych oraz przygotowaniu ilustracji, a także
w redagowaniu oryginalnego manuskryptu.

Participated in conceived the idea, participated in data collection, participated in data analysis
and figures preparation, and participated in draft the original manuscript.

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mój udział polegał na / my contribution was:

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manuskryptu.

Participated in conceived the idea, participated in data collection, and participated in draft the
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mój udział polegał na / my contribution was:

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Participated in data collection and participated in draft the original manuscript.

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eksperymentu, a także w redagowaniu oryginalnego manuskryptu.

Participated in conceived the idea, participated in data collection, participated in maintain the
experiment field, and participated in draft the original manuscript.

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Tomasz Szymura
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Udział w zbiorze danych, utrzymaniu eksperymentu, a także w redagowaniu oryginalnego manuskryptu.

Participated in data collection, participated in maintain the experiment field, and participated in draft the original manuscript.

18.04.2023 
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