Multispecies invasion reduces the negative impact of single alien plant species on native flora

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Abstract

Aim: In the current Anthropocene, many ecosystems are being simultaneously invaded by multiple alien species. Some of these invasive species become more dominant and have greater environmental impacts than others. If two potentially dominant species invade the same area, the combined impact has been reported to be either (a) domination by one species, that is, the competitive dominance of one invader, or (b) invasion meltdown, where the combined impact is much greater, that is, a synergistic effect. We studied the effects of the invasion of two alien plant species that are known to strongly decrease native plant species diversity: the Persian walnut *Juglans regia* and goldenrod *Solidago canadensis*.

Location: We examined native vegetation diversity in abandoned fields (in Poland) where neither species had invaded, only one species had invaded, and both species had invaded.

Methods: Field survey data were analysed using generalized linear mixed models and ordination techniques.

Results: When goldenrod invaded alone, it caused a larger decrease in species richness and cover (74%) than when walnut invaded alone (58%). When walnut and goldenrod co-occurred in abandoned fields, walnut was dominant and strongly decreased goldenrod density by 87%. However, the combined impact on native species diversity was much lower (15% decrease in native plant diversity) than when either goldenrod or walnut invaded alone.

Main conclusions: In contrast to many other studies, our study does not support the occurrence of an invasion meltdown. Instead, our results show that even when one invader dominates, its negative effect on plant diversity can be strongly modified by the presence of another invasive species.

KEYWORDS
biodiversity, competition, competitive hierarchy, dominant invader, facilitation, invasion ecology, invasion meltdown, nitrogen, theory of coexistence
Globalization, trade and human migrations have intensified in the Anthropocene and have caused the breakdown of most geographical barriers that used to separate species ranges; as a result, several species have experienced geographic range increases. Many of these species can become invasive and cause biodiversity loss in their non-native ranges (Bennett, Vellend, Lilley, Cornwell, & Arcese, 2013; Crooks, 2005; Moroń et al., 2009; White et al., 2008). Most alien species invade and transform habitats and therefore increase the vulnerability of native ecosystems to invasions by multiple other alien species (Bennett et al., 2013; Essl et al., 2011; Hobbs et al., 2006; White et al., 2008).

Habitats invaded by multiple alien species may be more strongly affected than sites invaded by a single species (Inderjit, Cadotte, & Colautti, 2005; Pisula & Meiners, 2010; Simberloff & Von Holle, 1999). The invader-invader interactions may evolve in a mutually-advantageous way that facilitates new invasions. Their effects accumulate, leading to a meltdown of the native ecosystem (Green et al., 2011; Rodriguez, 2006; Simberloff & Von Holle, 1999). Since the seminal paper by Simberloff and Von Holle (1999), 100 articles that mention invasion meltdown have been published, but none of these studies have documented that the negative interactions between plant invaders positively affect native flora (for details, see Supporting Information Appendices S1 and S2). Thus, interactions among invasive plant species remain understudied (Hulme et al., 2013), and the vast majority of studies on invasive species consider a simple scenario in which only one invasive species affects the native community.

Competition for resources is a driving force that structures vegetation composition, and invasive species compete for resources among each other. Since invaders are often viewed as superior competitors (the "ideal weed" hypothesis: Elton, 1958; Sutherland, 2004), the competitive relationships among invasive species may also play a role in determining their combined impact on native communities (Vila & Weiner, 2004). A competitive hierarchy among invasive species may result in only the most competitive invader determining the impact on the affected native community. Alternatively, negative interactions among invasive species may reduce their combined impact. However, such alternative scenarios to the "invasion meltdown" interactions among invasive species have generally been overlooked in empirical studies (Rodriguez, 2006).

We examined the interaction between two co-occurring, highly competitive, widely distributed alien invasive species in Europe and determined their impact on native vegetation. The species examined were goldenrod (Solidago canadensis, Asteraceae), one of the 100 most widespread and harmful invasive plant species in the world (Moroń et al., 2009; Weber, 1998), and walnut (Juglans regia, Juglandaceae), whose invasion is a new phenomenon in Europe (Lenda, Knops, Skórka, Moroń, & Wojciechowski, 2018; Lenda et al., 2012). Goldenrod is native to North America, while walnut is native to Asia; thus, the two species have no mutual evolutionary history. Both species occur in abandoned fields of Central Europe that have been left fallow since the political transformation of 1989 (Lenda et al., 2012; Moroń et al., 2009; Rosin et al., 2016). This major change in land use has been a key environmental change that has triggered many invasions (Moroń et al., 2009; Lenda et al., 2012; Lenda et al., 2018). Both goldenrod and walnut are superior competitors for resources and have strong allelopathic effects (Abhilasha, Quintana, Vivanco, & Joshi, 2008; Pereira et al., 2007; Scharfy, Güsewell, Gessner, & Olde Venterink, 2010; Sun, Tan, Wan, Gu, & Zhu, 2006; Zhang, Jin, Tang, & Chen, 2009). Moreover, walnut is known to increase nitrogen content in soil (Andrianarisoa, Dufour, Bienaimé, Zeller, & Dupraz, 2016; Ercisli, Esitken, Turkkal, & Orhan, 2005). Locally, up to 80% of abandoned farmland can be covered by either goldenrod (Moroń et al., 2009; Tokarska-Guzik et al., 2012) or walnut (Lenda et al., 2012), which leads to a substantial loss in biodiversity (Moroń et al., 2009). In contrast, abandoned fields that are not dominated by either goldenrod or walnut have high native species richness and are important for biodiversity conservation (Skórka & Lenda, 2010; Tryjanowski et al., 2011). Most often, birch (Betula pendula, Betulaceae) is the native tree species that colonizes abandoned fields; the overshadowing characteristic of this species may change the habitat suitability of other species. Birch, however, is non-allelopathic.

In this study, we examined walnut, goldenrod and their combined impact on the diversity of native plants on abandoned fields in Poland, Central Europe. Since walnut seeds had been cached by birds before the fields were abandoned, walnut was typically one of the first species to become established in abandoned fields (Lenda et al., 2012). Moreover, we found no effect of goldenrod on the presence and density of walnut (Lenda & Skórka 2009; see also Methods); therefore, we examined only the influence of walnut on goldenrod. Six specific hypotheses were tested: (a) Both walnut and goldenrod, when growing alone, will decrease native plant diversity (i.e., species richness and coverage). (b) As the walnut is the superior invader (as a tree, it can outgrow other plants and intercept light, thus locally excluding goldenrod), a clear competitive hierarchy between these two invaders will be observed. (c) As a consequence of this competitive hierarchy, we predict that the presence of walnut will lead to the formation of circular goldenrod-free patches around walnut trees and thus promote native vegetation within goldenrod stands. Therefore, we assume that an invasion meltdown will not take place in the studied system. (d) The birch, a referential native tree species that is non-allelopathic, will not affect the density of the goldenrod and the native plant species. (e) Interactions between the two invasive plants will also be reflected in the pH, the soil contents of N and C and in the native plant community structure. (f) The composition of species in native plant communities will depend on the different amounts of N and C and the pH of the soil, which vary under different invasion scenarios. Specifically, we were interested in evaluating whether a walnut invasion filters for plant species that...
prefer high nitrogen content in the soil, as may be expected based on earlier studies of soil content in relation to walnuts (Andrianarisoa et al., 2016; Ercisli et al., 2005).

2 | METHODS

2.1 | Study species

We examined the impact on vegetation composition caused by two invasive alien plant species, goldenrod and walnut, as well as one native tree species, birch. Birch was a reference non-allelopathic species that was used to control for the effects of walnut, namely, to separate the effect of shadowing (exerted by both walnut and birch) from possible allelopathy (only walnut). When walnut and goldenrod are absent, silver birch is typically the dominant tree that establishes in abandoned agricultural fields (Bijak et al., 2013; Falinści, 1986). In Central Europe, goldenrods often occur in dense monospecific patches, covering up to hundreds of hectares (de Groot, Kleijn, & Jogan, 2007; Moroń et al., 2009). Goldenrod leaves out relatively late in spring but has a large impact on vegetation throughout the entire season because of its high accumulation of above-ground biomass, litter accumulation and growth rate and shading potential, achieving heights up to 2 m (de Groot et al., 2007; Herr, Chapuis-Lardy, Dassonville, Vanderhoeven, & Meerts, 2007; Moroń et al., 2009). Goldenrod also releases allelopathic chemicals that influence other plant species (Abhilasha et al., 2008; Chapuis-Lardy, Vanderhoeven, Dassonville, Koutika, & Meerts, 2006; Sun et al., 2006). Goldenrod shoot density is 150–200 per square metre, but this density may become even higher than 300 shots per square metre (Weber, 2000). Typically, one stem produces over 10,000 seeds (Bochenek et al., 2016; Werner & Platt, 1976). Seeds of invasive goldenrods display a high seed vigour that is maintained after storage in a wide range of temperatures and in both dry and moist conditions (Bochenek et al., 2016). Approximately 50% of goldenrod seeds germinate (Szymura et al. 2018). After the initial establishment of seeds, goldenrod reproduces vegetatively through rhizomes, and these clones occur as dense patches that comprise up to 90% of the total plant cover in abandoned fields (Moroń et al., 2009; Weber, 2000).

Walnut is a large tree that was introduced to Central Europe in the Middle Ages (Zdyb, 2010), and it is invasive in abandoned agricultural land (Lenda et al., 2012). Walnut produces large seeds; thus, its distribution in agricultural land is mostly related to animal dispersal (Lenda et al., 2018, 2012). Each year, corvids, namely, native rooks (Corvus frugilegus, Corvidae), cache a large number of walnut seeds in managed arable fields as a long-term food supply. Rooks forget the locations of many cached seeds, which causes a seed bank to develop in the soil; however, seeds and seedlings are usually destroyed during field work. After field abandonment, the seeds from the seed bank can sprout and grow into trees. Corvids do not cache seeds in abandoned fields (Lenda et al., 2012). Thus, the abandonment of fields with large undamaged walnut seed banks is a key factor that enables these seeds to establish as saplings and then trees. In addition, because the seeds are cached before fields are abandoned, walnut is one of the first species to establish in abandoned fields. Walnut also contains juglone, an allelopathic chemical that inhibits many other plant species (MacDaniels & Pinnow, 1976; Ponder & Tadros, 1985; Vander Wall, 2001). Thus, walnut may have a large competitive impact on other vegetation, both because it is a tree, that is, causing overtopping and shading, and because of its allelopathic effect (Chi et al., 2011; Ercisli et al., 2005). Because walnut seed caching by corvids is patchy, the establishment of the walnut in abandoned fields is also patchy; however, fields with a very high density of this tree species are common (Lenda et al., 2012).

2.2 | Study area and field selection

We conducted our study within a primarily agricultural landscape located near the towns of Kraków and Tarnów in southern Poland (Supporting Information Figure S1 in Appendix S2). In this area, approximately 15% of the agricultural fields have been abandoned in recent years, and many of them contain goldenrod, walnuts and/or native birches.

Within the local landscape, abandoned fields are either heterogeneous, meaning they contain a patchwork of different vegetation types, or relatively homogeneous, meaning they are dominated by one vegetation type. We examined plant species richness, plant cover (i.e., index of abundance) and species composition within these two types of abandoned fields (Supporting Information Figures S2 and S6–S15 in Appendix S2). Homogeneous fields are relatively small (approximately 0.4 ha), and each presents just one type of vegetation. Heterogeneous fields are larger (approximately 1 ha), and each contains several vegetation types. In heterogeneous fields, because the invaded and uninvaded sites are in close proximity in the same field, site characteristics such as soil and land-use history are much more similar than those of homogeneous fields (Usowicz et al., 2004). However, the homogeneous fields allowed us to examine whether the impact of the invasive species on the native vegetation was stronger than the impact of the site differences that can influence species composition. Moreover, plant species succession and invasion are very complex processes, and ecological processes and species associations may be different, for example, in small patches where the impact of margins and the surrounding matrix is stronger than that in larger fields (Bergholz et al., 2017; Honnay, Endels, Vereecken, & Hermy, 1999). Therefore, we decided to include these two types of fields to encompass this complexity and to ensure that the effects of the invasion of the two alien species were consistent across different types of abandoned fields.

We selected 10 heterogeneous abandoned fields that had been used for cereal cultivation before abandonment. The fields were chosen based on four criteria: (a) similar size (approximately 1 ha), (b) currently surrounded by the same cereal crops, (c) agricultural abandonment occurred between 10 and 15 years ago, and (d) similar clay soil. Soil selection was based on our data from earlier studies in these landscapes (e.g., Moroń et al., 2009; Lenda et al., 2012;
Lenda, Wittek, Moroń, & Wojciechowski, 2013, Lenda et al., 2018) and on published soil maps (scale 1:5,000) issued by the Polish Ministry of Agriculture (Witek, 1965). These maps are also available online (http://miip.geomalopolska.pl/imap/?gpmap=gps83).

Each heterogeneous field contained six different vegetation patches dominated by (a) native vegetation without birch (the control, reference type), (b) native birch in native vegetation, (c) walnut, (d) goldenrod, (e) goldenrod and birch, or (f) goldenrod and walnut (Supporting Information Figure S2a in Appendix S2). In each field, we established 12 circular plots (2 m diameter; area of 3.14 m²), and there were two plots in each of the different vegetation patches summing up to a total of 120 plots in all the heterogeneous fields. The plot size was chosen so that it would fit under the birch and walnut canopy. All the plots were located at least 2 m from the field boundary to avoid edge effects. The plots dominated by native vegetation and goldenrod were placed at least 15 m apart from either walnut or birch trees. The plots were selected randomly but had to meet the abovementioned criteria to effectively test the stated hypotheses.

As in the heterogeneous fields, we selected two circular plots (3.14 m²) in the homogeneous fields; the plots were placed within 10 separate fields of a given type (60 homogeneous fields in total). Each field was dominated by one of the six different vegetation types: (a) native vegetation without birch, (b) native birch in native vegetation, (c) walnut, (d) goldenrod, (e) goldenrod and birch, or (f) goldenrod and walnut (Supporting Information Figure S2b in Appendix S2). The total number of plots was the same as that in the heterogeneous fields.

Each studied field (either homogeneous or heterogeneous) was surrounded by managed crop fields. However, other abandoned fields were frequently in the vicinity (but did not share a border with the studied fields). The cover of goldenrod in abandoned fields within a 500 m radius from the field border was 13 ± 10% (mean ± SD); however, many goldenrods also grow along road edges and in field margins.

2.3 | Plant and soil sampling

Plant species were counted in all circular plots (120 in heterogeneous fields and 120 in homogeneous fields) in two surveys. The first survey was performed at the end of May, and the second survey was conducted at the end of July or the beginning of August. During the surveys, we noted the coverage of each plant species in the herb layer and classified the coverage into 21 categories (i.e., <1%, 1%–5%, 6%–10%, 95%–100%). Surveys in the homogeneous fields were performed in 2012, while the heterogeneous fields were surveyed in 2013. Moreover, to test whether the density of goldenrods around walnut trees decreased, we measured the diameter of goldenrod-free circular patches for 200 walnuts growing in goldenrods in the studied fields. We attempted to measure these circles under birches and walnuts in native vegetation, but they were unidentifiable (see Results).

Three soil samples (0–15, 15–30, 30–45 cm below the surface) were taken in each plot in May (360 samples from the heterogeneous fields and 360 from the homogeneous fields). The weather conditions during soil sampling were similar during both years (Supporting Information Appendix S2). The three soil samples from each plot were dried and mixed before analysis. We determined the amounts of soil organic carbon and soil total nitrogen in the collected soil using a Vario-Max analyser, while the soil pH was determined using a pH metre (Radiometer) in a slurry of soil and 1 M KCl (soil/solution ratio of 1:2.5).

2.4 | Data analysis and statistics

For both the heterogeneous and the homogeneous fields, we examined the relationship between alpha species richness and invasive plant cover. To perform the statistical analyses, plant cover designations were changed as follows: the category <1% was entered as 1, the category 1%–5% was entered as 5, the category 6%–10% as 10, and so on. Moreover, each species was scored for nitrate preferences according to the Ellenberg scale (Ellenberg & Leuschner, 2010). Values of this index vary from 1 (nitrate-avoiding species) to 9 (highly nitrophilous species). Mean values (weighted by species coverage) were calculated for each plot and survey.

The relationship between goldenrod, walnut and birch and native flora was analysed using two generalized linear mixed models (GLMMs). In the two models, the dependent variables were (a) richness of native species (GLM1), and (b) coverage (sum of the percentage coverage of all native species—GLM2). The results of each survey were used as a single data record, and each model was based on 480 such data records (i.e., 2 plots per field × 20 fields × 6 combinations of birch, walnut and goldenrod × 2 surveys). The presence of birch, walnut and goldenrod were the three explanatory variables. Additionally, we considered the two interactions: between the presence of birch and goldenrod, as well as between the presence of walnut and goldenrod. Moreover, the type of field (homogeneous vs. heterogeneous) was included as a separate fixed factor. We entered the field identity (ID), plot ID and survey ID as the three random factors to account for the spatial dependency among the data records. We used a Poisson error distribution and a log-link for the GLM1, and we used a Gaussian error with an identity link for the GLM2. The full models were then checked for spatial autocorrelation of their residuals using Moran’s I statistic, which was computed for the 15 distance classes. The values of Moran’s correlation did not exceed 0.062 for any of the classes; this result indicated the lack of a spatial dependency of the residuals.

We then used a multimodel inference (Burnham & Anderson, 2002) to identify the variables that best explained the variation in plant species richness and coverage among the plots. Each GLMM was used as a full model, and we calculated Akaike’s information criterion (AICc) for each possible model with the help of the “MuMIn” package (Bartoń, 2017). The models with an ΔAICc < 4 were determined to be worth consideration (Burnham & Anderson, 2002) and were included in full averaging. The averaged parameter estimates were presented as the final result of the modelling.
Additionally, we used the ordination method to investigate species-specific associations with the six types of plots (control plots with native herb vegetation, native birch in native vegetation, walnut, goldenrod, goldenrod and birch, and goldenrod and walnut) and soil characteristics in the heterogeneous and homogeneous fields. We used partial canonical correspondence analysis (CCA) because the length of the longest gradient in the detrended correspondence analysis exceeded three in both heterogeneous and homogeneous fields. We used the mean of the two vegetation surveys for species cover estimates. Soil carbon, nitrogen and pH as well as field coordinates (homogeneous fields) and field identity (heterogeneous fields) were used as covariates in both CCAs. We used mean cover because there was strong overlap between plant composition in the first survey and the second survey, as indicated by co-correspondence analysis (see details in Supporting Information Figure S3 in Appendix S2). Moreover, separate CCAs were performed for the first and second surveys and resulted in very similar findings (results not shown). The CCAs were performed using CANOCO 5.1 software (Šmilauer & Lepš, 2014). The significance of the explanatory variables was tested using 1,000 Monte Carlo permutations restricted with a blocking structure (plots within fields in the case of heterogeneous fields), with the p-values adjusted for the false discovery rate. In addition to the CCA, the GLMMs with Gaussian error and an identity link were built to test the association between the types of plots and the mean value of the Ellenberg nitrogen preference index for the heterogeneous and homogeneous fields (GLMM3 and GLMM4 presented in Supporting Information Appendix S2).

3 | RESULTS

We found a total of 93 native species in the heterogeneous fields and 57 native species in the homogeneous fields (Tables S1 and S2 in Supporting Information Appendix S2).

3.1 | Impact of invasions on native plant diversity

Species richness was highest in the control plots (native vegetation, Figure 1, Table 1). The plots with birch also had high species richness (similar to the control plots). The separate occurrence of walnut or goldenrod alone had clear negative effects on the native plant species richness compared to that of the control plots (Figure 1, Table 1). Additionally, the impact of goldenrod tended to be significantly stronger than the impact of walnut (Figure 1, Table 1). A similar pattern was found for plant coverage (Figure 1). However, we recorded a significant positive interaction between the effect of

![Figure 1](image-url)
walnut and the effect of goldenrod; in other words, plots that were invaded simultaneously by both invasive plants had a higher native species richness and coverage than did plots invaded by walnut or goldenrod alone (Figures 1 and 2, Table 1). This means that the effects of walnut and goldenrod are not additive—in contrast, the negative impact of these two alien species on native flora seems to be reduced when these alien species co-occur.

The density of walnuts (78.2 walnuts ± 0.6 SE per hectare, \( n = 10 \) fields) in native vegetation in homogeneous fields did not differ from the density of walnuts (80.8 walnuts ± 1.5 SE per hectare, \( n = 10 \) fields) growing in goldenrods (t test = 0.784, degrees of freedom = 11.7, \( p = 0.448 \)). The presence of walnut negatively impacted the density of goldenrod growing below, which resulted in circular goldenrod-free patches around each walnut tree (GLMM \( F_{3,90} = 233.890, p < 0.001 \), Figure 2). The mean size of these distinctive circular patches was 3.46 m ± 0.05 m SE, min = 2.02 m, max = 5.92 m, \( n = 200 \) walnuts growing in goldenrods sampled in different fields (Supporting Information Appendix S2). In cases where walnuts grew in goldenrods where the native plant community was described, the mean size of these circular patches was similar (mean = 3.41 m ± 0.12 m SE, \( n = 40 \)), and there was no difference in the size of these circular patches between homogeneous (mean = 3.53 m ± 0.20 m SE, \( n = 20 \)) and heterogeneous fields (mean = 3.29 m ± 0.13 m SE, \( n = 20 \), t test, \( t = 1.015 \), degrees of freedom = 33.288, \( p = 0.317 \), Supporting Information Appendix S2). We did not find these circular patches under walnuts growing

### TABLE 1

Averaged parameter estimates (and 95% CIs) of the GLMMs explaining plant species richness and pooled plant coverage

| Model description | Effect | B (95% CI) | \( p \) |
|-------------------|--------|------------|--------|
| GLMM 1            | Intercept | 2.78 (2.69; 2.88) | <0.001 |
| Response: Species richness | Field type: homogeneous | -0.16 (-0.27; -0.05) | 0.005 |
| \( \Delta AICc \) Null: 426.6 | Birch | -0.09 (-0.21; 0.03) | 0.133 |
|                   | Goldenrod | -1.23 (-1.35; -1.12) | <0.001 |
|                   | Walnut | -0.72 (-0.85; -0.59) | <0.001 |
|                   | Goldenrod × birch | 0.02 (-0.10; 0.14) | 0.760 |
|                   | Goldenrod × walnut | 1.72 (1.54; 1.90) | <0.001 |
| GLMM 2            | Intercept | 121.18 (106.13; 136.22) | <0.001 |
| Response: Coverage | Field type: homogeneous | 0.39 (-5.67; 6.45) | 0.899 |
| \( \Delta AICc \) Null: 495.5 | Birch | -13.08 (-23.04; -3.12) | 0.010 |
|                   | Goldenrod | -98.75 (-107.72; -89.78) | <0.001 |
|                   | Walnut | -35.80 (-45.78; -25.81) | <0.001 |
|                   | Goldenrod × birch | 8.98 (-4.59; 22.56) | 0.195 |
|                   | Goldenrod × walnut | 128.63 (115.08; 142.19) | <0.001 |

Note. The \( \Delta AICc \) value of the null model (i.e., intercept only) is given in the first column. Parameters that do not overlap with zero are marked in bold and accompanied by \( p \)-values. Field type—homogeneous versus heterogeneous, Birch—effect of native birch, Goldenrod—effect of alien goldenrod, Walnut—effect of alien walnut. The intercept is a reference category—native vegetation.

**FIGURE 2** The effect of vegetation type within the abandoned fields on the mean cover of alien goldenrods.
in native vegetation (Supporting Information Appendix S2). Under native birches growing in goldenrod stands, we did not find the same type of circular patches with reduced goldenrod density (Figure 2, Supporting Information Appendix S2).

### 3.2 Impact of vegetation type on species composition

The CCA for heterogeneous fields showed that the first two ordination axes were statistically significant \( (F = 3.2, p < 0.001) \) and explained 13.4% of the variation in species composition, of which 65.2% was further explained by the vegetation type after accounting for the differences in soil properties among the plots and field identities (Figure 3). The CCA for the homogeneous fields showed that the first two ordination axes were also statistically significant \( (F = 7.4, p < 0.001) \) and explained 10.5% of the variation in plant species composition, of which 70.0% was further explained by vegetation type after accounting for the differences in soil properties among plots and field locations (Figure 3). In both analyses, along the first ordination axis, there was a clear separation between the species-rich uninvaded plant communities and the plots where walnuts grew together with goldenrod (Figure 3). These two types of vegetation were separated from species-poor communities invaded solely by goldenrod or walnuts along the second ordination axis (Figure 3). In both CCAs, the forward selection of variables indicated that the vegetation types contributing the most to plant species ordination were walnuts growing alone and walnuts growing with goldenrod, and the same result was found for the control plots (Table 2). The impact of walnuts growing with goldenrod on species composition had a different impact on the native plant community than the impact observed in the control plots.
with native birch, and Control—native vegetation without birch. Our study shows that the effect of invasive species on native plant diversity within the different vegetation types was also associated with the soil properties. Specifically, we found that walnut was the only vegetation type that significantly increased soil pH and total organic carbon and nitrogen (for details, see text and Supporting Information Figure S4 in Appendix S2). These findings were further confirmed by comparing the Ellenberg values for the nitrophyte index between the vegetation types in both field types (Supporting Information Table S3, Figure S5 in Appendix S2). Namely, the native plants growing under walnuts had larger Ellenberg values related to nitrate preferences than did the plants in other vegetation types (Supporting Information Figure S5 in Appendix S2).

4 | DISCUSSION

Our study shows that the effect of invasive species on native plant diversity depends on the presence of other invasive plant species in the same habitat. To grow and reproduce, all plants inhabiting the same space need similar resources; thus, competition between two alien species is very likely (Chesson, 2000; Kuebbing, Souza, & Sanders, 2013). Here, we show for the first time that the co-occurrence of invasive alien plant species may be much more beneficial for native flora than when a single invasive species invades a habitat alone. To understand the current mechanisms of invasions, such multispecies studies are important because there are at least 13,168 naturalized plant species globally, which is approximately equal to the number of native flora in Europe (Van Kleunen et al., 2015), and more species are colonizing the same areas (Pyšek et al., 2017).

4.1 | The individual impact of the invasive walnut and goldenrod on plant diversity

Walnut has been invasive since the 1990s (Lenda et al., 2012). However, studies of its invasion have mostly focused on the reasons for its release from a 700-year lag phase. The factors that have been identified as important are the coincidence in time among politically related land-use alterations (e.g., land abandonment), seed sources and behavioural changes of native dispersers (Lenda et al., 2012, 2017). Here, we demonstrated that walnut decreased native plant diversity in abandoned agricultural land. This effect may be caused by canopy shading, as walnut trees have dense foliage that strongly influences the composition of understory vegetation (Zdyb, 2010). However, birch is also known to have a shading effect (Olsrud & Michelsen, 2009); thus, the influence of walnut on plant diversity is most likely the result of its allelopathy, which our native control tree does not exhibit. Juglone, the walnut plant’s secondary metabolite, is secreted into the soil by the entire walnut tree, including its leaf litter and roots (Cosmulescu & Trandafir, 2011) and is toxic to many plants (Cui, Cai, Jiang, & Zhang, 2011; Ercisli et al., 2005; Sytykiewicz, 2011; Terzi, 2008; Terzi & Kocacaliskan, 2010). The walnut also changes soil properties, for example, its presence increases pH and soil total carbon and nitrogen. This increased soil fertility is associated with a change in vegetation composition and specifically with an increased abundance of nitrophilous species. We also found more litter under walnut trees than under birch trees (M. Lenda, P. Skórka, personal observations), and this may lower light levels, which can further decrease the seed germination of other plant species (Li, Zheng, Xie, Zhao, & Gao, 2017; Offord, Meagher, & Zimmer, 2014). Therefore, we suggest that the effect of alien walnut on vegetation is likely not caused solely by lower light intensity but also by a combination of the plant’s secondary metabolites, soil chemistry and fertility changes, as has been demonstrated in grassland ecosystems (Harpole et al., 2016; Hautier et al., 2014).

| Variable               | % variance explained | % contribution | F    | p    |
|------------------------|----------------------|----------------|------|------|
| Heterogeneous fields   | Total = 13.4%        |                |      |      |
| Goldenrod & walnut     | 4.8                  | 35.8           | 5.3  | 0.001|
| Control                | 3.2                  | 23.9           | 3.6  | 0.001|
| Birch                  | 2.6                  | 19.4           | 3.0  | 0.001|
| Walnut                 | 2                    | 14.9           | 2.4  | 0.001|
| Homogeneous fields     | Total = 11.6%        |                |      |      |
| Goldenrod & walnut     | 5.1                  | 44.0           | 6.1  | 0.001|
| Walnut                 | 1.9                  | 16.4           | 2.3  | 0.001|
| Birch                  | 1.8                  | 15.5           | 2.2  | 0.001|
| Control                | 2.1                  | 18.1           | 2.5  | 0.003|

Note. Percentage of variance explained by each statistically significant (F test and p-value are presented) variable and its contribution to the CCA ordination are given. Explanation of variable codes: Goldenrod & walnut—stand of native vegetation invaded both by alien walnut and goldenrod, Walnut—stands of native vegetation invaded by alien walnut, Birch—stands of native vegetation with native birch, and Control—native vegetation without birch.
Goldenrod substantially decreased native plant diversity. The reduction in local plant biodiversity by goldenrod has been reported in other studies, and once this plant colonizes a habitat, it soon out-competes and overshadows smaller native plants and reduces the number of their pollinators (de Groot et al., 2007; Moroń et al., 2009). Moreover, exclusive stands of goldenrod have always had a much more harmful effect than that of the invasive walnut, as the diversity components were much lower in goldenrod than in other vegetation types. The reason why goldenrod exerts a more harmful effect than walnut on native flora may be that it reaches a high density, with some invaded areas turning into monospecific goldenrod patches (Moroń et al., 2009; Skórka, Lenda, & Tryjanowski, 2010, Supporting Information Appendix S2); another reason may be allelopathy (Abhilasha et al., 2008; Sun et al., 2006). Contrary to goldenrod, walnut has not yet created dense forests, and its trees are usually scattered within a single patch; thus, its impact may be limited. However, walnut invasion is a relatively new, dynamic ongoing process, with an increasing number of invaded habitats (Lenda et al., 2018).

4.2 | Do invasive species interact with each other?

Relationships between living organisms, especially plants, are never shaped by one-to-one interactions. Resources are limited, and there are many other species in the environment that utilize and depend on essentially only a few resources, such as water, light and nutrients. In our study, walnut significantly decreased the cover of goldenrod growing underneath it. One of the explanations of the observed phenomenon may be walnut’s strong allelopathic effect. In addition, goldenrod seeds have a photoblastic characteristic; thus, the shading of the walnut trees and the increased litter layer may limit goldenrod seed germination (Fenner & Thompson, 2005; Górski, Górski, & Stasiak, 2013). In contrast to walnut, we found no impact of the presence of birch on goldenrod density. Therefore, the shading and increased thickness of litter may be less important than the allelopathic effect of juglone. If juglone is the explanation for why walnut decreases goldenrod density, using juglone as a natural herbicide may provide a way to control goldenrod invasions. However, this hypothesis needs to be verified experimentally.

Our literature search found only two studies in which negative interactions were confirmed between invasive alien species (Belote & Weltzin, 2006; Wundrow, Carrillo, Gabler, Horn, & Siemann, 2012, Supporting Information Appendices S1 and S2). Wundrow et al. (2012) found that the presence of the invasive alien alligatorweed (Alternanthera philoxeroides), a rooted plant, decreased the establishment of new individuals of the alien invasive water hyacinth (Eichhornia crassipes), which is a free-floating plant. In contrast, the presence of alligatorweed increased the growth of the hyacinth in already established patches, with an overall positive effect on the success of the water hyacinth. Belote and Weltzin (2006) demonstrated a mutually detrimental relationship between two invasive alien plants: Japanese stillgrass (Microstegium vimineum) interfered with Japanese honeysuckle (Lonicera japonica) when they occurred together in forests. In this interaction, M. vimineum was the superior competitor to L. japonica, which was explained by the reduced access to light caused by the first species (Belote & Weltzin, 2006).

4.3 | Why is the joint impact of walnut and goldenrod on plant diversity lower than their individual impacts?

Species richness and the cover of native plants were much higher when both walnut and goldenrod invaded the same area than when each species invaded an area alone. Thus, our results provide a rare empirical example of how negative interactions between invasive species can alleviate their individual impacts on native vegetation. In general, when only a single, highly competitive species invades, its effect is often a decrease in native biodiversity (Vila et al., 2011). However, this effect may change when several highly competitive species invade a single area (Chesson, 2000; Simberloff & Von Holle, 1999). When multiple highly competitive species invade, their combined impact will be shaped by the interactions between them, and the combined effect can be lower than the individual effect of each invasive species. However, as far as we are aware, our study is the first to demonstrate this for plant species (Supporting Information Appendices S1 and S2). Preisser and Elkinton (2008) demonstrated a similar negative interaction between herbivores, which resulted in a lower combined negative impact on native vegetation composition (Preisser & Elkinton, 2008).

We found that the native vegetation diversity was similar at sites that had been co-invaded by both walnut and goldenrod compared with the uninvaded control areas with birch. However, in contrast to this result, the species composition was quite different. Thus, while goldenrod possibly filters for native species from plant communities that already were present, our data are consistent with the hypothesis that walnuts growing with goldenrod create novel plant communities. More plant species are present in stands invaded by both walnut and goldenrod than in stands that have been invaded by only walnut. However, several specific species, for example, Geum urbanum, Geum rivulare and Urtica dioica, were commonly found with walnut. Thus, the presence of walnut may create a favourable site for a subset of native species that can co-exist with walnut when the area is also invaded by goldenrod. Interestingly, the species that grow with walnut are typically highly nitrophilous. Thus, in addition to the direct allelopathic effects of walnut, walnut-induced soil changes may also contribute to changes in the species composition of native plant communities. Considering that there are 5,789 naturalized alien plant species in Europe (Lambdon et al., 2008) and that some of those species may be in the lag phase, multiple invasions may be one of the most important factors that will shape plant communities in post-agricultural landscapes in future.

4.4 | The evolutionary history of co-invading invasive species

Goldenrod originates from North America, while walnut originates from Asia. Thus, these species have no common evolutionary history.
Both species evolved in different environments with different climates, soils, microorganisms and plant species associations. Therefore, we hypothesize that goldenrod, because it has never interacted with walnut, may be just as sensitive to juglone as native species that also have no mutual evolutionary history with walnut. Our results are similar to those of Callaway and Aschehoug (2000), who showed that knapweed (Centaurea diffusa) had a much stronger harmful effect on North American species growth and physiology in its invasion range than in the species’ native range in Europe and Asia. For the “invasion meltdown” phenomenon to occur, a common evolutionary history that shaped the competitive interactions between co-invading species should be important. However, because of the current global mixing of species, many co-invading species have no common evolutionary history, and their interactions may be unpredictable and may not differ from the competitive interactions with native species.

4.5 | Conclusion

In our study, we found a negative interaction between two invasive species that, when combined, had a less negative impact on the native flora. Walnut trees growing in goldenrod stands excluded goldenrod from their surroundings and created suitable habitat patches for native plants. Our results contrast with those of other studies that have largely confirmed the invasion meltdown hypothesis for plant species (Rodríguez, 2006; Simberloff & Von Holle, 1999). Our findings support the hypothesis that multiple invaders do not always facilitate each other but can possibly compete with each other, and this competition can lower their negative impact on native flora.

Thus, better evaluations of the impact of these species on native biodiversity are needed to propose effective mitigation measures. Our results may suggest that the use of single-species studies to investigate the effects of a single invasive plant on native flora can lead to misleading conclusions when other invasive species are present but not considered in analyses. To better understand the impact of invasive alien species on native biodiversity, a broader approach is necessary, as the impacts of several co-occurring invasive species may not be additive.

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DATA AVAILABILITY

The data that support the findings of this study are available on the Dryad repository at: https://doi.org/10.5061/dryad.9f0n877.

REFERENCES

Abhilasha, D., Quintana, N., Vivanco, J., & Joshi, J. (2008). Do allelopathic compounds in invasive Solidago canadensis s.l. restrain the native European flora? Journal of Ecology, 96, 993–1001.

Andrianarisoa, K. S., Dufour, L., Bienaimé, S., Zeller, B., & Dupraz, C. (2016). The introduction of hybrid walnut trees Juglans nigra regia cv. NG23 into cropland reduces soil mineral N content in autumn in southern France. Agroforestry Systems, 90, 193–205.

Bartoń, K. (2017). MuMIn: Multi-Model Inference. R Package Version 1.40.0. Retrieved from https://CRAN.R-project.org/package=MuMIn

Belote, R. T., & Weltzin, J. F. (2006). Interactions between two co‐dominant, invasive plants in the understory of a temperate deciduous forest. Biological Invasions, 8, 1629–1641. https://doi.org/10.1007/s10530-005-3932-8

Bennett, J. R., Vellend, M., Lilley, P. K., Cornell, W. K., & Arcese, P. (2013). Abundance, rarity and invasion debt among exotic species in a patchy ecosystem. Biological Invasions, 15, 706–716. https://doi.org/10.1007/s10530-012-0320-x

Bergholz, K., May, F., Giladi, I., Ristow, M., Ziv, Y., & Jeltsch, F. (2017). Environmental heterogeneity drives fine-scale species assembly and functional diversity of annual plants in a semi-arid environment. Perspectives in Plant Ecology, Evolution and Systematics, 24, 138–146. https://doi.org/10.1016/j.ppees.2017.01.001

Bijak, S., Zasada, M., Bronisz, A., Bronisz, K., Czajkowski, M., Ludwiśiak, Ł., ... Wojtan, R. (2013). Estimating coarse roots biomass in young silver birch stands on post-agricultural lands in central Poland. Silva Fennica, 47, 963. https://doi.org/10.14214/sf.963

Bochenek, A., Synowiec, A., Kondrat, B., Szymczak, M., Lahuta, L. B., & Golaszewski, J. (2016). Do the seeds of Solidago gigantea Aiton have physiological determinants of invasiveness? Acta Physiologiae Plantarum, 38, 159.

Burnham, K. P., & Anderson, D. R. (2002). Model selection and multi-model inference: A practical information-theoretic approach. New York, NY: Springer.

Callaway, R. M., & Aschehoug, E. T. (2000). Invasive plants versus their new and old neighbors: A mechanism for exotic invasion. Science, 290, 521–523. https://doi.org/10.1126/science.290.5491.521

Chapuis-Lardy, L., Vanderhoeven, S., Dassonville, N., Koutika, L. S., & Meerts, P. (2006). Effect of the exotic invasive plant Solidago gigantea on soil phosphorus status. Biology and Fertility of Soils, 42, 481–489. https://doi.org/10.1007/s00374-005-0039-4

Chesson, P. (2000). Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics, 31, 343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Chi, W. C., Fu, S. F., Huang, T. L., Chen, Y. A., Chen, C. C., & Huang, H. J. (2011). Identification of transcriptome profiles and signaling pathways for the allelochemical juglone in rice roots. Plant Molecular Biology, 77, 591–607. https://doi.org/10.1007/s11103-011-9841-6

Cosmulescu, S., & Trandafir, I. (2011). Variation of phenols content in walnut (Juglans regia) leaves. South Western Journal of Horticulture, Biology and Environment, 2, 25–33.

Crooks, J. A. (2005). Lag times and exotic species: The ecology and management of biological invasions in slow-motion. Ecoscience, 12, 316–329.

Cui, C., Cai, J., Jiang, Z., & Zhang, S. (2011). Effects of walnut (Juglans regia L.) root exudates on germination, seedling growth and enzymatic activities of turnip (Brassica rapa L.). Allelopathy Journal, 28, 237–250.
de Groot, M., Kleijn, D., & Jogan, N. (2007). Species groups occupying different trophic levels respond differently to the invasion of seminatural vegetation by Solidago canadensis. Biological Conservation, 136, 612–617.

Ellenberg, H., & Leuschner, C. (2010). Vegetation mitteleuropas mit den Alpe. Stuttgart, Germany: Verlag Eugen Ulmer.

Elton, C. S. (1958). The ecology of invasions by animals and plants. London, UK: Methuen.

Ercisli, S., Esitken, A., Turkkal, C., & Orhan, E. (2005). The allelopathic effects of juglone and Walnut leaf extracts on yield, growth, chemical and PNE compositions of strawberry cv. Fern. Plant Soil and Environment, 6, 283–287.

Essl, F., Dullinger, D., Rabitsch, W., Hulme, P. E., Hubler, K., Jarosik, V., ... Pyshek, P. (2011). Socioeconomic legacy yields an invasion debt. Proceedings of the National Academy of Sciences of the United States of America, 108, 203–207. https://doi.org/10.1073/pnas.1011728108

Faliński, J. B. (1986). Sukcesja roślinności na nieużytkach porolnych jako przejaw dynamiki ekosystemu wywołanego spod długotrwałej presji antropogenicnej. Cz. 1 i 2. Wiadomosci Botaniczne, 30, 115–126.

Fenner, M., & Thompson, K. (2005). The ecology of seeds. Cambridge: Cambridge University Press.

Górski, T., Górska, K., & Stasiak, H. (2013). Inhibition of seed germination by far red radiation transmitted through leaf canopies. Polish Journal of Agronomy, 13, 10–38.

Green, P. T., O’Dowd, D. J., Abbott, K. L., Jeffery, M., Retallick, K., & Mac Nally, R. (2011). Invasive meltdown: Invader-invader mutualism facilitates a secondary invasion. Ecology, 92, 1758–1768. https://doi.org/10.1890/11-0050.1

Harpole, W. S., Sullivan, L. L., Lind, E. M., Firn, J., Adler, P. B., Borer, E. T., ... Wragg, P. D. (2016). Addition of multiple limiting resources reduces grassland biodiversity. Nature, 537, 93–96. https://doi.org/10.1038/nature19324

Hautier, Y., Seabloom, E. W., Borer, E. T., Adler, P. B., Harpole, W. S., Hillebrand, H., ... Hector, A. (2014). Eutrophication weakens stabilizing effects of diversity in natural grasslands. Nature, 508, 521–525.

Herr, C., Chapuis-Lardy, L., Dassonville, N., Vanderhoeven, S., & Meerts, P. (2007). Seasonal effect of exotic invasive plant Solidago gigantea on soil pH and P fractions. Journal of Plant Nutrition and Soil Science, 170, 729–738.

Hobs, R. J., Arico, S., Aronson, J., Baron, J. S., Bridgewater, P., Cramer, V. A., ... Zobel, M. (2006). Novel ecosystems: Theoretical and management aspects of the ecological world order. Global Ecology and Biogeography, 15, 1–7.

Honnay, O., Endels, P., Vereecken, H., & Hermy, M. (1999). The role of patch area and habitat diversity in explaining native plant species richness in disturbed suburban forest patches in northern Belgium. Diversity and Distribution, 5, 129–141.

Hulme, P. E., Pyshek, P., Jarošík, V., Pergl, J., Schaffner, U., & Vila, M. (2013). Bias and error in understanding plant invasion impacts. Trends in Ecology and Evolution, 28, 212–218. https://doi.org/10.1016/j.tree.2012.10.010

Inderjit, K., Cadotte, M. W., & Colautti, R. I. (2005). The ecology of biological invasions: past, present and future. In K. Inderjit (Ed.), Invasive plants: Ecological and agricultural aspects (277, pp. 1-5). Basel, Switzerland: Birkhauser-Verlag.

Kuebbing, S. E., Souza, L., & Sanders, N. J. (2013). Effects of cooccurring non-native invasive plant species on old-field succession. Forest Ecology and Management, 324, 196–204.

Lambdon, P. W., Pyshek, P., Basnou, C., Hejda, M., Arianoutsou, M., Essl, F., ... Hulme, P. E. (2008). Alien flora of Europe: Species diversity, temporal trends, geographical patterns and research needs. Preslia, 80, 101–149.

Lenda, M., Knops, J. M. H., Skórka, P., Moroń, D., & Wojciechowski, M. (2018). Cascading effects of changes in land use on the invasion of the walnut Juglans regia in forest ecosystem. Journal of Ecology, 106, 671–686.

Lenda, M., & Skórka, P. (2009). Walnut Juglans regia – a new, potentially invasive species in native flora. Chrony Przyrodę Ojczysta, 65, 261–270.

Lenda, M., Skórka, P., Knops, J. M. H., Moroń, D., Tworek, S., & Wojciechowski, M. (2012). Plant establishment and invasions: An increase in a seed disperser combined with land abandonment causes an invasion of the non-native Walnut in Europe. Proceedings of the Royal Society B: Biological Sciences, 279, 1491–1497. https://doi.org/10.1098/rspb.2011.2153

Li, J., Zheng, Z., Xie, H., Zhao, N., & Gao, Y. (2017). Increased soil nutrition and decreased light intensity drive species loss after eight years grassland enclosures. Scientific Reports, 7, 44525. https://doi.org/10.1038/srep44525

MacDaniels, L. H., & Pinnow, D. L. (1976). Walnut toxicity, an unsolved problem. Northern Nut Growers Association Annual Report, 67, 114–122.

Moroń, D., Lenda, M., Skórka, P., Szentgyorgyi, H., Settele, J., & Wojciechowski, M. (2009). Wild pollinator communities are negatively affected by invasion of alien goldenrods in grassland landscape. Biological Conservation, 142, 1322–1332.

Offord, C. A., Meagher, P. F., & Zimmer, H. C. (2014). Growing up or growing out? How soil pH and light affect seedling growth of a relictual rainforest tree. AoB Plants, 6, plu011. https://doi.org/10.1093/aobpla/plu011

Olrusd, H. M. K., & Michelsen, A. (2009). Effects of shading on photosynthesis, plant organic nitrogen uptake and root fungal colonization in a subarctic mire ecosystem. Botany-Botanique, 87, 463–474. https://doi.org/10.1139/B09-021

Pereira, J. A., Oliveira, I., Sousa, A., Valenata, P., Andrade, P. B., Ferreira, I. C. F. R., ... Estevinho, L. (2007). Walnut (Juglans regia L.) leaves: Phenolic compounds, antimicrobial activity and antioxidant potential of different cultivars. Food and Chemical Toxicology, 45, 2287–2295.

Pisula, N. L., & Meiners, S. J. (2010). Relative allelopathic potential of invasive plant species in a young disturbed woodland. The Journal of the Torrey Botanical Society, 137, 81–87.

Ponder, F., & Tadros, S. H. (1985). Juglone concentration in soil beneath black walnut interplanted with nitrogen-fixing species. Journal of Chemical Ecology, 11, 937–942. https://doi.org/10.1007/BF01012079

Preisser, E. L., & Elkinton, J. S. (2008). Exploitative competition between invasive herbivores benefits a native host plant. Ecology, 89, 2671–2677. https://doi.org/10.1890/08-0299.1

Pyshek, P., Pergl, J., Essl, F., Lenzenzer, B., Dawson, W., Kreft, H., ... Van Kleunen, M. (2017). Naturalized alien flora of the world: Species diversity, taxonomic and phylogenetic patterns, geographic distribution and global hotspots of plant invasion. Preslia, 89, 203–274. https://doi.org/10.23855/preslia.2017.203

Rodriguez, L. (2006). Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. Biological Invasions, 8, 927–939. https://doi.org/10.1007/s10530-005-5103-3

Rosin, Z. M., Skórka, P., Pütt, T., Žmihorski, M., Ekner-Grzyb, A., Kwiecinski, Z., & Tryjankowski, P. (2016). Villages and their old farmsteads are hot spots of bird diversity in agricultural landscapes. Journal of Applied Ecology, 53, 1363–1372. https://doi.org/10.1111/1365-2664.12715

Scharfy, D., Güsewell, S., Gessner, M. O., & Olde Venterink, H. (2010). Invasion of Solidago gigantea in contrasting experimental plant communities: Effects on soil microbes, nutrients and plant-soil feedbacks. Journal of Ecology, 98, 1379–1388. https://doi.org/10.1111/j.1365-2745.2010.01722.x

Simberloff, D., & Von Holle, B. (1999). Positive interactions of nonindigenous species: Invasive meltdown? Biological Invasions, 1, 21–32.
Skórka, P., & Lenda, M. (2010). Abandoned fields as refuges for butterflies in agricultural landscapes of Eastern Europe. In E. L. Harris, & N. E. Davies (Eds.), Insect habitats: Characteristics, diversity and management (pp. 83–103). New York, NY: Nova Science Publishers.

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

Śmilauer, P., & Lepš, J. (2014). Multivariate analysis of ecological data using CANOCO 5 (2nd ed.). Cambridge: Cambridge University Press.

Sun, B. Y., Tan, J. Z., Wan, Z. G., Gu, F. G., & Zhu, M. D. (2006). Allelopathic effects of extracts from Solidago canadensis L. against seed germination and seedling growth of some plants. Journal of Environmental Sciences, 18, 304–309.

Sutherland, S. (2004). What makes a weed a weed: Life history traits of native and exotic plants in the USA. Oecologia, 141, 24–39. https://doi.org/10.1007/s00442-004-0412-2

Sytykiewicz, H. (2011). Expression patterns of glutathione transferase gene (GstI) in maize seedlings under juglone-induced oxidative stress. International Journal of Molecular Sciences, 12, 7982–7995. https://doi.org/10.3390/ijms12117982

Szymura, M., Szymura, T. H., Wolski, K., & Świerszcz, 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

Terzi, I. (2008). Allelopathic effects of Juglone and decomposed walnut leaf juice on muskmelon and cucumber seed germination and seedling growth. African Journal of Biotechnology, 7, 1870–1874.

Terzi, I., & Kocacališkan, I. (2010). The effects of gibberellic acid and potassium on overcoming the effects of juglone stress on seed germination and seedling growth. Turkish Journal of Botany, 34, 67–72.

Tokarska-Guzik, B., Dajdok, Z., Zając, M., Zając, A., Urbisz, A., & Danielewicz, W. (2012). Rośliny obcego pochodzenia w Polsce ze szczególnym uwzględnieniem gatunków inwazyjnych. Warszawa, Poland: Generalna Dyrekcja Ochrony Środowiska.

Tryjanowski, P., Hartel, T., Báldi, A., Szymański, P., Tobolka, M., Herzon, I., … Żmihorski, M. (2015). Conservation of farmland birds faces different challenges in Western and Central-Eastern Europe. Acta Ornithologica, 46, 1–12. https://doi.org/10.3161/000164515X89857

Usowicz, B., Hajnos, M., Sokolowska, Z., Józefaciuk, G., Bowanko, G., & Kossowski, J. (2004). Spatial variability of physical and chemical soil properties in a field and commune scale. Acta Agrophysica, 103, 1–90.

Van Kleunen, M., Dawson, W., Essl, F., Pergl, J., Winter, M., Weber, E., … Pyšek, P. (2015). Global exchange and accumulation of non-native plants. Nature, 525(7567), 100–103.

Vander Wall, S. B. (2001). The evolutionary ecology of nut dispersal. Botanical Review, 67, 74–117. https://doi.org/10.1007/BF02857850

Vila, M., & Weiner, J. (2004). Are invasive plant species better competitors than native plant species? – Evidence from pair-wise experiments. Oikos, 105, 229–238. https://doi.org/10.1111/j.0030-1299.2004.12682.x

Vila, M., Espímar, J. L., Hejda, M., Hulme, P. E., Jarosik, P. E., Maron, J. L., … Pyšek, P. (2011). Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. Ecology Letters, 14, 702–708. https://doi.org/10.1111/j.1461-0248.2011.01628.x

Weber, E. (1998). The dynamics of plant invasions: A case study of three exotic goldenrod species (Solidago L.) in Europe. Journal of Biogeography, 25, 147–154. https://doi.org/10.1046/j.1365-2699.1998.01119.x

Weber, E. (2000). Biological flora of Central Europe: Solidago altissima L. Flora, 195, 123–134.

Werner, P. A., & Platt, W. J. (1976). Ecological relationships of co-occurring goldenrods (Solidago: Compositae). American Naturalist, 110, 959–971. https://doi.org/10.1086/283120

White, P. C., Ford, A. E., Clout, M. N., Engeman, R. M., Roy, S., & Saunders, G. (2008). Alien invasive vertebrates in ecosystems: Pattern, process and the social dimension. Wildlife Research, 35, 171–179. https://doi.org/10.1071/WR08058

Witek, T. (1965). Treś i metody sporządzania wielkoskalowych map glebowo-roślinnych. Roczniki Gleboznawcze, 40, 99–117.

Wundrow, E. J., Carrillo, J., Gabler, C. A., Horn, K. C., & Siemann, E. (2012). Facilitation and competition among invasive plants: A field experiment with alligatorweed and water hyacinth. PLoS ONE, 10, e48444. https://doi.org/10.1371/journal.pone.0048444

Zdyb, H. (2010). Eurasian walnut. Warszawa, Poland: PWN Warszawa.

Zhang, S. S., Jin, Y. L., Tang, J. J., & Chen, X. (2009). The invasive plant Solidago canadensis L. suppresses local soil pathogens through allelopathy. Applied Soil Ecology, 41, 215–222. https://doi.org/10.1016/j.apsis.2008.11.002

BIOSKETCH

Magdalena Lenda obtained her PhD in 2015 at the Jagiellonian University in Poland with her thesis on invasion processes of alien plants due to environmental changes and Internet trade. Magda’s research interests embrace ecology of invasive species, plant dispersers and pollinators network functioning, ecosystem services, effects of policy on biodiversity and ecology of large mammals. As a former student of psychology, she is also interested in how nature affects human mental wellbeing and health. She is currently Overseas Postdoctoral Fellowship at CEED/CBCS, University of Queensland, Australia, and works on inclusion invasion risk in the land sharing and land sparing dilemma.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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