

Invader–pollinator paradox: Invasive goldenrods benefit from large size pollinators

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Abstract

Aim: Mutualistic interactions between alien plants and native pollinators are needed to enable plant invasions. Although the increasing abundance of invasive plants in a habitat causes a dramatic decline of native pollinators, pollination services received by invaders are often sustained. This invader–pollinator paradox might be attributed to differences in pollination effectiveness and varying vulnerability to invasion among pollinators with different life history traits. In an experimental study, we explored the relationships between pollinator body size, pollination effectiveness and abundance of invasive species.

Location: Kraków area, Poland.

Methods: We placed a pair of potted invasive goldenrods (*Solidago gigantea*) at 25 sites differing in goldenrod abundance (cover: 0%–100%). Floral visitation rate of the potted goldenrods, as well as seed set and viability, was noted.

Results: Species richness of pollinators visiting inflorescences decreased with the increase of the goldenrod cover, whereas the floral visitation rate remained unchanged. However, the seed set was positively related to the goldenrod cover. Body size of floral visitors was structured along with the goldenrod cover so that pollinators' size increased with the cover. Also, the seed set of the potted plants, as well as goldenrod seed viability, depended positively on the body size of visiting pollinators.

Main conclusions: Invasive goldenrods did not suffer from pollinator shortage and ineffective pollination, especially in habitats densely covered by the invader, due to the presence of large-bodied pollinators. Our study highlights that pollination and reproduction of invasive plants might be sustained through ecological filtering, affecting the composition of pollinators with traits increasing pollination effectiveness.

KEYWORDS

alien species, bees, flies, plant invasions, pollen limitation, pollination, pollinator limitation, traits

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1 | INTRODUCTION

Globalization has accelerated the introduction and spread of alien species across all continents (Amano et al., 2016). Thus, recognition of basic mechanisms behind successful biological invasions allows a better understanding of ecological processes, which are shaping the state of biodiversity worldwide (Richardson, 2010). Many hypotheses designed to explain invasions are grouped around biotic characteristics as the most important factors affecting the success of alien species (Catford et al., 2009). Biotic characteristics include the properties of invading species and native communities, as well as their interactions (Catford et al., 2009; Tylianakis et al., 2008). After introduction, alien species can lose and gain biotic interactions, and these novel ecological relationships shape an invasive species' impact on a native community (Mitchell et al., 2006; Morales & Aizen, 2006). New mutual interactions between alien and native species can boost the invasive spread (Aizen et al., 2008; Richardson et al., 2000). Otherwise, the inability to establish biotic relationships between native and invasive species can stop the colonization of a new habitat (Levine et al., 2004).

Animal pollination is crucial to successful plant invasions (Burns et al., 2013), as almost 58% of alien plant species in Central Europe are, at least partially, dependent on insect pollinators (Pyšek et al., 2011). Insect pollination seems especially limiting to self-incompatible alien plants, as plants with self-pollination ability are more likely to establish outside their historical range (Razanajatovo et al., 2016). It has been shown that most invasive plant species are sufficiently pollinated by native or invasive pollinators (Chittka & Schürkens, 2001; Pyšek et al., 2011; Richardson et al., 2000). On the other hand, plant invasions can negatively impact the pollinator communities, for example a high abundance of alien plants dramatically decreases pollinator abundance (Bezemer et al., 2014; Bjerknes et al., 2007; Moroń et al., 2019; Potts et al., 2010, 2016). Thus, the lack of a shortage of pollination services received by invasive plants is a paradox of the invader–pollinator relationship (Figure 1). This paradox might be attributed to ecological filtering, that is differences in vulnerability to invasion, which structures pollinator populations according to life history traits related to pollination effectiveness (Frund et al., 2013). Mobility traits, such as body size, are linked to how pollinators use resources in a landscape (Moroń et al., 2017), as well as their pollination effectiveness (Abrol, 2012; Ne'eman et al., 2010). Therefore, it may be expected that pollinators with large body

sizes are able to avoid some of the negative impacts caused by invasive plants by covering longer distances (Greenleaf et al., 2007) and foraging in uninvaded areas in their home range. Also, because pollinators' body size is a good predictor of crops' fruit set (Garibaldi et al., 2015), larger pollinators might be effective pollinators of invasive plants' flowers, if they gather more pollen and transport it over longer distances (Kerr et al., 2019).

North-American goldenrods *Solidago* spp. are among the most invasive species in Europe and Asia (Axmacher & Sang, 2013; Weber, 2001). The species, in invaded sites, forms dense mono-specific stands frequently covering dozens of hectares (Moroń et al., 2009; Skórka et al., 2010). Goldenrod inflorescences are insect-pollinated and need cross-pollination because of their self-incompatibility (Kabuce, 2006). An individual shoot may produce more than 10,000 seeds, which can be dispersed over long distance by wind, whereas the local population size's increase is mainly the result of clonal growth (Kabuce, 2006; Weber, 2000). Earlier findings showed that, in habitats invaded by alien goldenrods, there is a dramatic abundance-dependent decline of the pollinator community suggesting the emergence of intra-specific competition for pollinators (Fenesi et al., 2015; Groot et al., 2007; Moroń et al., 2009, 2019). Thus, invasive goldenrods are excellent species to test whether pollination function in invasive species is dependent on pollinators with particular life history traits, (body size, in this case), in habitats of varying invader abundances during the course of invasion. We performed a field experiment, placing pairs of potted goldenrods at sites which differed in goldenrod cover (0%–100%). Floral visitors of planted goldenrods were noted, as were the seed set and their viability, produced by the plants. We expected that, on sites densely covered by invasive goldenrods, pollination services would be provided by large-bodied pollinators able to withstand the invasion effects and pollinate goldenrods effectively.

2 | METHODS

2.1 | Study area

The study was performed in the grassland landscape located in the valley of the Vistula river near the city of Kraków, Southern Poland (Figure 2). Using current and historical vegetation data, we mapped the wet meadows (Dubiel, 1995, 1996; Kornaś & Medwecka-Kornaś,

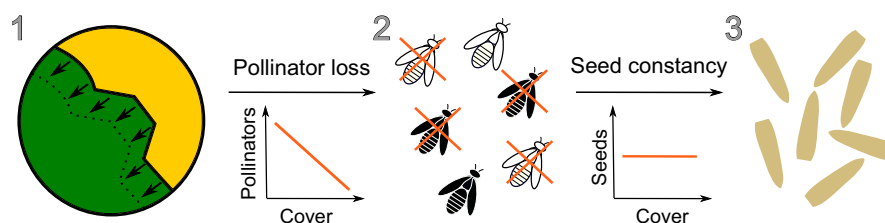


FIGURE 1 Conceptual model of the invader–pollinator paradox. With the increasing invasion (1), the native pollinators decrease (2). However, decrease of native pollinators (2) does not cause shortage in pollination services received by invasive plants (3)

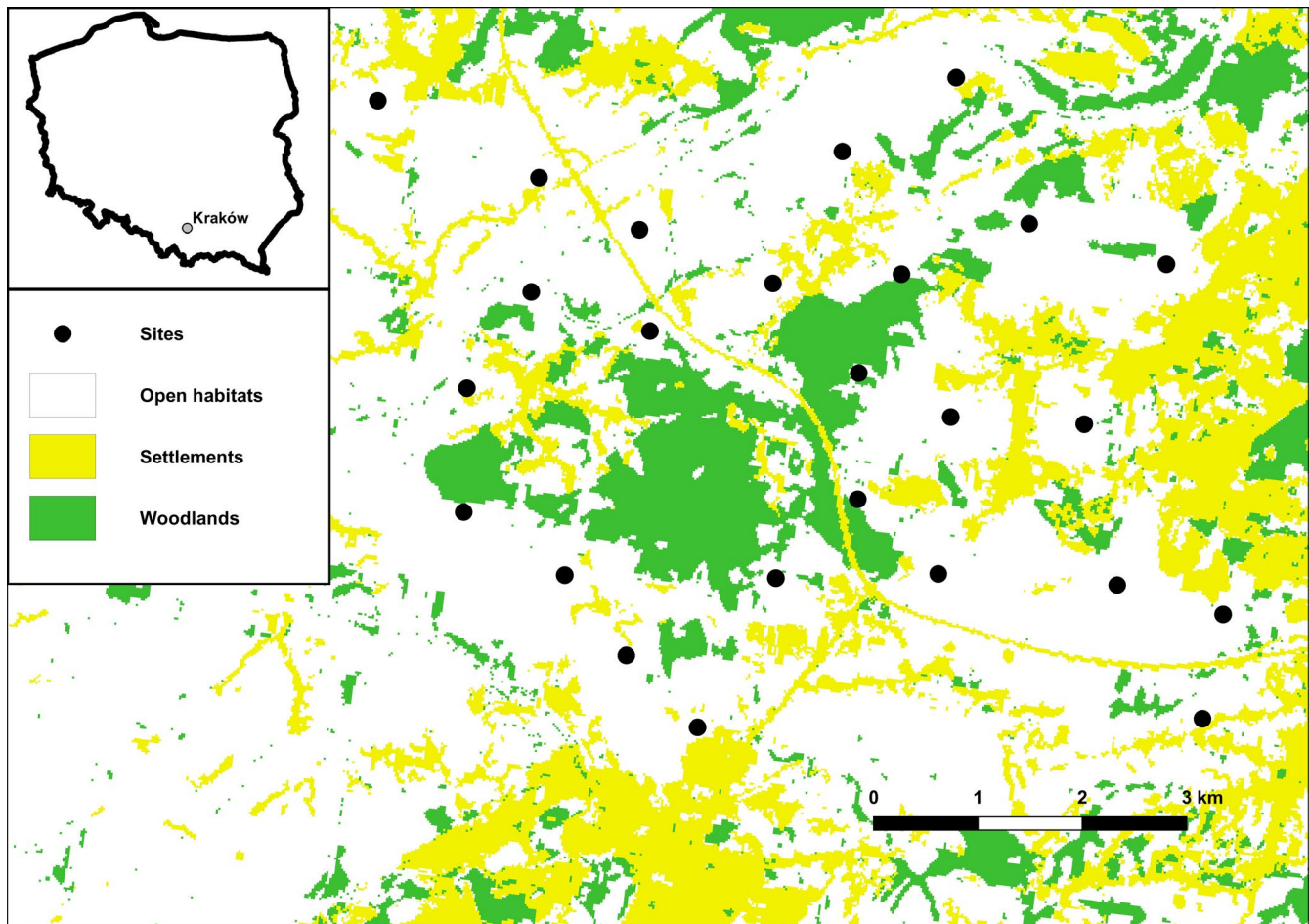


FIGURE 2 Location of 25 study sites in the Krakow region, Southern Poland

1974; Moroń et al., 2009; Pępkowska, 2002) where soil is periodically saturated with water. The meadows have a similar geological history, climate, soil properties and dominant vegetation type, that is dominated by *Molinietum caeruleae* (Gradziński, 1974; Kornaś & Medwecka-Kornaś, 1974; Langer & Szczepanowicz, 1996). Since the late 1980s, the meadows have been maintained by mowing, grazing or burning at several-year intervals which have resulted in differences in invasive goldenrod cover.

From all the mapped meadows, we selected 25 patches of meadows 1.13 ± 0.18 km (mean \pm SD) apart, on average (Figure 2). We ensured that cover of invasive goldenrods ranged from 0% to 100% ($38.36 \pm 37.48\%$). To calculate goldenrod cover within meadows, the study sites were carefully inspected and all patches of invasive goldenrods were mapped with the help of GPS. To control for the confounding effects of potential spatial gradients (size of site, number of native flowering plants and the cover of human settlements, farmland, grassland and woodland in the surrounding landscape), sites were selected in a relatively homogenous landscape. We used Spearman's rank correlation test to assess correlations between spatial environmental gradients and goldenrod cover. The sizes of the sites (6.81 ± 7.07 ha) and number of native flowering plant species (0.90 ± 0.52 species) were not correlated with goldenrod cover (site size: $r_s = -.171$, $p = .412$, Figure S1a; native

plants: $r_s = -.353$, $p = .079$, Figure S1b). The goldenrod cover of selected sites did not correlate with the cover of farmland ($r_s = -.124$, $p = .566$; 1.25 ± 1.91 ha, Figure S1c), woodland ($r_s = .065$, $p = .756$; 20.58 ± 12.27 ha, Figure S1d), human settlements ($r_s = -.022$, $p = .917$; 7.59 ± 6.51 ha, Figure S1e), grassland ($r_s = -.168$, $p = .421$; 46.56 ± 10.15 ha, Figure S1f) or goldenrod ($r_s = .040$, $p = .915$; $22.64 \pm 17.94\%$, Figure S1g) in a 500 m buffer around the study sites. Native plants were surveyed at four permanent plots, (each of 4 m²), randomly distributed at each site. The size of sites and land use covers were measured with the help of QGIS 2.18 (QGIS Development Team, 2018).

2.2 | Experimental setup

To standardize site-related differences in resources other than pollinators available for goldenrods, we decided to plant goldenrods in pots. Thus, from a patch of goldenrod located in the mapped meadow complex, we collected about one hundred *Solidago gigantea* stems with the root systems, in June. We chose *S. gigantea*, instead of the other co-occurring invasive *Solidago* spp. (*S. canadensis* and *S. graminifolia*), because of its higher survival during experimental processing and high abundance in the landscape. We ensured that

all the selected stems had developed inflorescence buds and were similar in size. After careful excavating, individual stems were immediately replanted to 5-L pots filled with potting soil to standardize soil conditions during the development of inflorescences. To avoid damage caused by animals or humans, the plants were transferred to the sites just before bloom at the beginning of August.

We confirmed *S. gigantea* self-incompatibility, as none of the 10 planted goldenrods with inflorescences isolated by plastic bags to protect against cross-pollination produced seeds (Figure S2). Inflorescences covered by mesh to protect against insect pollination produced significantly fewer seeds compared to planted goldenrods with open flowers (Wilcoxon test; seeds per inflorescence: 0.14 vs. 7.2, $W = 0$, $p < .001$, Figure S2). We confirmed that invasive goldenrods under experimental and natural conditions produced similar quantities of inflorescences and seeds (Figure S2). Due to goldenrod self-incompatibility, and in order to protect sources of pollen, especially in sites sparsely covered by goldenrods, we placed two pots with plants belonging to two different goldenrod clones at each site. We ensured that the clones' pollen could successfully pollinate each inflorescence, resulting in seed production which was confirmed by a lack of relationship between the seed set produced by inflorescences of potted goldenrods and the distance to the nearest naturally growing conspecific as shown by the generalized linear mixed models (GLMM) fitted with a negative binomial distribution and the site identity as a random factor ($Z = -.94$, $R^2 = .03$, $p = .350$; Figure S3). Two pots with plants belonging to two different clones were selected for each study site in such a manner as to ensure they would bloom at the same time, and placed there, with a distance of 10 m between the pots (buried in the ground). We also ensured that there was no correlation between the number of inflorescences of potted plants with goldenrod cover (GLMM with a Gaussian distribution and the site identity as a random factor; $t = -1.48$, $R^2 = .04$, $p = .145$; Figure S4). The presence of other flowers in close proximity can affect the number of pollinator visits to goldenrod flowers. Thus, to standardize the closest surroundings of planted goldenrods, we cleared a circle (2 m across) around each pot of all flowering plants. Potted plants shed blooms in mid-September. We collected stem fragments when seeds were fully developed (by the end of October) and stored these at -4°C till May.

2.3 | Surveys

We surveyed pollinating insects visiting potted goldenrod inflorescences. Each observation lasted 15 min and was repeated two to six times for each plant (depending on the duration of the potted plant's flowering period) from mid-August till mid-September, between 09:00 and 17:00, during favourable weather conditions. Altogether, each potted plant was observed for 61 ± 14 min (mean \pm SD), which is above the recommended duration of observation needed to obtain the flower visitation rate (Fijen & Kleijn, 2017). Whenever possible, floral visitors were identified to species level. In other cases, pollinators were collected and identified in the laboratory. Before pollinator

observations, we noted the number of blooming inflorescences of potted goldenrods. However, we did not find a significant relationship between the number of inflorescences of potted plants and the number of pollinator visits (GLMM with a negative binomial distribution and with the site identity as a random factor; bees: $Z = 1.22$, $R^2 = .02$, $p = .223$; flies: $Z = -.13$, $R^2 = .00$, $p = .899$; Figure S5a) or between the number of flowering native species and the number of pollinator visits (GLMM with a negative binomial distribution and with the site identity as a random factor; bees: $Z = -.02$, $R^2 = .00$, $p = .983$; flies: $Z = 1.60$, $R^2 = .06$, $p = .110$; Figure S5b). The order and time of day at which the sites were checked were random. From each potted plant, 100 seeds were evenly collected from multiple inflorescences, resulting in 5,000 seeds overall and sown on petri dishes in May. We recorded all germinated seedlings (those with a developed radicle or hypocotyl) and stopped observation when two weeks passed without the appearance of any new seedlings.

2.4 | Statistical analysis

To take into account the role of life history trait spectrum in pollination of invasive goldenrods, pollinator body size, flight period, food preferences, nesting preferences, parasitism and sociality were obtained from a review of the literature (Banaszak & Romasenko, 1998; Celary, 1991, 1995, 1999; Celary & Dylewska, 1988; Dylewska, 1987; Dylewska & Wiśniowski, 2003; Pesenko et al., 2000; Scheuchl, 2000; Speight, 2011; van Veen, 2004; Westrich, 1990) or based on direct measurements (body size) of at least 10 specimens stored in collections at the Polish Academy of Sciences and The Jan Kochanowski University. Pollinator body size and flight period were collected for all pollinator species. Food and nesting preferences, parasitism and sociality traits were accessed for bees. Hoverflies are not dependent on a particular group of plants as food, do not build nests and are not parasitic or social species, thus no data were collected for them. For each trait obtained only for bees, species were divided into two groups: food preferences (food specialists or non-food specialists), nesting preferences (nesting in the ground or above the ground), parasitism (parasite or non-parasite) and sociality (social or solitary). Body size was measured as body length (mm). Flight period meant seasonal activity of adults and was given in months. Bee species of which larvae feed on the pollen of a particular species or family of plants were considered as food-specialized, while species building nests in the ground or using soil cavities were considered as ground nesters. Cuckoo species were considered as parasitic and species which take care of their broods (at least the first generation) were considered as social.

All the variables had 50 records (two per site), if applicable, expressed in terms of a potted plant. To check the species richness of flower visitors, the seed set of potted plants and the number of floral visits per time (visitation rate) according to goldenrod cover, we used the generalized linear mixed-effects models with a negative binomial distribution with the site identity (ID) as the random factor and the sampling effort (duration of observation

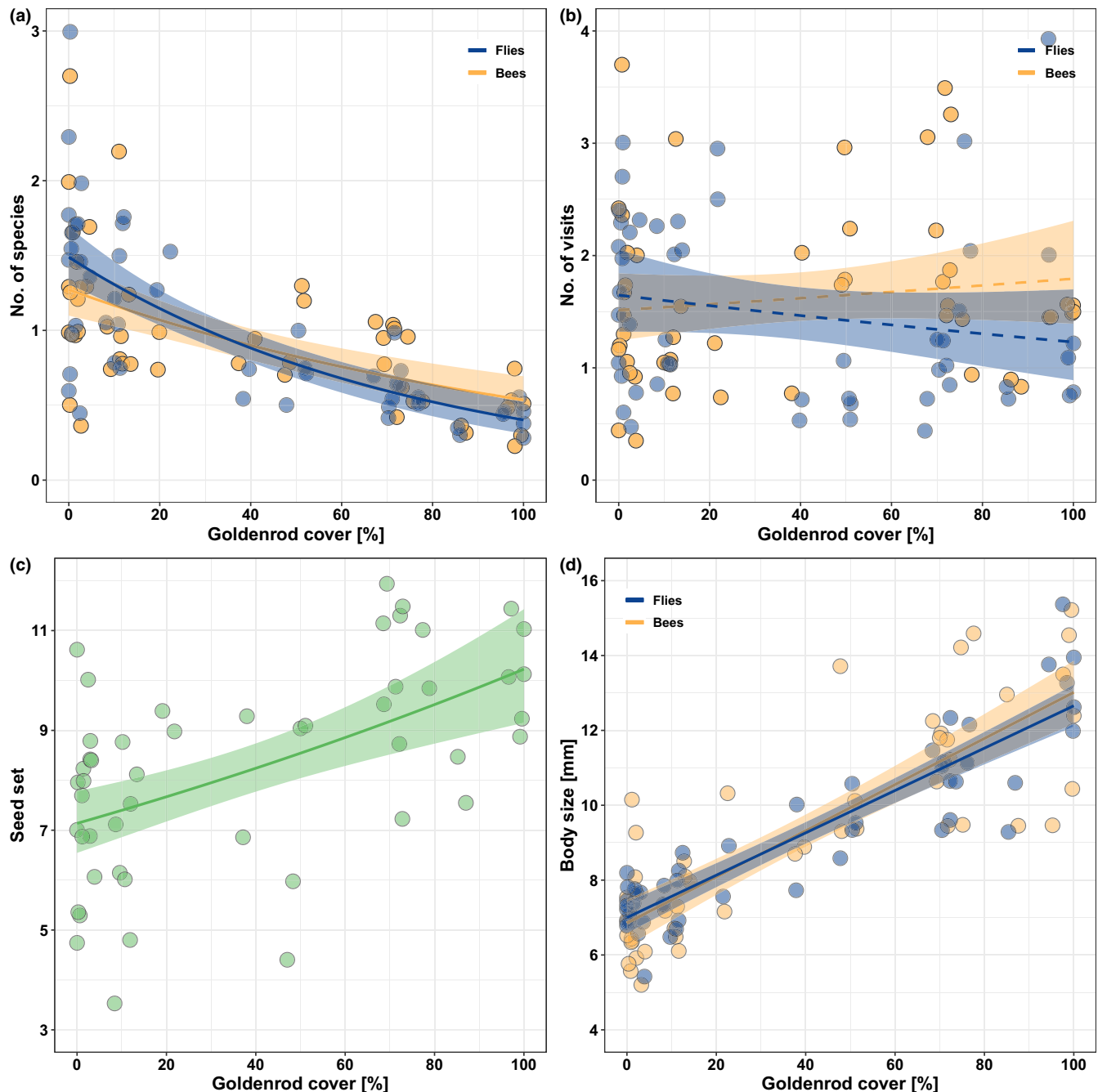


FIGURE 3 Relationship between potted goldenrods' visitor species richness (a), number of visits per 15 min (b), seed set per inflorescence (c), visitors' body size (d) and sites' cover by goldenrods. Points represent each of 50 potted plants. 95% CI are marked with polygons. Solid fitted lines represent significant relationships and dashed lines non-significant ones. Jittering was added to aid visualization

or inflorescence number) as an offset. GLMM with a negative binomial distribution and with site ID as the random factor and the inflorescence number as an offset was applied to check the relationship between seed set and body size, whereas GLMM with a binomial distribution and with site ID as the random factor was used to check the relationship between seed viability and body size. To find the relationship between traits and goldenrod cover, we built GLMM with a binomial distribution (for nesting preferences and

sociality) or a Gaussian distribution (for body size and flight period) both with site ID as random factors. Because there were only ten food-specialized and two parasitic species visits, these traits were not analysed. All data analysis and visualizations were undertaken using R ver. 4.0.2 (R Development Core Team, 2020) and the following packages: DHARMa ver. 0.3.3.0 (Hartig & Lohse, 2020), ggplot2 ver. 3.3.2 (Wickham et al., 2020), lme4 ver. 1.1.23 (Bates et al., 2020), lmerTest ver. 3.1.2 (Kuznetsova et al., 2020), MuMIn

ver. 1.43.17 (Bartoń, 2020) and vegan ver. 2.5.6 (Oksanen et al., 2019).

3 | RESULTS

During 3,030 min of observation of goldenrod inflorescences, we counted 604 visits by individual pollinating insects. Bees formed the most frequently observed pollinator group, accounting for 53% of visiting insects. Flies comprised 46% of insects inspecting inflorescences of potted goldenrods. Butterflies were only a very minor fraction of pollinators (1% of the total). Among pollinators, the most dominant species were *Apis mellifera* (9% of all visits), *Syrphid pipiens* (6%) and *Pipizella viduata* (4%).

3.1 | The invader–pollinator paradox

Increasing cover of goldenrod correlated with a decline in species richness of pollinators visiting goldenrod inflorescences of about 60% (bees: $Z = -4.01$, $R^2 = .30$, $p < .001$; flies: $Z = -5.59$, $R^2 = .48$, $p < .001$; Figure 3a, Figure S6a). Conversely, the pollinator visitation rate to goldenrod inflorescences did not change across the range of goldenrod cover (bees: $Z = 0.80$, $R^2 = .02$, $p = .423$; flies: $Z = 1.56$, $R^2 = .07$, $p = .110$; Figure 3b, Figure S6b). However, we found a positive relationship between goldenrod cover and seed set ($Z = 4.17$, $R^2 = .28$, $p < .001$; Figure 3c, Figure S6c). Inflorescences of potted goldenrods produced about 30% more seeds at densely covered sites compared to sparsely covered ones.

3.2 | Traits

Increasing cover of goldenrod was positively correlated with pollinator body size by about 50% (bees: $t = 10.55$, $R^2 = .69$, $p < .001$; flies: $Z = 13.46$, $R^2 = .81$, $p < .001$; Figure 3d). Larger pollinator species (~50% bigger) were associated with densely covered areas of goldenrods. However, pollinator communities were not structured along goldenrod cover gradient according to their flight period (bees: $t = 1.19$, $R^2 = .04$, $p = .245$; flies: $t = 1.48$, $R^2 = .04$, $p = .153$), nesting preferences (bees: $Z = -0.18$, $R^2 = .00$, $p = .854$) and sociality (bees: $Z = 0.54$, $R^2 = .01$, $p = .587$) traits.

3.3 | Production and viability of goldenrod seeds

The increased presence of larger pollinator species was positively associated with goldenrod seed production, leading to a 35% increase in yield and 20% increase in seed viability (seed set; bees: $Z = 3.48$, $R^2 = .22$, $p < .001$; flies: $Z = 4.23$, $R^2 = .28$, $p < .001$; viability; bees: $Z = 2.43$, $R^2 = .12$, $p = .015$; flies: $Z = 3.23$, $R^2 = .22$, $p = .001$; Figure 4a,b).

4 | DISCUSSION

Dense stands of invasive plants, similar to mass-flowering crops (Westphal et al., 2003), can have a strong negative effect on insect pollinators (Potts et al., 2016), although most studies show that invasive plant species are not pollinator- or pollen-limited (Pyšek et al., 2011; Richardson et al., 2000; Vilà et al., 2009). However, it

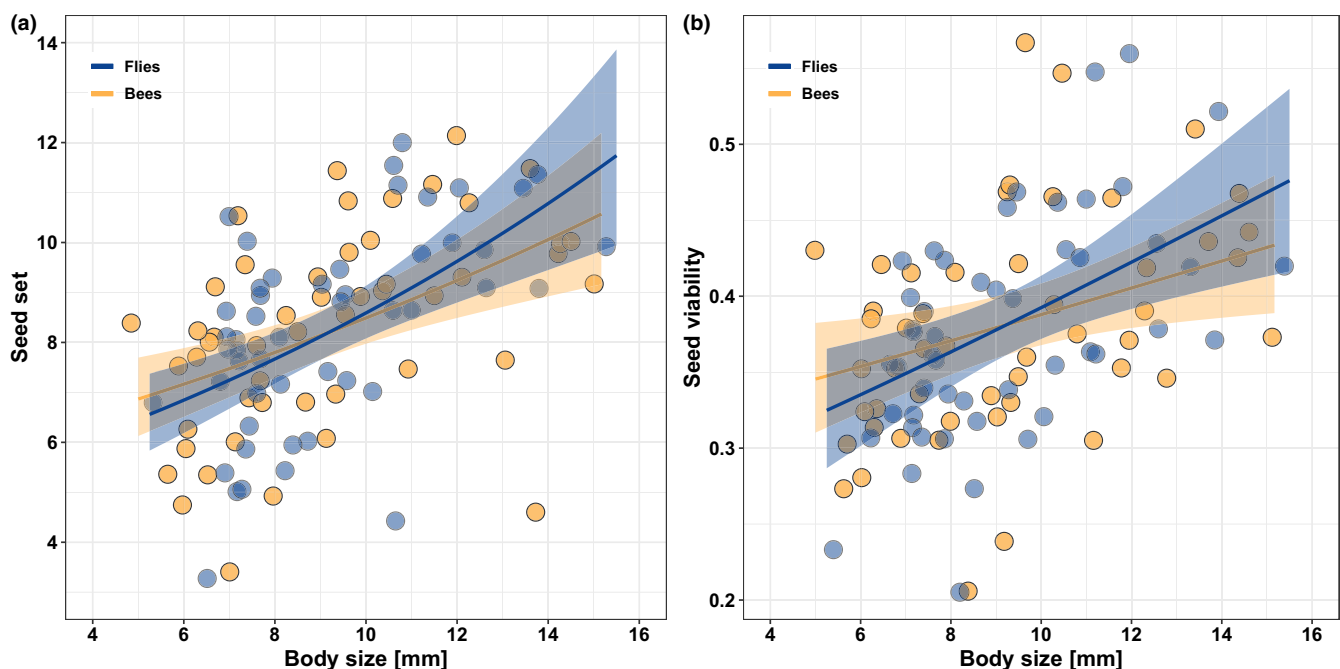


FIGURE 4 Relationship between the seed set per inflorescence (a) as well as seed viability (b) of potted goldenrods and body size of flower visitors. Legend as in Figure 3

could be expected that, with the increasing density of invaders, the magnitude of the negative impact on the pollinator community would also increase (Morón et al., 2009), thus pollination services for the invader would decline too (Figure 1). For example, it has been shown that, with increasing alien plant abundance, native plants experience a decrease in pollen deposition (Dietzsch et al., 2011). Nevertheless, none of the published studies, to our best knowledge, link pollinator deficiency of invader plants with their density. However, along with other studies concerning invasive plants (Pyšek et al., 2011), we did not find pollen limitation of potted goldenrods, even if we accounted for goldenrod cover. Whereas pollinator species richness decreased with goldenrod cover and their visitation rates remained unchanged, the body size of pollinators increased. This translates into an observed deficit of some trait-based groups of insects visiting inflorescences of the invader (for example, small-bodied bees and flies) with increasing goldenrod cover. However, the decrease of small-bodied pollinators was balanced by increasing visitation of the alien plants by large-bodied pollinators, probably as a result of ecological filtering (Sydenham et al., 2015). The invasive goldenrods did not suffer from insufficient pollination, even in habitats completely covered by dense stands of the invader, because of the possible role played by large-bodied pollinators in goldenrod pollination. Thus, our results show that biotic interactions with pollinators of different life history traits may be important factors affecting the success of alien species (Catford et al., 2009).

The factor that affected numbers of all pollinator groups visiting goldenrod inflorescences was goldenrod cover, but its impact differed between the pollinators of different body sizes. As expected, for small-bodied bees and flies, dense stands of goldenrods formed an adverse environment (Groot et al., 2007; Morón et al., 2009), which resulted in decreased pollinator richness. It is notable that the total number of insects recorded was small, which is typical for goldenrod stands (Morón et al., 2009). Nevertheless, numbers of large-bodied pollinators visiting the inflorescences increased as goldenrod cover increased on the sites. This may suggest that only highly mobile species such as large-bodied pollinators (Greenleaf et al., 2007; Wolf & Moritz, 2008), can deal with the negative impact of the invasion. Goldenrods successfully outcompete native plants (Lenda et al., 2019), so floral resources are scarce before the relatively short goldenrod flowering period and abundant once it begins (Morón et al., 2009). Thus, species living in an invaded habitat and able to cover greater distances can find resource-rich uninvaded patches, which is especially important before the goldenrod flowering period. On the other hand, larger pollinators living outside the invaded area are able to cross the boundaries of goldenrod patches, often avoided by smaller insects (Morón et al., 2019), and reach the interior during the flowering period to use abundant flower resources. Moreover, some pollinators (mostly honey bees in the studied region) are supported by humans, thus avoiding the direct negative impacts of goldenrod invasion, such as the reduction in native plant diversity (Morón et al., 2009).

Seed set and seed viability of the potted plants were positively affected by the body size of pollinators visiting the inflorescences.

Goldenrods need cross-pollination to develop viable seeds (Kabuce, 2006). Taking into consideration that the plant forms often one-clonal patches, effective pollination probably requires the pollen to be carried between inflorescences of different patches. Small-bodied pollinators cover short distances while collecting food (Greenleaf et al., 2007), at least in comparison with large-bodied ones (Ratnieks, 2000), thus might more frequently transfer goldenrod pollen within a clone. However, this hypothesis needs to be tested by measuring the pollen metrics, for example pollen deposition, to fully understand the effects of life history traits in the pollination of invasive plants.

Although most bees have behavioural and morphological adaptations (Michener, 2000), to carry pollen, their contribution to the pollination of goldenrods is not more effective than that of flies. An explanation of this pattern might be that flies, unlike bees, are not central-place foragers (Brock, 2015), so they are not restricted by nest location in their movement through a landscape. Thus, even if flies are not able to transport as much pollen as bees, pollen may be transferred among distant goldenrod patches, leading to more effective pollination (Rader et al., 2020). However, the existence of a trade-off between pollen load and distance of pollen source for pollination effectiveness needs to be tested.

An alternative explanation could be competition between pollinator species. For example, bees might outcompete flies for goldenrod floral resources. However, we did not find evidence of competition between bees and flies (Figure S7). Moreover, ecological filtering, as a hypothesis explaining the results, is supported by the significant nestedness of the pollinator community, indicating that species-poor sites constituted subsets of species-rich sites (Figure S8). Also, because floral food sources are positively related to goldenrod cover and visitation rate remains unchanged, relaxation of competition for resources can be assumed at densely covered sites. Additionally, it could be possible that the pollination behaviour of bees and flies changes with goldenrod abundance. For example, pollinators might spend more time on an inflorescence at sites densely covered by goldenrods, which would change pollination effectiveness. However, there was no significant correlation between goldenrod cover and the duration of pollinators' visits (Figure S9).

The invader–pollination paradox can have a non-linear character because inflorescences could receive decreased pollen deposition (reduced pollinator availability) but maintain seed set if there are enough flower visitors to fertilize all ovules (Aizen & Harder, 2007). Accordingly, we should expect, at most, the maintenance of seed set with the increase of invasive species cover. However, we found an increase of seed set along the cover gradient (Figure 3c). Moreover, the decrease of species richness at invaded sites was significant, with the number of pollinator species decreasing more than twofold (Figure 3a). Thus, both size-related quality and size-related quantity of pollinators seem important in pollination ecology of invasive goldenrods (Aizen & Harder, 2007).

Invasive plants, including goldenrods, are widely considered to have an adverse density-dependent effect on pollinator populations (Morón et al., 2019; Muñoz & Cavieres, 2008). However, studies so

far have not universally supported this negative impact and it is likely to be strongly context-dependent and to vary according to the traits of the invaders and the invaded community (Stout & Tiedeken, 2017). Furthermore, since the impacts of invasive plants are likely to be specific to the plant species and its ecology, our understanding is likely to be limited to globally widespread, problematic plant species. Thus, more studies of the ecology of invasive plants and flower visitors are required before generalizations about the invader–pollinator paradox can be made.

Because goldenrods are self-incompatible, it may be expected that potted plants received more viable cross-pollen as the cover increased. This in turn might affect seed set and seed viability. To lower this possibility, we potted two plants of different clones to ensure sources of pollen independently from goldenrod cover. Moreover, we did not find a statistically significant relationship between the seed set produced by inflorescences of potted goldenrods and the distance to the nearest naturally growing conspecific (Figure S3). Also, the observed pattern of seed set along the cover of naturally growing goldenrods mirrored the pattern found for potted plants (Figure S6c). Thus, although the level of cross-pollination was not controlled in our study, we assume that the effect of goldenrod cover on the seed set of potted plants was not mimicked by the pollen supply.

Preventing the introduction of invasive species seems to be the most cost-effective solution for biological risk management (Keller et al., 2007). However, in the case of established alien species that dominate in native habitats, their further expansion should be prevented (Zalba & Ziller, 2007). Large-bodied pollinators seem to be key pollinators of invasive goldenrods, especially at sites dominated by the invader. Although goldenrods are capable of effectively outcompeting local native plants, due to, for example, fast clonal growth or a strong allelopathic effect (Lenda et al., 2019; Ridenour & Callaway, 2001), seeds are important for long-distance dispersal (Kabuce, 2006). Taking into consideration that propagule pressure is an important factor determining the success of invasions (Catford et al., 2009), large-bodied pollinators could boost the invasion through sustaining feedback processes (Gaertner et al., 2014), that is densely covered sites are still the source of propagules despite the loss of pollinator diversity. Thus, identifying life history traits of pollination insects and invasive plants, particularly in habitats which are greatly changed by invaders, is important in risk management models concerning the spread of invasions.

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DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.c2fqz6171>.

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BIOSKETCH

Dawid Moroń is a community ecologist interested in understanding factors affecting pollinator communities in globalized world. His research also includes the behavioural and evolutionary ecology of social insects, especially ants. Recently, he has studied the effects of invasive species, environmental pollution and human alteration of landscapes on temperate zone insect pollinators. In his research, he places emphasis on novel habitats which can be important in biodiversity management, especially in highly changed landscapes.

Authors contributions: D.M. and P.S. conceived the idea; E.M., D.M. and P.S. collected the data; D.M. analysed the data; and D.M., P.S., E.M, M.L. and M.W. wrote and edited the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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