

# Invasive goldenrods affect abundance and diversity of grassland ant communities (Hymenoptera: Formicidae)

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**Abstract** Goldenrods (*Solidago* sp.) are currently one of the most invasive plant species in Central Europe. They threaten abandoned semi-natural wet grasslands which are extremely vulnerable to plant succession and invasions. We assessed whether *Solidago* invasion affects ants, keystone organisms essential to proper ecosystem functioning and to the existence of myrmecophilous *Phengaris* butterflies. Ten meadows containing 60 plots with and without goldenrods were studied. We found a strong, negative dependence between the presence of goldenrod cover and the number of ant nests (more than 50 % reduction compared to control) as well as the number of species, and changes in species composition. *Myrmica* ants, essential hosts for *Phengaris* larvae, were among the most affected species by goldenrod invasion. Immediate action should be undertaken for restoration and maintenance of biodiversity hot-spots affected by goldenrod invasion.

**Keywords** Goldenrod · Invasion · *Maculinea* butterflies · *Solidago canadensis* · *Solidago gigantea* · Semi-natural grasslands

## Introduction

The invasion of alien goldenrods (*Solidago gigantea* and *S. canadensis*, Asteraceae) is one of the major threats for semi-natural habitats in Central Europe. Introduced from North America in the first half of the nineteenth century as

an ornamental plant, goldenrods began to spread rapidly into new areas, successfully competing and displacing native flora (Weber 1998). Their success is due to strong colonization ability—single plants grow rapidly up to 2 m height and can produce up to ten thousand light, wind-dispersed, seeds (Kabuce and Priede 2010). Moreover, they propagate extremely efficiently by rhizomes, the primary proliferation route in stable populations (Hartnett and Bazzaz 1985; Weber 2011). Goldenrods also produce allelopathic compounds, effectively inhibiting the growth of other plants (Abhilasha et al. 2008; Callaway and Aschehoug 2000). The expansion of alien goldenrods is also reinforced by a lack of herbivores (Jobin et al. 1996), viruses and pathogens (Mitchell and Power 2003). Additionally, smaller or slower growing plant species receive less light, resulting in the displacement of native flora (Banta et al. 2008). Uncontrolled growth of *Solidago* may lead to a reduction in both the number of indigenous plant species and the degree of plant cover by more than 50 % (Moroń et al. 2009). In consequence, goldenrods establish stable and widespread monocultures, with high densities of sprouts. Such large changes in vegetation also bring further consequences for organisms at higher trophic levels, both herbivores and predators (de Groot et al. 2007; Moroń et al. 2009; Skórka et al. 2010; Fenesi et al. 2015). An investigation into the climatic niche of *Solidago* showed that its range and density will increase, mainly in the south-eastern part of Europe (Weber 2001).

The abandonment of traditional management (mowing, cattle grazing) of semi-natural grasslands (Luoto et al. 2003; Joyce 2014) results in rapid succession within these areas and encroachment of invasive species on previously unavailable habitat, threatening biodiversity (Queiroz et al. 2014). Meadows are among the most endangered habitats in Europe. From the twentieth century, the areas occupied

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by semi-natural grassland have been reduced by at least 80 % of their original area (Joyce 2014). Semi-natural meadows are considered to be valuable for nature protection in Europe and fall under Annex I of the Habitats Directive of the “Natura 2000” network. They are characterized by relatively high biodiversity (Habel et al. 2013) including rare and endangered species closely associated with this specific biotope.

Ants are considered keystone species with an environmental influence disproportionately large in relation to their biomass (Folgarait 1998; Crist 2009). In one season, ants are able to consume 3 % of the primary productivity of meadows and in the case of predatory ants up to 40 % of the biomass (Petal 1980). Ants also have an important role in modifying the physico-chemical properties of the soil. Corridor and nest building by ants not only increases the porosity of the soil by bioturbation, but also alters the pH and chemical composition, facilitating soil colonization by microbiota and hence increasing the rate of decomposition (Frouz and Jilková 2008). Moreover, ant activity can significantly affect vegetation. The creation of nests favors the colonization of plant roots by mycorrhizal fungi (Dauber et al. 2008) and disturbance to the soil can improve the development of annual plants, some of which are exclusively associated with anthills (Dostál 2007). Ants also spread plant seeds enabling expansion into new areas (Servigne and Detrain 2008). In the case of plant species that use obligatory myrmecochory, displacement of associated ants may cause a significant reduction in population size and may lead to local extinction (Gorb et al. 2013).

There are also strong links between ants and other invertebrates, i.e. aphids and numerous lycaenid butterflies, including the scarce large blue *Phengaris teleius*, the dusky large blue *P. nausithous* and alcon blue *P. alcon*. All are obligatory parasites of the ant genus *Myrmica*, spending major parts of their life cycles in ant nests (Thomas et al. 1989; Thomas and Settele 2004). Metapopulations of blue butterflies in Kraków are considered to be one of the largest in Europe (Nowicki et al. 2007) and have been afforded habitat protection in the “Dębnicko-Tyniecki meadow area” of the Natura 2000 network. As an umbrella species, their preservation entails protection for multiple coexisting species and the whole semi-natural meadow habitat.

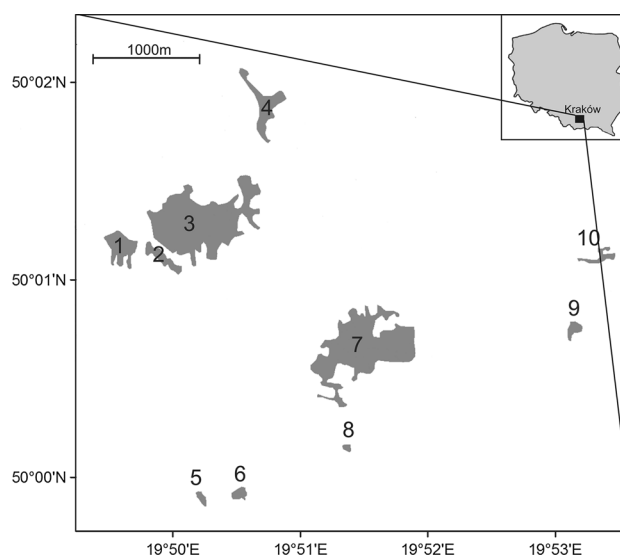
Because of the unique interactions between different meadow species, interspecific competition among ants can play an important role in the functioning of the whole habitat. Among native meadow-inhabiting ants, *Lasius niger* is a highly competitive species, resistant to changes and thus dominant in disturbed habitats. It may displace other species of ants such as *L. flavus*, and *Myrmica* sp. However, in the case of habitats with high stability, these species may be able to effectively compete with *L. niger* (Wynhoff et al. 2011).

Ants are sensitive to environmental changes and it is relatively easy to estimate their density, making them useful bioindicators (Underwood and Fisher 2006). Some studies have shown changes in ant communities due to abandonment of semi-natural grassland (Dauber et al. 2006; Wynhoff et al. 2011) suggesting that the quickly progressing invasion of goldenrod can also have an impact on this group of insects.

Our aim was to assess whether the invasion of goldenrods on semi-natural grassland areas triggered changes in species composition and population density of meadow-inhabiting ants. We checked whether and how goldenrods affect ant communities by assessing the number of ant species, the density of ant nests and proportion of *L. niger* in the total nest number of *Myrmica* and *Lasius* species. A negative impact of goldenrods would imply that the invasion is harmful not only to ants, but also indirectly to *Phengaris* butterflies as well as to the functioning of the ecosystem.

## Materials and methods

The study was conducted in ten semi-natural wet grasslands located in the south-eastern part of Kraków (Fig. 1) which belong to a meadow complex inhabited by *Phengaris* butterfly metapopulations (Nowicki et al. 2007). Five of them are situated in the “Dębnicko-Tyniecki meadow area” Natura 2000 network. Until recently, these meadows were extensively managed. At present, because of the abandonment of traditional use in all of the surveyed areas,



**Fig. 1** Location of the studied meadows in the Kraków region, southern Poland

there is a serious problem with uncontrolled spreading of goldenrod populations.

On each meadow, six  $5 \times 5$  m square plots were randomly selected (Łomnicki 2010): three covered with goldenrods (*Solidago canadensis* and *S. gigantea*) and three controls. Overall 60 plots were studied. Google Earth photos of each meadow were put on axes according to cardinal directions ('x' and 'y' axes demarcated east–west and north–south orientations, respectively). Points on axes were selected using random numbers; their intersection determined coordinates. Next, the list of coordinates was entered into a GPS device. These coordinates determined the southwestern corner of each plot. Plots were located at least 20 m from each other. Goldenrod cover on each plot was quantified using the Braun-Blanquet Cover-Abundance Scale (Wikum and Shanholtzer 1978; Wysocki and Sikorski 2002) in five categories: (1—<10 % of goldenrod cover; 2—10–25 % of goldenrod cover; 3—25–50 % of goldenrod cover; 4—50–75 % of goldenrod cover; 5—75–100 % of goldenrod cover). With the exception of two cases (plot cover approximately 65 %—category 4), we took into consideration only two categories: 1 ('control' plot) and 5 ('goldenrod' plot). Hence if the coordinates did not meet the requirements (i.e. unsuitable meadow type or proximity to other plots), we reiterated the random selection procedure until we obtained 3 plots in each meadow type (3 'goldenrod' and 3 'control').

Each square was investigated in terms of ant nest presence. The study plots were searched systematically to detect all ant nests. Several ant workers were collected from each nest and preserved in 75 % ethyl alcohol for further identification. All samples were collected in the period from 8 June to 9 September 2012, with the exception of a single square, which was inspected on 31 August 2011. Ants were identified using the key of Radchenko et al. (2004). *M. scabrinodis* and *M. sabuleti* were grouped together as "*M. scabrinodis*" because of the minor morphological differences between the species making proper identification contentious. The only certain method in this case seems to be chromatography (Guillem et al. 2012), but due to the very large number of contentious samples and low probability of finding *M. sabuleti* in this area, this species was omitted in the analysis.

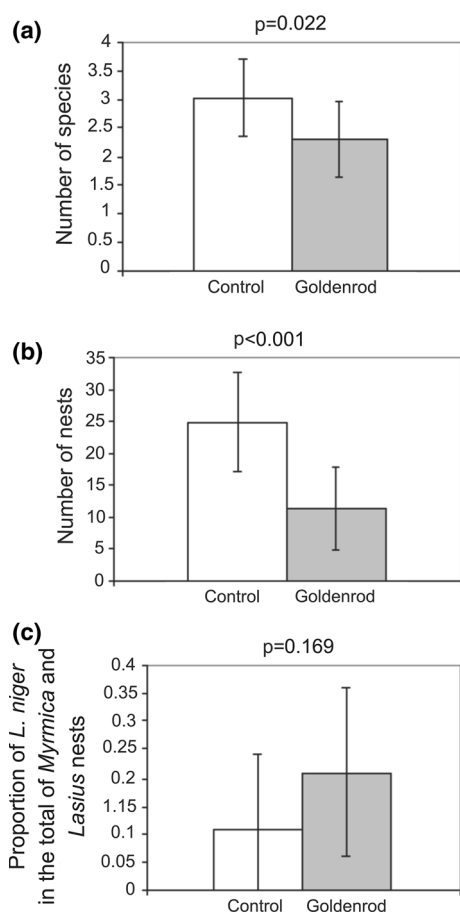
Because of non-normal distributions of the collected data, Mann–Whitney *U* tests were applied to compare the numbers of nests of *Myrmica* as well as individual ant species between goldenrod and control plots. Next, the average (1) number of ant species, (2) number of ant nests and (3) proportion of *L. niger* ants in the total nest number of *Myrmica* and *Lasius* species were calculated for plot type (goldenrod vs. control) on each meadow separately. The mean values for each meadow were used to examine differences between control and goldenrod plots. The Student's *t* test for paired samples

with a 95 % confidence interval was applied to evaluate the impact of goldenrods on the number of ant nests. Data was square-rooted to obtain a normal distribution. In the case of the number of ant species as well as the proportion of *L. niger* ants in the total nest number of *Myrmica* and *Lasius* species, data distributions were non-normal even after transformation. Hence, non-parametric Wilcoxon sign-ranked tests were used to check for differences between control and goldenrod meadows. A two-dimensional non-metric multi-dimensional scaling (NMDS) ordination plot was calculated for visualization of the species composition in both meadow types. One-way PERMANOVA was performed to test for potential differences in ant composition between control and goldenrod plots. Similarly, average nest numbers of each species for each meadow were used to examine differences between control and goldenrod plots. The Bray–Curtis distance was used as a dissimilarity measure because it is well suited for species abundance data (Quinn and Keough 2002). Analyses were done in StatSoft Statistica 12 and PAST 3.

## Results

We found a total of 1087 ant nests belonging to seven species. *Myrmica* was the most common in the ant assemblage and was more numerous in control than in goldenrod plots (mean  $\pm$  SD:  $5.19 \pm 8.55$ ;  $2.12 \pm 5.24$ , respectively; Mann–Whitney *U* test  $U = 155.0$ ;  $Z = 4.360$ ;  $P < 0.0001$ ). Differences in the number of nests between control and goldenrod plots were statistically significant in the case of *M. ruginodis* and *M. scabrinodis* (81 % for *M. ruginodis*: Mann–Whitney *U* test  $U = 330.5$ ,  $Z = 1.993$ ,  $P = 0.046$ ; 63 % for *M. scabrinodis*:  $U = 176.0$ ,  $Z = 4.082$ ,  $P < 0.001$ ). Non-significantly lower densities in goldenrod plots were found for *M. rubra* and *L. flavus* (39 % for *M. rubra*: Mann–Whitney *U* test  $U = 442.0$ ,  $Z = 0.113$ ;  $P = 0.910$ ; 65 % for *L. flavus*:  $U = 357.5$ ,  $Z = 1.649$ ,  $P = 0.099$ ). The only species that sustained densities and even showed a slightly higher frequency in goldenrod plots (by 2 %, Mann–Whitney *U* test  $U = 447.0$ ,  $Z = 0.041$ ,  $P = 0.968$ ) was *L. niger*. Single nests of *M. gallienii* and *Formica sp.* ants occurred only in the control plots.

The number of species per plot (mean  $\pm$  SE) averaged  $3.03 \pm 0.69$  for the control and  $2.3 \pm 0.66$  for the goldenrod plots and this difference was statistically significant (Wilcoxon-ranked test,  $N = 10$ ,  $T = 5.00$ ,  $Z = 2.293$ ,  $P = 0.022$ ; Fig. 2a). Moreover, there was a two-fold difference in the number of ant nests in the control compared to goldenrod plots ( $24.97 \pm 7.83$  and  $11.27 \pm 6.54$ , respectively, Student's *T* test for paired samples  $N = 10$ ,  $DF = 9$ ,  $T = 8.871$ ,  $P < 0.001$ ; Fig. 2b). There was also a slightly higher proportion of *L. niger* nests in goldenrod



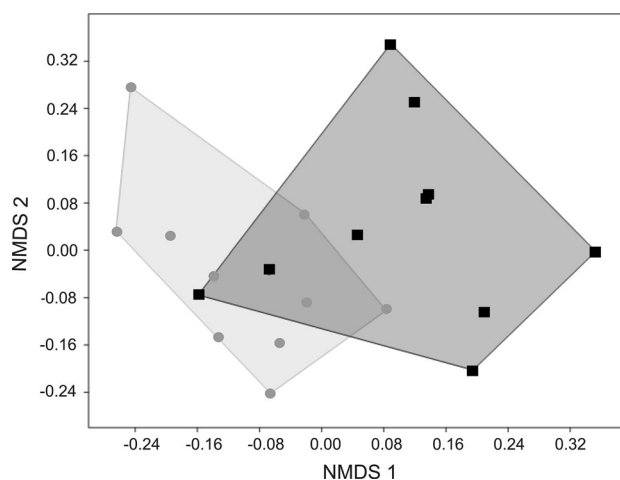
**Fig. 2** The average ( $\pm$ SD) number of species (a); number of nests (b) and ratio of the number of *L. niger* nests in the total nest number of *Myrmica* and *Lasius* species (c) in control (white bars) and goldenrod (gray bars) squares

( $0.21 \pm 0.15$ ) compared to control plots ( $0.11 \pm 0.13$ ), but this difference was non-significant (Wilcoxon-ranked test,  $N = 10$ ,  $T = 14.00$ ,  $Z = 1.376$ ,  $P = 0.169$ ; Fig. 2c).

The NMDS ordination plot suggested a possible difference in community structure between control and goldenrod plots (Fig. 3). A stress value of 0.146 suggests sufficient representation in reduced dimensions (Quinn and Keough 2002). Coefficients of determination between distances along each ordination axis and the original distances explained 46 and 36 % of differences in ant communities between control and goldenrod plots (Fig. 3). One-way PERMANOVA revealed differences in ant species composition between control and goldenrod plots ( $N_{\text{permutation}} = 9999$ ,  $SS = 3.49$ ,  $MS = 2.767$ , Pseudo-F = 4.701,  $P = 0.003$ ).

## Discussion

Our results revealed a strong negative effect of goldenrod on the average number of ant species and ant nest density. The lower species number in goldenrod plots was



**Fig. 3** NMDS ordination plot of ant species composition in control (grey circles, light grey polygon) and goldenrod (black squares, dark grey polygon) meadows. Fractions of explained variation:  $R^2_{\text{NMDS1}} = 0.458$ ,  $R^2_{\text{NMDS2}} = 0.357$

statistically significant despite the relatively low ant species diversity. Strikingly, a more than 50 % reduction occurred in density of ant nests on goldenrod plots. Ant species composition also significantly differed between control and goldenrod plots. Species negatively affected by goldenrods included *L. flavus*, *M. scabrinodis*, *M. ruginodis* and *M. rubra*. The first two species are thermophilic and prefer heavily insolated areas with low vegetation (Radchenko et al. 2004). Hence, the high shading associated with goldenrod invasion most probably degraded high-quality habitat previously available for these species. The status of *M. scabrinodis* (the most numerous species in the control plots) is particularly interesting, because its considerable decline on goldenrod plots indicates a significant change in habitat conditions. Surprisingly, populations of *M. ruginodis* were the most affected. Compared to other ants of the genus *Myrmica* found in this study, this species prefers shaded and slightly cooler habitats such as woodlands (Elmes et al. 1998; Radchenko et al. 2004). This habitat requirement suggests that *M. ruginodis* could potentially find favorable conditions within invaded patches. The presence of goldenrod guarantees the availability of honeydew and nectar (on which *M. ruginodis* as well as *M. rubra* forage; Radchenko et al. 2004), but not before July. Ant workers in areas with goldenrod forage over longer distances (Lenda et al. 2013), which may indicate lower food availability in areas invaded by goldenrod. Further studies are required to resolve the detailed mechanism of the negative effect of goldenrod on particular species. All observed *Myrmica* species are host ants of *Phengaris* butterflies (Witek et al. 2008). In the context of previous studies showing significant correlations between local extinctions of hosts and parasites (Koh et al. 2004),

goldenrods may also have a negative effect on these flagship species. In the context of extreme local specificity of *P. alcon* for *M. scabrinodis* ants (Sielezniew and Stankiewicz 2002) as well as the high specificity of *P. nausithous* for *M. rubra*, goldenrod invasion potentially threatens these two butterfly species to a higher degree than the more flexible *P. teleius* which does not show local specialization to host ants (Thomas and Elmes 1998; Witek et al. 2008).

Our results suggest that only *L. niger* is able to sustain numerous nests in an environment changed by goldenrod. As a polyphagous species known for its high resistance to environmental change (Radchenko et al. 2004), *L. niger* seems to be an opportunist not threatened by invasion. The number of nests of *L. niger* can even increase because they probably start to occupy free niche space after the decline of other ant species for which the goldenrod environment is unfavorable. Although Wynhoff et al. (2011) showed that *L. niger* can displace competing species (*L. flavus*, *Myrmica* sp.) if habitat conditions undergo a sudden change for other reasons, e.g. heavy mowing, our study design precluded an assessment of this mechanism.

Litt et al. (2014) reviewed the literature concerning effects of invasive plants on arthropods. They found that the abundance and richness of ant species decreased with invasion of various plants (including goldenrod, see Lenda et al. 2013) in almost 50 % of recent studies and increased in only 7 %. They suggest two main explanations for this decline. First, deterioration in the food base due to a decrease in the diversity and coverage of native plants could have triggered a decline in nectar-feeding ants (mainly *M. rubra* and *M. ruginodis*). Goldenrod is a strongly melliferous plant, but the time of flowering is probably too short and too late to provide enough food for invertebrates (Moroń et al. 2009). Moreover, an overall decline in species richness and densities of different groups of invertebrates in areas with goldenrod (de Groot et al. 2007; Skórka et al. 2007; Moroń et al. 2009; Fenesi et al. 2015) may cause a decrease in the amount of available food for carnivorous ant species (Litt et al. 2014), mainly *M. scabrinodis*. Many species of ants also feed on the honeydew produced by aphids. However, the effect of displacement of native plants by goldenrod on aphids is unknown. Second, the decline in ant diversity and abundance could be due to changes in microclimatic conditions (temperature, moisture, light intensity) caused by modifications in structural characteristics (increasing cover, plant height) as well as in litter accumulation and in soil characteristics (nutrients, salinity, pH) (Standish 2004; Wolkovich et al. 2009; Talley et al. 2012), which may be important especially for thermophilic species such as *M. scabrinodis*.

The impact of goldenrod invasion has already been studied in other groups of animals with a documented

decrease in species richness, diversity and abundance of butterflies, wild bees and hoverflies but only a decrease in abundance in the case of ground beetles (de Groot et al. 2007; Skórka et al. 2007; Fenesi et al. 2015). The strength of these relationships depended on the trophic position occupied by the group of insects, i.e. the most strongly affected species were food specialists associated with native plants (de Groot et al. 2007). Such specialists include *Phengaris* butterflies which beside *Myrmica* ants also need obligatory host plants in their life cycle. Because invaded parts of meadows are characterized by a significantly lower number of flowering *Sanquisorba officinalis* and *Gentiana pneumonanthe* host plants (unpublished data), goldenrods may threaten *Phengaris* butterflies as well as other coexisting meadow species. So far no negative demographic trends in *Phengaris* butterfly metapopulations were noticed in the study area (Kajzer-Bonk et al. 2013). However, goldenrod invasion has only recently commenced (Moroń et al. 2009), and a large part of this particular meadow complex is still in good condition. Moreover, the abundance of *S. officinalis* does not affect densities of *Phengaris* butterflies (Nowicki et al. 2007). Notably, *S. officinalis* is typically the last native flowering plant in patches invaded by goldenrod (personal observation). Hence, the negative effect of goldenrod invasion may be delayed and later expressed as a co-extinction and a sudden collapse of *Phengaris* populations.

Despite evidence of the negative effects of goldenrod invasion (Skórka et al. 2007; Moroń et al. 2009), no efforts have been made to restore this valuable area. Our findings again show that immediate conservation actions should be undertaken to suppress goldenrod invasion in grassland habitats. One way is to systematically mow twice per season in May and August before seed production and remove the remaining biomass (Meyer and Schmid 1999; Weber 2000; Dölle and Schmidt 2009). Even small fragments of grasslands utilized in a traditional and continuous manner can increase the chances of survival of typical meadow species. Proper management after goldenrod removal involves not mowing the whole area at the same time—uncut fragments constitute a refuge for many species that can later recolonize mown areas (Dauber et al. 2006). An alternative method can be controlled burning of meadow fragments, which is probably much less destructive for grassland fauna than it is believed by many conservationists (Nowicki et al. 2015). Properly conducted active grassland protection allows the restoration of ant species richness (Dahms et al. 2010) and preservation of the whole ecosystem.

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