

## *Solidago canadensis* impacts on native plant and pollinator communities in different-aged old fields



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### Abstract

Secondary succession in former arable fields (i.e. old fields) might be altered by the colonization of invasive alien species, with possible community-wide impacts, hindering the ability of old fields to become species-rich communities. However, the effects of invasive species on local communities have rarely been addressed in the light of secondary succession. Therefore, we studied the impact of the highly invasive *Solidago canadensis* on plant and pollinator communities along a gradient of invasion severity in old fields with different ages (1–20 years since last ploughing) in Southern Transylvania, Romania. We asked whether the invasion of *S. canadensis* causes shifts in (1) the composition and diversity of plant communities, and (2) pollinator communities along the successional gradient. Further, we asked (3) to what extent the presence of *S. canadensis* affected flower visitation of native plant species by pollinators. According to our results, the invasion reduced the native plant species richness throughout succession, although the most profound negative effect on plant diversity and vegetation naturalness was exerted in older successional communities. The invasion of *S. canadensis* had a negative effect on the abundance of bees irrespective of the old field age; however, there was no similar negative effect on hoverflies. Native flowers experienced reduced visitation by wild bees, honey bees and hoverflies due to the augmented presence of *S. canadensis*. Therefore, the invasion of this perennial plant species diverts the trajectory of vegetation succession, alters the mutualistic links between the native elements of these old fields, and causes a non-desired alternative stable states to be installed.

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## Zusammenfassung

Die sekundäre Sukzession auf ehemaligen Feldern könnte durch die Besiedelung mit invasiven fremden Arten verändert werden, die möglicherweise die ganze Gemeinschaft beeinflussen, indem sie die Entwicklung hin zu artenreichen Gemeinschaften erschweren. Indessen wurden die Einflüsse von invasiven Arten auf lokale Gemeinschaften selten in Hinblick auf die sekundäre Sukzession betrachtet. Wir untersuchten deshalb den Einfluss der hoch-invasiven Kanadischen Goldrute (*Solidago canadensis*) auf Pflanzen- und Bestäubergemeinschaften entlang eines Gradienten unterschiedlich starker Invasion auf alten Feldern unterschiedlichen Alters (1 bis 20 Jahre seit dem letzten Pflügen) in Süd-Transsilvanien (Rumänien). Wir fragten, ob Invasion durch die Goldrute Veränderungen in der Zusammensetzung und Diversität der Pflanzen- und Bestäubergemeinschaften entlang des Sukzessionsgradienten hervorruft. Desweiteren fragten wir, inwieweit die Anwesenheit der Goldrute den Blütenbesuch an einheimischen Pflanzen beeinflusst. Die Invasion reduzierte den Artenreichtum der einheimischen Pflanzen über die gesamte Sukzession hinweg, aber der stärkste negative Effekt auf die Pflanzendiversität und die Natürlichkeit der Vegetation erfolgte in den älteren Sukzessionsgemeinschaften. Die Goldruten-Invasion hatte unabhängig vom Alter der Felder einen negativen Effekt auf die Abundanz der Bienen, aber es gab keinen gleichartigen Effekt auf die Schwebfliegen. Einheimische Pflanzen erfuhren einen reduzierten Blütenbesuch durch Wildbienen, Honigbienen und Schwebfliegen, der der vermehrten Anwesenheit der Goldrute geschuldet war. Deshalb ändert die Invasion durch diese ausdauernde Pflanzenart den Verlauf der Vegetationssukzession, ändert die mutualistischen Verbindungen zwischen den einheimischen Arten der ehemaligen Felder und verursacht die Etablierung eines unerwünschten, alternativen stabilen Zustandes.

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## Introduction

Over the last few decades, various social and economic changes have driven the abandonment of extensive areas of formerly arable lands in several parts of the world. If these areas are left alone and propagule sources are available, secondary succession takes place and diverse semi-natural vegetation can be formed in short time (Stoate et al. 2009). Former arable lands (hereafter old fields) may support farmland biodiversity and provide valuable ecosystem services (e.g. pollination) at the beginning of secondary succession (Tscharntke, Batáry, & Dormann 2011) and their conservation value may increase in the later stages (Corbet 1995). However, reaching a stage of diverse secondary vegetation is not free from challenges, as old fields are highly susceptible to invasion by alien plant species (Catford et al. 2012). Non-native invasive species are likely to colonize the freshly abandoned croplands because of increased soil nutrient availability associated with previous fertilizer applications, and limited competition for resources (Standish, Cramer, & Hobbs 2008). Longer-lived alien species can persist until the later stages of succession, therefore perturbing natural succession pathways and altering the pattern of vegetation recovery (Meiners, Pickett, & Cadenasso 2002). By preventing the establishment of late-successional species, alien plant invasion may cause the invaded habitats to remain in the early successional stages for a long time (Cramer, Hobbs, & Standish 2008).

The establishment of invasive plants may influence not only the native flora and the trajectory of its secondary succession, but can also have an impact on the related

invertebrate communities, such as pollinator insects (van Hengstum, Hooftman, Oostermeijer, & van Tienderen 2014). Former studies presented highly controversial results, reporting either positive (Bartomeus, Vilà, & Santamaría 2008) or negative effects (de Groot, Kleijn & Jogan 2007; Morón et al. 2009) on pollinator abundance and diversity. Invasive plants are reported to influence the abundance and diversity of smaller, mostly solitary wild bees (Apoidea) of limited dispersal ability (Gathmann & Tscharntke 2002), as well as hoverflies (Syrphidae) and bumblebees, which generally have larger foraging ranges (Greenleaf, Williams, Winfree, & Kremen 2007). Therefore, invasive species might threaten biodiversity not only at the local level, but at the landscape scale as well (Hejda, Pyšek, & Jarošík 2009). Moreover, invasive plant species can also act indirectly on ecological communities by weakening the mutualistic links between native plants and their pollinators (Aizen, Morales, & Morales 2008) by luring pollinators away from native plants, either partially (Baskett, Emery, & Rudgers 2011) or completely (Bartomeus et al. 2008). This expansion of plant preference for pollination can result in fewer pollinator visits, pervasive interspecific pollen transfer (Baskett et al. 2011), and consequently, decreased reproduction success and diversity of the native flora. Despite these possible detrimental effects, the direct effect of invasive plant species on secondary succession of old fields is relatively understudied (Flory & Clay 2010), while the effects of invasive species on the pollinator communities along the successional trajectory has so far never been studied.

Here, we focus on a large-scale biological invasion phenomenon in southern Transylvania, Romania. Large-scale abandonment of arable lands has occurred over the last two decades due to a significant class of absentee landowners and the decreasing profitability of traditional subsistence agriculture (Fischer, Hartel, & Kuemmerle 2012). *Solidago canadensis* L. (Canada goldenrod) is the most successful invasive colonizer of these old fields, often becoming dominant even at the landscape scale. Its impact on the species richness of vascular plants and pollinators has already been studied in other countries (de Groot et al. 2007; Morón et al. 2009). However, these studies analysed only the final stage of invasion, when the invasive species had already established dominance in the community, and compared this stage with non-invaded, semi-natural communities, representing only the two contrasting extremes of the invasion gradient.

To fill these gaps in our knowledge regarding the impact of invasion on both plant and pollinator communities over the course of secondary succession on old fields along a continuous gradient of invasion, we initiated a large-scale field study. We aimed to answer the following questions: (1) Does the invasion of *S. canadensis* cause shifts in the composition and diversity of plant communities over the course of secondary succession of old fields? (2) Does abundance and species richness of pollinators change due to the invasion of the old fields? (3) To what extent does the presence of *S. canadensis* affect flower visitation of native plant species by pollinators? To answer these questions, we studied the effect of *S. canadensis* density (0–80% relative cover) in 36 old fields with various ages (1–20 years since the last ploughing).

## Materials and methods

### The invasive species

*S. canadensis* is a rhizomatous, patch-forming perennial herb of the Asteraceae. It has become an exceptionally successful invasive species since its introduction to Europe in the 18th century and is now widespread throughout the continent (Weber 1998). In addition to its prolific vegetative propagation (Meyer & Schmid 1999), *S. canadensis* releases chemicals that inhibit the growth, germination and survival of native plants (Abhilasha, Quintana, Vivanco, & Joshi 2008), and change the soil composition by diverting nutrients and minerals (Zhang, Wang, Qian, & Li 2009).

### Location and study sites

Our study area was located in the middle section of the Târnava Mare Valley in Southern Transylvania, Romania (Fig. 1A). Climate is classified as moderate continental. Mean annual rainfall is approximately 650 mm, while mean

annual temperature is 8 °C (Drăgulescu 2003). The region has been designated as Natura 2000 Site of Community Interest (Sighişoara-Târnava Mare Natura 2000 site, ROSCI0227) because 18 habitats listed in the EU Habitats Directive Annex I can be found in this region.

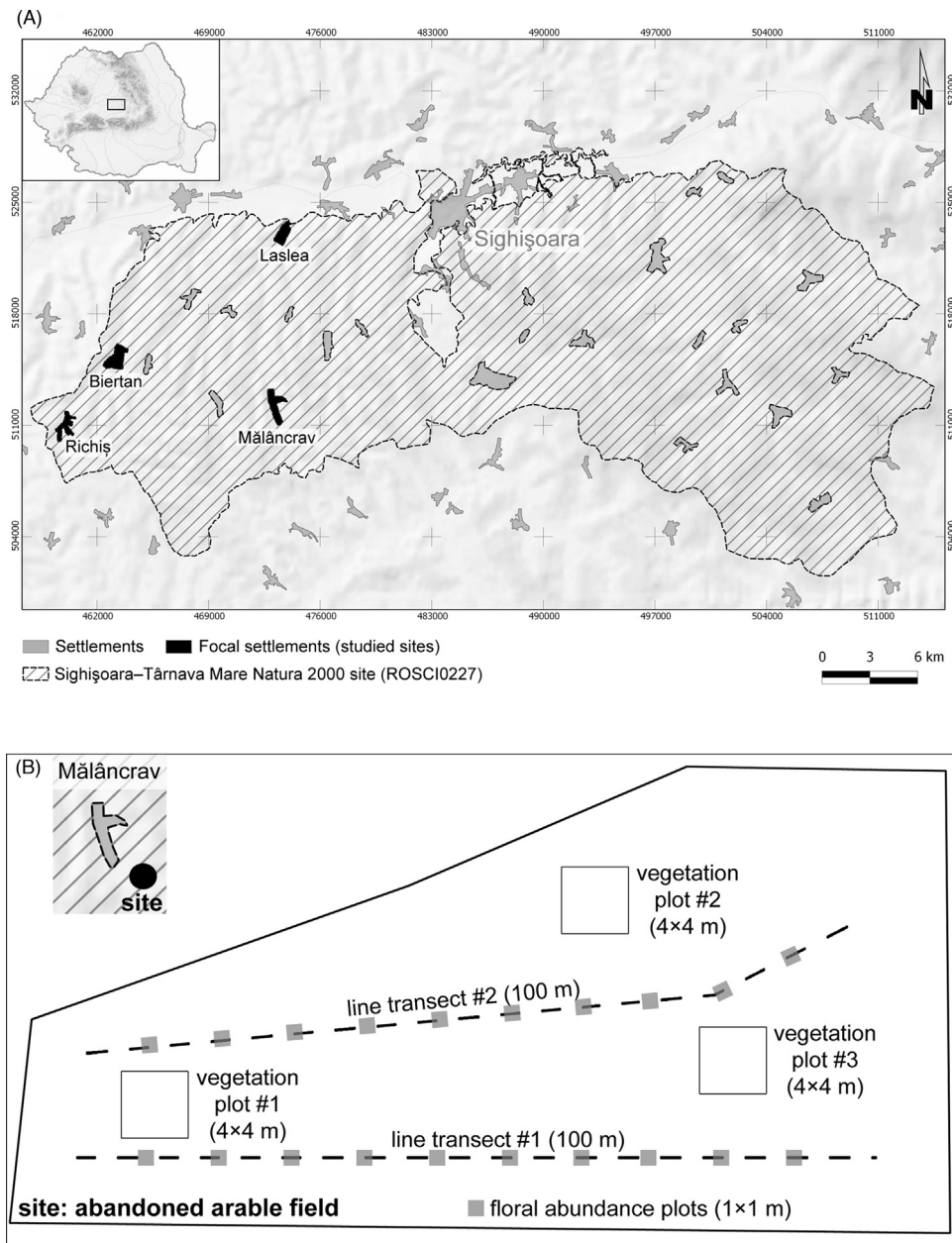
We examined the succession of vegetation and pollinator communities in this site using a chrono-sequence of old fields representing different stages of succession (space for time substitution, sensu Pickett 1989). We chose old fields with a known abandonment date in the vicinity of four villages (Biertan, Laslea, Malâncrav, Richiş; Fig. 1A). Abandonment here can be defined as the cessation of ploughing, though other uses and activities such as mowing or grazing may be present in the fields. These old fields may also be infrequently burned by locals. The 36 fields examined ranged in age from 1 to 20 years since abandonment. These sites were also chosen to represent the whole range of *S. canadensis* abundance from highly to less invaded areas (relative cover 0–80%). Most sites were quite small (mean area: 1.3 ha, range: 0.08–2.7 ha). The year of last ploughing, and current land-use practices were determined by interviewing landowners, and based on that information, we categorized the old fields as mown, grazed or without management. To determine whether the sites had been recently burned, or not, we looked for local signs of fire (burned trees and shrubs, incinerated litter or grass tussocks) and asked local people.

### Vegetation survey

Percent cover of vascular plant species with a resolution of 1% was visually estimated within three 4 × 4 m plots per site (Fig. 1B). We assigned 0.5% to species with a cover smaller than 1% (species represented by one small individual or by seedlings only). The level of invasion was characterized in each plot by the relative cover of *S. canadensis* and averaged over the three plots at site level. The surveys were conducted once per site in May–June 2012.

In order to accurately depict compositional changes during the course of succession, we calculated the following variables for each site:

- (1) *Native vascular plant species richness and diversity.* Species richness was calculated by averaging the number of species in the three plots per site. The Shannon diversity index of each site was calculated based on the proportional cover of each species. *S. canadensis* was not included in the calculation.
- (2) *Naturalness.* All plant species were assigned to one of the three naturalness groups according to Sanda, Popescu, Doltu, and Doniță (1983): (i) species of natural and semi-natural habitats, hereafter called “grassland species”, (ii) species common to both natural and ruderal communities, hereafter “generalist species”, and (iii) species of ruderal communities, hereafter “ruderal species”. The



**Fig. 1.** Map of the study area with the Natura 2000 site delineated. The four villages, where the sampling took place are shown in black (A). Schematic map showing sampling design (B).

proportion of each category was calculated for each site and used in subsequent analyses.

- (3) *Functional guilds.* The proportion of the main functional groups was taken into account by distinguishing (i) graminoid species belonging to the Poaceae, Cyperaceae or Juncaceae, (ii) legume species of the Fabaceae and (iii) forbs, i.e. herbaceous plants belonging to other families. As the presence of tree and shrub species never exceeded 1% average cover at site level, we excluded those species from the calculation of this variable.

### Pollinator sampling

We sampled pollinator insects in 22 sites (out of 36 sites with botanical surveys). We selected these sites to cover the whole range of successional age (1 to 20 years) and low to high densities of *S. canadensis* cover. The sites were at least 250 m from each other. Pollinators were sampled along two 100 m transects per study site; each transect assigned was at least 15 m from the field edge and 15 m apart from each other (Fig. 1B). We surveyed the pollinators twice: first during the

peak flowering season of indigenous vegetation (21–25 July 2012) and second during the peak flowering of *S. canadensis* (19–23 August 2012). Transect counts were performed between 9 a.m. and 6 p.m. under favourable weather conditions with little wind and few clouds at most. A pair of observers walked along each transect for 20 min and recorded all insects actively pollinating, flying or perching on the vegetation. In the case of active pollination, the visited plant species was also recorded. Pollinators were hand-netted and preserved in 96% ethanol for later identification at the species level.

We distinguished four pollinator groups: honey bee (*Apis mellifera* L.), bumblebees (*Bombus* spp.), other wild bees (Apoidea: Colletidae, Melittidae, Halictidae, Megachilidae, Andrenidae, Apidae except *Bombus* spp. and honey bee), and hoverflies (Syrphidae). Bumblebees and other wild bees were analysed separately because these two groups have different biological traits in terms of floral requirements, flying abilities and sociality (Gathmann & Tscharntke 2002; Greenleaf et al. 2007; Michener 2007), and therefore different responses to landscape and local scale environmental conditions were expected. Although there are some semi-social species and/or genera among the collected bees (e.g. some *Halictus* spp.), we use ‘solitary bees’ in the current paper for wild bees other than bumblebees.

As the presence of pollinators depends on the pollen and nectar supply, we gathered additional botanical information: flowering plant species and the number of flowers at species level were recorded at ten 1 × 1 m quadrates placed equidistantly along the same two transects per site (Fig. 1B). We counted the number of heads in the case of Asteraceae species and simple umbels for Apiaceae, but refer to both as flowers for the sake of simplicity.

We calculated several variables to detect potential changes in the pollinator communities during succession:

- (1) *Abundance of each pollinator group* (bumblebees, solitary bees, honey bee, hoverflies) per transect was calculated as the number of individuals per group per transect;
- (2) *Species richness of bumblebees, solitary bees and hoverflies*; species data from the two transects per site were pooled because of the relatively low species numbers;
- (3) *Number of visited flowers other than *S. canadensis** was calculated as the total number of flowers visited (actively pollinated) by each pollinator group per transect.

## Statistical analyses

All statistical analyses were carried out in the R statistical environment version 3.0.1 (R Core Team 2013). We built separate linear mixed-effects models (LMMs) for each vegetation and pollinator variable using the *nlme* package (Pinheiro et al. 2013).

For vegetation data, the dependent variables were plant species richness, diversity, naturalness and functional guilds, all calculated from the data collected in the three 4 × 4 m plots per site. We included old field age, the proportional cover of *S. canadensis* and field area (in ha) as continuous fixed variables, land-use type (mown, grazed, without management), anthropogenic fire (burned, unburned) as fixed factors, and village (4 levels) as a random term. In addition, the pairwise interaction between fixed variables and proportional cover of *S. canadensis* was also included in the models.

For pollinator variables (abundance and species richness of pollinator groups and the number of visited flowers except *S. canadensis*) land-use, fire, sampling period (July vs. August) were included as fixed factors. The proportional cover of *S. canadensis*, field area, old field age, species richness of flowering plants, the number of flowers of native species and the number of *S. canadensis* flowers (collected from the ten 1 × 1 m quadrates placed along the pollinator transects) were built in as fixed covariates. The two-way interactions between *S. canadensis* cover and the other five explanatory variables (except flower variables) were also included in the models. We included study site nested within village as a random effect for abundance and number of visited flowers; we used only village as a random effect for species richness of pollinators because data from the two transects per sites were pooled due to low number of available species at the transect level.

In each case, we started with saturated models (Appendix A) and removed non-significant variables using backward stepwise selection, except those that were part of a significant interaction. We extracted the contrasts for retained significant terms as follows: the contrasts for covariates or interactions between covariate and factors, based on differences of least square means, were extracted using the *lsmeans* function of the *lsmeans* package (Lenth 2013). For land-use types, Tukey contrasts were performed using the *glht* function of *multcomp* package (Hothorn, Bretz, & Westfall 2008). Contrasts for interactions between covariates cannot be computed, hence we drew regression surface plots with the dependent variable and the interacting covariates. Normality of the residuals was tested using the Shapiro–Wilk test and homoscedasticity of the residuals verified by plot diagnosis. Abundance variables were log-transformed prior to analyses to reach normal residual distribution. We calculated effect sizes (partial *r*) and their 95% confidence intervals (Nakagawa & Cuthill 2007) to present the biologically meaningful magnitude by which the significant explanatory variables influenced plant and pollinator abundance and diversity.

Before building LMMs, we tested all predictor variables for multicollinearity by calculating the variance inflation factor (VIF) using *vif* function of the *fmsb* package in R. VIF values were <2 in all cases, so no multicollinearity was detected in any of the performed models (Rogerson 2001).

**Table 1.** The effects of *Solidago canadensis* cover, age of the old fields and land-use (M – mown, W – without management) on vegetation characteristics according to the linear mixed-effects models. Positive effects are indicated by “+” and negative effects by “–”. Effect sizes (Partial *r*) and their 95% confidence interval are also shown. *p*-Values of significant effects are in bold. Significant interactions between the covariates *S. canadensis* cover and old field age have no contrasts but are plotted on Fig. 2.

|                               | df    | <i>F</i> | <i>p</i>         | Contrasts | Effect size | 95% C.I.     |
|-------------------------------|-------|----------|------------------|-----------|-------------|--------------|
| <b>Richness and diversity</b> |       |          |                  |           |             |              |
| Plant species richness        |       |          |                  |           |             |              |
| <i>S. canadensis</i> cover    | 1, 29 | 4.43     | <b>0.044</b>     | –         | 0.09        | –0.24; 0.43  |
| Old field age                 | 1, 29 | 32.88    | <b>&lt;0.001</b> | +         | 0.72        | 0.38; 1.06   |
| SCC × OFA                     | 1, 29 | 3.09     | 0.088            |           |             |              |
| Diversity                     |       |          |                  |           |             |              |
| <i>S. canadensis</i> cover    | 1, 29 | 20.43    | <b>&lt;0.001</b> | –         | 0.24        | –0.09; 0.58  |
| Old field age                 | 1, 29 | 6.07     | <b>0.019</b>     | +         | 0.61        | 0.27; 0.95   |
| SCC × OFA                     | 1, 29 | 15.19    | <b>&lt;0.001</b> |           | –0.58       | –0.92; –0.24 |
| <b>Naturalness</b>            |       |          |                  |           |             |              |
| Grassland species             |       |          |                  |           |             |              |
| <i>S. canadensis</i> cover    | 1, 29 | 0.01     | 0.956            |           |             |              |
| Old field age                 | 1, 29 | 53.51    | <b>&lt;0.001</b> | +         | 0.80        | 0.46; 1.14   |
| SCC × OFA                     | 1, 29 | 5.30     | <b>0.028</b>     |           | –0.39       | –0.73; –0.05 |
| Generalist species            |       |          |                  |           |             |              |
| <i>S. canadensis</i> cover    | 1, 29 | 0.94     | 0.339            |           |             |              |
| Old field age                 | 1, 29 | 21.43    | <b>&lt;0.001</b> | –         | –0.72       | –1.06; –0.38 |
| SCC × OFA                     | 1, 29 | 10.69    | <b>0.002</b>     |           | 0.51        | 0.17; 0.86   |
| Ruderal species               |       |          |                  |           |             |              |
| Old field age                 | 1, 31 | 45.09    | <b>&lt;0.001</b> | –         | –0.76       | –1.11; –0.42 |
| <b>Functional guilds</b>      |       |          |                  |           |             |              |
| Graminoids                    |       |          |                  |           |             |              |
| <i>S. canadensis</i> cover    | 1, 29 | 1.56     | 0.221            |           |             |              |
| Old field age                 | 1, 29 | 9.53     | <b>0.004</b>     | +         | 0.21        | –0.12; 0.55  |
| SCC × OFA                     | 1, 29 | 5.78     | <b>0.022</b>     |           | 0.40        | 0.06; 0.74   |
| Legumes                       |       |          |                  |           |             |              |
| <i>S. canadensis</i> cover    | 1, 27 | 5.42     | <b>0.027</b>     | +         | 0.52        | 0.18; 0.86   |
| Old field age                 | 1, 27 | 8.10     | <b>&lt;0.008</b> | +         | 0.68        | 0.34; 1.02   |
| SCC × OFA                     | 1, 27 | 8.39     | <b>0.007</b>     |           | –0.48       | –0.82; –0.14 |
| Land-use                      | 1, 27 | 4.47     | <b>0.021</b>     | W > M     | –0.47       | –0.81; –0.13 |
| Forbs                         |       |          |                  |           |             |              |
| <i>S. canadensis</i> cover    | 1, 30 | 12.30    | <b>0.001</b>     | –         | –0.50       | –0.84; –0.16 |
| Old field age                 | 1, 30 | 38.31    | <b>&lt;0.001</b> | –         | –0.74       | –1.09; –0.40 |

In addition, all dependent variables were tested for spatial autocorrelation (see Appendix A).

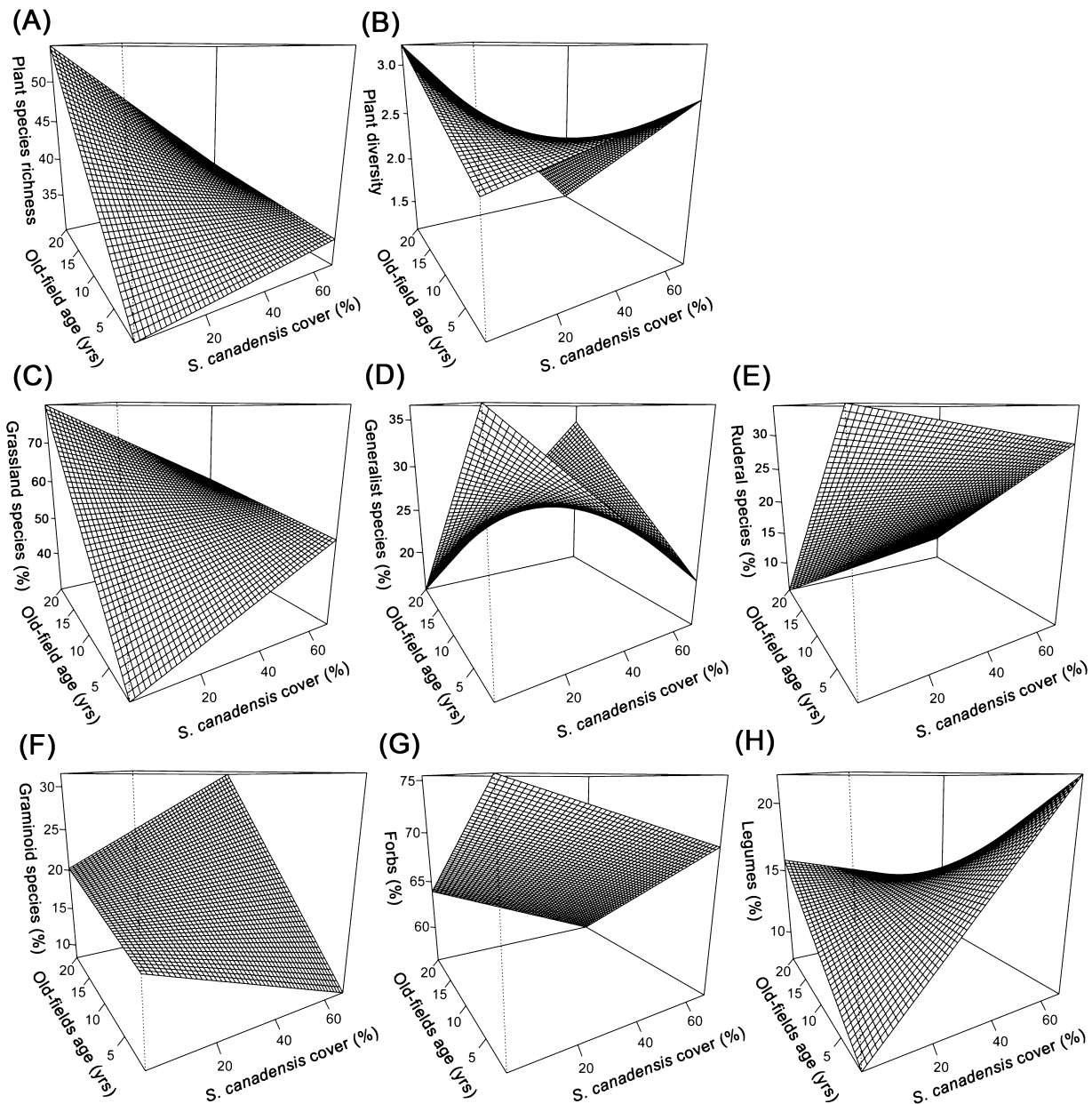
## Results

### Species richness, diversity and composition of plant community

The old field age, the proportional cover of *S. canadensis*, and their interactions were important sources of variation for all vegetation variables (Table 1). Plant species richness and diversity increased with field age. The density of *S. canadensis* was negatively associated with the number of plant species irrespective of old field age and with the diversity of older fields (Table 1, Fig. 2A and B).

The proportion of grassland species increased, while that of generalist and ruderal species decreased with old field age. The effect of *S. canadensis* cover was non-significant in all three naturalness groups. However, *S. canadensis* did significantly interact with old field age, as the proportion of grassland species decreased, and that of generalist species increased in the older fields, while the abundance of generalist species declined in younger fields with higher *S. canadensis* cover (Table 1, Fig. 2C–E).

In the case of the plant functional guilds, the proportion of graminoids and legumes increased, while that of forbs decreased with old field age (Table 1). Despite their temporal decline, forbs were the dominant group throughout succession. High *S. canadensis* cover was associated with increased proportion of legumes in younger sites, and that of graminoid species in older fields, while the proportion of forbs decreased



**Fig. 2.** Plant species richness (A), plant diversity (B), the proportion of three plant naturalness groups (grassland species (C), generalist species (D) and ruderal species (E)), and the proportion of three functional guilds (graminoids (F), forbs (G) and legumes (H)) plotted against the increasing proportional cover of *Solidago canadensis* and old field age.

irrespective of old field age (Fig. 2F–H). Land-use type predicted only the proportion of legumes, which was smaller in mown and grazed sites than in sites without management (Table 1).

### Abundance and species richness of pollinators

The abundance of solitary bees was significantly decreased by *S. canadensis* cover in July ( $F = 6.33$ ,  $p = 0.022$ ), but no such effect was found in August (Table 2, Fig. 3A). The abundance of solitary bees was influenced by land-use,

sampling time and species richness of actually flowering plants (Table 2). The abundance of bumblebees was decreased by *S. canadensis* cover in July ( $F = 6.78$ ,  $p = 0.018$ , Fig. 3A) and marginally significantly increased in August ( $F = 3.03$ ,  $p = 0.099$ , Fig. 3B). Bumblebees were present in higher abundance in July than in August, and enhanced by both native and *S. canadensis* flower abundance. The abundance of honeybees decreased with *S. canadensis* cover and old field age. The abundance of hoverflies showed the opposite pattern with higher values in August than in July. Hoverfly abundance was enhanced by the field area and by the abundance of *S. canadensis* flowers (Table 2).

**Table 2.** The effects of *S. canadensis* cover, old field age, land-use (G – grazed, W – without management), sampling time (July, August) and several vegetation parameters on the abundance and species richness of different pollinator groups according to the linear mixed effect models. Flower abundance refers to all flowers except those of *S. canadensis*. Positive effects are indicated by “+”, negative effects by “–”. Effect sizes (Partial *r*) and their 95% confidence interval are also shown. *p*-Values of significant effects are in bold.

|                                       | df    | <i>F</i> | <i>p</i>         | Contrasts     | Effect size | 95% C.I.     |
|---------------------------------------|-------|----------|------------------|---------------|-------------|--------------|
| <b>Abundance</b>                      |       |          |                  |               |             |              |
| Solitary bees                         |       |          |                  |               |             |              |
| <i>S. canadensis</i> cover            | 1, 15 | 4.19     | 0.059            | (–)           |             |              |
| Land-use                              | 2, 15 | 3.80     | <b>0.046</b>     | W > G         | –0.64       | –1.08; –0.19 |
| Sampling time                         | 1, 63 | 38.87    | <b>&lt;0.001</b> | Jul > Aug     | –0.58       | –1.03; –0.13 |
| Flowering plant species richness      | 1, 63 | 21.81    | <b>&lt;0.001</b> | +             | 0.48        | 0.03; 0.93   |
| SCC × ST                              | 1, 63 | 7.29     | <b>0.009</b>     | July: –       | 0.32        | –0.13; 0.77  |
| Bumblebees                            |       |          |                  |               |             |              |
| <i>S. canadensis</i> cover            | 1, 17 | 1.14     | 0.301            |               |             |              |
| Sampling time                         | 1, 62 | 31.48    | <b>&lt;0.001</b> | Jul > Aug     | –0.60       | –1.05; –0.15 |
| Flower abundance                      | 1, 62 | 9.18     | <b>0.004</b>     | +             | 0.28        | –0.17; 0.73  |
| <i>S. canadensis</i> flower abundance | 1, 62 | 4.53     | <b>0.037</b>     | +             | 0.05        | –0.40; 0.50  |
| SCC × ST                              | 1, 62 | 12.21    | <b>0.001</b>     | Jul–; Aug (+) | 0.41        | –0.04; 0.86  |
| Honey bee                             |       |          |                  |               |             |              |
| <i>S. canadensis</i> cover            | 1, 16 | 13.06    | <b>0.002</b>     | –             | –0.68       | –1.13; –0.23 |
| Old field age                         | 1, 16 | 8.11     | <b>0.012</b>     | –             | –0.58       | –1.03; –0.13 |
| Hoverflies                            |       |          |                  |               |             |              |
| Area                                  | 1, 17 | 4.94     | <b>0.040</b>     | +             | 0.54        | 0.09; 0.99   |
| Sampling time                         | 1, 64 | 7.25     | <b>0.009</b>     | Jul < Aug     | –0.04       | –0.49; 0.41  |
| <i>S. canadensis</i> flower abundance | 1, 64 | 35.03    | <b>&lt;0.001</b> | +             | 0.59        | 0.15; 1.04   |
| <b>Species richness</b>               |       |          |                  |               |             |              |
| Solitary bees                         |       |          |                  |               |             |              |
| Sampling time                         | 1, 38 | 19.02    | <b>&lt;0.001</b> | Jul > Aug     | –0.52       | –0.97; –0.07 |
| Flowering plant species richness      | 1, 38 | 21.30    | <b>&lt;0.001</b> | +             | 0.60        | 0.15; 1.05   |
| Bumblebees                            |       |          |                  |               |             |              |
| Sampling time                         | 1, 39 | 4.25     | <b>0.046</b>     | Jul > Aug     | –0.31       | –0.76; 0.14  |
| Hoverflies                            |       |          |                  |               |             |              |
| Area                                  | 1, 37 | 12.22    | <b>0.001</b>     | +             | 0.50        | 0.05; 0.95   |
| Flower abundance                      | 1, 37 | 14.35    | <b>0.001</b>     | +             | 0.58        | 0.13; 1.03   |
| <i>S. canadensis</i> flower abundance | 1, 37 | 6.07     | <b>0.019</b>     | +             | 0.38        | –0.07; 0.83  |

The species richness of solitary bees was higher in July than in August and increased with the number of flowering plant species. Similarly, more bumblebee species were found in July than in August. The species richness of hoverflies increased with field area and the flower abundance of both native species and *S. canadensis* (Table 2).

## Flower visitation

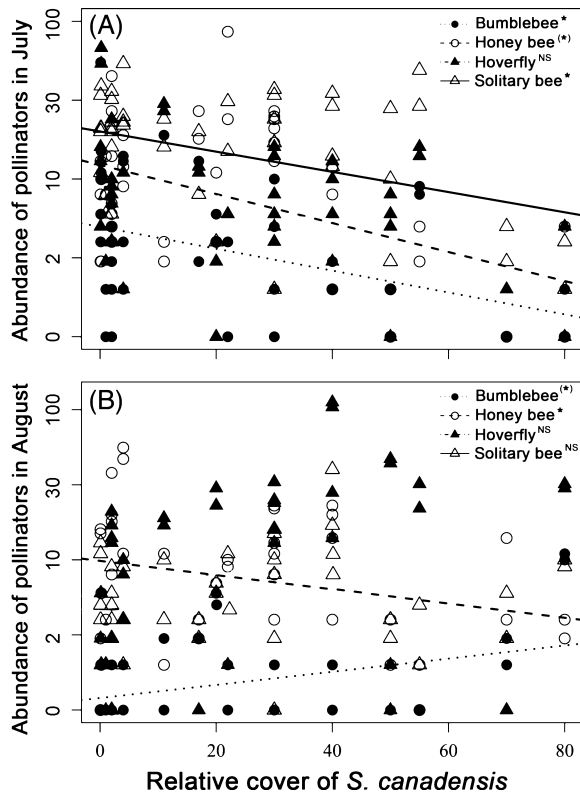
In general, the number of flowers (excluding *S. canadensis*) visited by bumblebees and solitary bees was higher in July than in August (Table 3). The flower visitation of indigenous plant species by solitary bees and honey bees was positively influenced by the number of flowering species. The abundance of flowers (excluding *S. canadensis*) had a positive effect on the number of bumblebee-visited flowers (Table 3). Further, the increasing cover of *S. canadensis* had a significant negative effect on the flower visitation of

native species by solitary bees, honey bees and hoverflies (Table 3, Fig. 4). In addition, we found a significant interaction between sampling time and *S. canadensis* cover: the number flowers (excluding *S. canadensis*) visited by bumblebees was slightly decreased by *S. canadensis* in July (Fig. 4A) but marginally significantly increased in August (Fig. 4B).

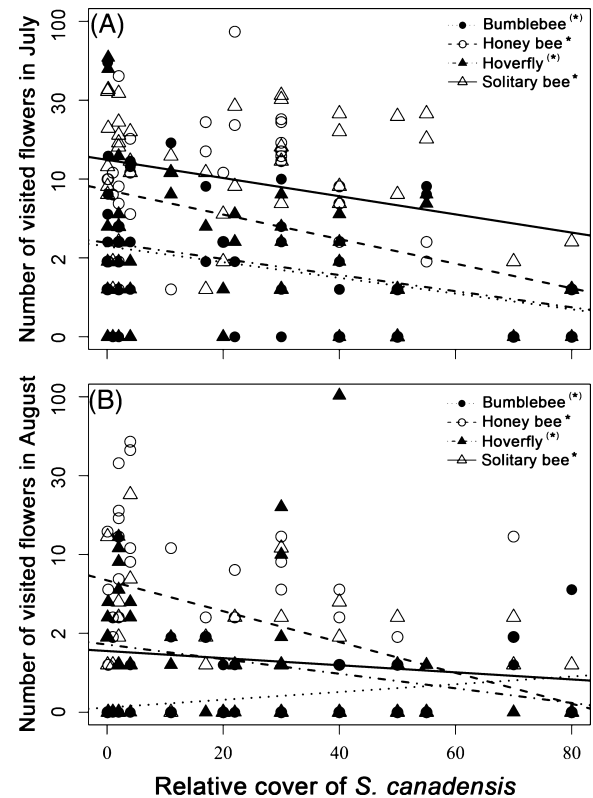
## Discussion

### Effects of *S. canadensis* invasion on different-aged old field plant communities

Although it was already known that plant communities invaded by *S. canadensis* might suffer shifts in diversity and composition (de Groot et al. 2007; Morón et al. 2009), we are the first to report reduced species richness and altered



**Fig. 3.** Abundance of four pollinator groups (honey bee, bumblebees, solitary bees, hoverflies) plotted against the increasing proportional cover of *S. canadensis* before its flowering in July (A) and during its mass blooming in August (B). Note that y-axis has log-scale. Statistically significant and marginally significant results are marked with \* and (\*\*) and with regression lines; NS – non-significant regressions.



**Fig. 4.** Number of visited flowers except *Solidago canadensis* plotted against the increasing proportional cover of *S. canadensis* in July (A) and in August (B). Note that y-axis has log-scale. Statistically significant and marginally significant results are marked with \* and (\*\*) and with regression lines; NS – non-significant regressions.

**Table 3.** The effects of *S. canadensis* cover, old field age, sampling time and several vegetation parameters on the number of flowers (excluding *S. canadensis*) visited by different pollinator groups according to linear mixed effect models. Flower abundance refers to all flowers except those of *S. canadensis*. Positive effects are indicated by “+”, negative effects by “–”. Effect sizes (Partial *r*) and their 95% confidence interval are also shown. P-values of significant effects are in bold.

|                                                             | df    | F     | p                | Contrasts         | Effect size | 95% C.I.     |
|-------------------------------------------------------------|-------|-------|------------------|-------------------|-------------|--------------|
| Number of visited flowers (excluding <i>S. canadensis</i> ) |       |       |                  |                   |             |              |
| Solitary bees                                               |       |       |                  |                   |             |              |
| <i>S. canadensis</i> cover                                  | 1, 17 | 11.47 | <b>0.004</b>     | –                 | –0.47       | –0.92; –0.02 |
| Sampling time                                               | 1, 64 | 81.71 | <b>&lt;0.001</b> | Jul > Aug         | –0.72       | –1.17; –0.27 |
| Flowering plant species richness                            | 1, 64 | 13.76 | <b>&lt;0.001</b> | +                 | 0.42        | –0.03; 0.87  |
| Bumblebees                                                  |       |       |                  |                   |             |              |
| <i>S. canadensis</i> cover                                  | 1, 17 | 1.08  | 0.313            |                   |             |              |
| Sampling time                                               | 1, 63 | 36.64 | <b>&lt;0.001</b> | Jul > Aug         | –0.54       | –0.99; –0.09 |
| Flower abundance                                            | 1, 63 | 8.37  | <b>0.005</b>     | +                 | 0.29        | –0.16; 0.74  |
| SCC × ST                                                    | 1, 63 | 6.54  | <b>0.013</b>     | Jul (–); Aug: (+) | 0.31        | –0.14; 0.76  |
| Honey bee                                                   |       |       |                  |                   |             |              |
| <i>S. canadensis</i> cover                                  | 1, 17 | 15.74 | <b>0.001</b>     | –                 | –0.63       | –1.08; –0.18 |
| Flowering plant species richness                            | 1, 65 | 3.70  | 0.059            | (+)               | 0.23        | –0.22; 0.68  |
| Hoverflies                                                  |       |       |                  |                   |             |              |
| <i>S. canadensis</i> cover                                  | 1, 17 | 4.31  | 0.053            | (–)               | –0.45       | –0.90; 0.01  |

naturalness and functional composition in the context of secondary succession.

The early years of vegetation succession are usually characterized by a wide array of disturbance-tolerant ruderal species and fast colonizing generalist species (Ruprecht 2006). *Solidago canadensis* displaced the native generalist species in young successional fields, which might slow down the secondary succession, as generalist species would lead the community to the next stage of succession by outcompeting disturbance-tolerant ruderal species (Catford et al. 2012). *Solidago canadensis* can monopolize resources and hinder the colonization of other species due to its quick capacity for vegetative expansion and a dynamic foraging strategy (Bartha et al. 2014). Only native legumes were able to increase their importance during the early years of the succession, probably due to their nitrogen-fixing ability.

In older successional fields, the species turnover decreases, and biotic filters can be particularly important (Pickett, Cadenasso, & Bartha 2001). If a monopolist species becomes dominant (fast-growing clonal species tending to eliminate other species, sensu Falińska 1991), it may outcompete the subordinate species and may have a strong negative impact on local diversity (Bartha et al. 2014). *S. canadensis* seems to be a monopolist species as it negatively influenced the species richness of forbs and the diversity of the older fields. It outcompeted species belonging to the same functional group (perennial non-nitrogen-fixing forbs), but seemed to facilitate or have no effect on graminoid species. Fargione, Brown, and Tilman (2003) proved that the strongest inhibitory effects of resident plants are on introduced plants of the same functional guild. Our results indicate that this relationship may work inversely as well: the invasive species might out-compete the natives belonging to the same functional group.

Most of the grassland specialists are expected to enter the community at mid-successional stages, because they are adapted to colonize the few available microsites under a closed canopy (Bartha et al. 2014). However, the increased presence of disturbance-tolerant generalists and the decreased proportion of the grassland specialists in the invaded old fields underlines that if this invasive species is abundant, secondary succession slows down, or even halts at a prolonged earlier successional state (Cramer et al. 2008) instead of recovering towards semi-natural grassland vegetation. Similar results were found in mid-successional old fields invaded by *S. gigantea* as well, having very strong negative impact on succession (Bartha et al. 2014).

### Effect of *S. canadensis* on the abundance and species richness of pollinators

The decreased plant species richness and especially the decline of forbs led to food resources becoming more limited for pollinators in the old fields we studied (see also de Groot et al. 2007). As a more diverse and flower rich plant community can harbour a more diverse and stable pollinator

assemblage over time (Ebeling, Klein, Schumacher, Weisser, & Tschamtkke 2008), it is understandable why the abundance of solitary bees and bumblebees declined in July, the pre-blooming period of the invader (see also de Groot et al. 2007; Morón et al. 2009; Lenda, Skórka, & Morón 2010). However, in August, the myriad of flowers produced by *S. canadensis* had a positive effect on the abundance of bumblebees and on the abundance and species richness of the mostly generalist hoverflies. Therefore, this invasive species might serve as an alternative food resource for certain pollinators during its flowering period, especially for bumblebees that have still persistent colonies until late summer/early autumn, and for late-emerging hoverflies (see also de Groot et al. 2007). From this point of view, *S. canadensis* may indirectly act as facilitator by maintaining larger pollinator populations throughout the flowering season (Bjerknes, Totland, Hegland, & Nielsen 2007).

*S. canadensis* is considered one of the most important plants yielding unifloral honey sources in Central Europe (Farkas & Zajácz 2007). Therefore, a highly interesting finding is that the increasing cover of *S. canadensis* significantly decreased the abundance of honey bees, even during mass flowering. Although honey bees are important pollinators of *S. canadensis*, they are likely to begin visiting goldenrod flowers only when the abundance of other flowering plant species has declined (Gross & Werner 1983). As the traditionally managed landscape we studied is a diverse mosaic of croplands, old fields and managed grasslands (pastures or hayfields), pollinators can easily find other pollen sources in the vicinity of the invaded old fields.

Although plant species richness and composition went through considerable alteration along the 20 years of succession, neither solitary bees nor hoverflies showed any difference among old fields of different age. Therefore, the bimodal species richness distribution of pollinators along secondary succession presented by Steffan-Dewenter and Tschamtkke (2001) could not be replicated for bees or for hoverflies in our study. This is because neither the number of flowering species, nor the number of flowers depended on the age of old fields (data not shown). One exception was the honey bee, which seemed to prefer plant species typical of the beginning of succession in younger old fields.

### Indirect effects of invasion: Flower visitation of native species

Plants and their pollinators are tightly intertwined components of ecological communities, therefore the adverse effect of *S. canadensis* might have further indirect repercussions as well. Alien plant species can have a strong effect on the pollination success of native species, often competing with them by causing either reduced pollinator visitation rates or increased heterospecific pollination of native flowers. However, in some cases, both at local and landscape scales, these often mass-flowering invasives may facilitate native plant

pollination by increasing pollinator densities (Bjerknes et al. 2007).

We found a negative correlation between the cover of *S. canadensis* and flower visitation of native plants (hereafter flowers) by bees and hoverflies. On the one hand this result might be the consequence of an indirect competition for pollination between the superior invasive and suppressed native species, competing possibly for light, space, soil nutrients. On the other hand, the positive effect of *S. canadensis* on bumblebees and hoverflies suggests also direct competition for pollination between invasive and native species in August due to the large amount of pollen and nectar provided by *S. canadensis*. The lower frequency of flower visitation induced by invasives can possibly result in a pollination deficit in native species (Chittka & Schürkens 2001). The reduction in the pollinator pool by alien plants might thus corrupt the reproductive success of insect-pollinated native plants (Stout & Morales 2009). Although flowers of *S. canadensis* are self-incompatible and dependent on the presence of pollinators for seed production (Gross & Werner 1983), it can also vigorously spread locally by rhizomes, thus its reproductive gain is less affected by a decreased pollinator pool. Through this two-way competition by direct and indirect routes, *S. canadensis* can further propagate its dominance and, therefore, contribute to the development of an alternative, self-perpetuating stable state in which it dominates.

## Conclusions and recommendations

Without management interventions, degraded, alternative states driven by *S. canadensis*, instead of valuable secondary grasslands, might dominate the landscape for decades (this invasive species can persist in the fields for up to 50–75 years; Hartnett & Bazzaz 1983), and could arrest the natural trajectory of secondary succession in an earlier, less diverse phase. Therefore, we cannot allow spontaneous processes to revegetate the old fields invaded by *S. canadensis*. Instead, active management actions are needed to guide vegetation recovery.

Long-term experiments testing the effects of different land-use techniques on controlling *S. canadensis* are already available from Central-Eastern Europe (Horváth 2012). According to these experiments, a combination of prescribed disturbances, such as regular mowing and extensive autumnal grazing with cattle or sheep, could reduce the target invasive species' abundance and enhance the recovery of native vegetation.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2015.03.003>.

## 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.
- Aizen, M. A., Morales, C. L., & Morales, J. M. (2008). Invasive mutualists erode native pollination webs. *PLoS Biology*, 6, e31.
- Bartha, S., Szentes, S., Horváth, A., Ház, J., Zimmermann, Z., Molnár, C., et al. (2014). Impact of mid-successional dominant species on the diversity and progress of succession in regenerating temperate grasslands. *Applied Vegetation Science*, 17(2), 201–213.
- Bartomeus, I., Vilà, M., & Santamaría, L. (2008). Contrasting effects of invasive plants in plant–pollinator networks. *Oecologia*, 155, 761–770.
- Baskett, C. A., Emery, S. M., & Rudgers, J. A. (2011). Pollinator visits to threatened species are restored following invasive plant removal. *International Journal of Plant Sciences*, 172, 411–422.
- Bjerknes, A.-L., Totland, Ø., Hegland, S. J., & Nielsen, A. (2007). Do alien plant invasions really affect pollination success in native plant species? *Biological Conservation*, 138, 1–12.
- Catford, J. A., Daehler, C. C., Murphy, H. T., Sheppard, A. W., Hardesty, B. D., Westcott, D. A., et al. (2012). The intermediate disturbance hypothesis and plant invasions: Implications for species richness and management. *Perspectives in Plant Ecology*, 14, 231–241.
- Chittka, L., & Schürkens, S. (2001). Successful invasion of a floral market. *Nature*, 411, 653.
- Corbet, S. A. (1995). Insects, plants, and succession: Advantages of long-term set-aside. *Agriculture, Ecosystems & Environment*, 53, 201–217.
- Cramer, V. A., Hobbs, R. J., & Standish, R. J. (2008). What's new about old fields? Land abandonment and ecosystem assembly. *TREE*, 23, 104–112.
- Drăgulescu, C. (2003). *Cormo flora județului Sibiu* (Flora of Sibiu county) [in Romanian] Pelecanus. In Brașov, pp. 18–20.
- Ebeling, A., Klein, A. M., Schumacher, J., Weisser, W. W., & Tschardtke, T. (2008). How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos*, 117, 1808–1815.
- Falińska, K. (1991). *Plant demography in vegetation succession*. New York, NY: Kluwer Academic.

- Fargione, J., Brown, C. S., & Tilman, D. (2003). Community assembly and invasion: An experimental test of neutral versus niche processes. *PNAS*, *100*, 8916–8920.
- Farkas, A., & Zajácz, E. (2007). Nectar production for the Hungarian honey industry. *European Journal of Plant Science and Biotechnology*, *1*, 125–151.
- Fischer, J., Hartel, T., & Kuemmerle, T. (2012). Conservation policy in traditional farming landscapes. *Conservation Letters*, *5*, 167–175.
- Flory, S. L., & Clay, K. (2010). Non-native grass invasion suppresses forest succession. *Oecologia*, *164*, 1029–1038.
- Gathmann, A., & Tschardt, T. (2002). Foraging ranges of solitary bees. *Journal of Animal Ecology*, *71*, 757–764.
- Greenleaf, S. S., Williams, N. M., Winfree, R., & Kremen, C. (2007). Bee foraging ranges and their relationship to body size. *Oecologia*, *153*, 589–596.
- de Groot, M., Kleijn, D., & Jogan, N. (2007). Species groups occupying different tropic levels respond differently to the invasion of semi-natural vegetation by *Solidago canadensis*. *Biological Conservation*, *136*, 612–617.
- Gross, R. S., & Werner, P. A. (1983). Relationships among flowering phenology, insect visitors, and seed-set of individuals: Experimental studies on four co-occurring species of goldenrod (*Solidago*: Compositae). *Ecological Monographs*, *53*, 95–117.
- Hartnett, D. C., & Bazzaz, F. A. (1983). Physiological integration among intracolonial ramets in *Solidago canadensis*. *Ecology*, *64*, 779–788.
- Hejda, M., Pyšek, P., & Jarošík, V. (2009). Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology*, *97*, 393–403.
- van Hengstum, T., Hooftman, D. A. P., Oostermeijer, J. G. B., & van Tienderen, P. H. (2014). Impact of plant invasions on local arthropod communities: A meta-analysis. *Journal of Ecology*, *102*, 4–11.
- Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, *50*, 346–363.
- Horváth, R. (2012). Az agresszív gyomok terjedésének megakadályozása. In L. Viszló (Ed.), *A természetkímélő gyepgazdálkodás: Hagyományőrző szemlélet, modern eszközök* (pp. 171–188). Csákvár: Pro Vértes Természetvédelmi Közalapítvány.
- Lenda, M., Skórka, P., & Moroń, D. (2010). Invasive alien plant species – A threat or an opportunity for pollinating insects in agricultural landscapes? In T. H. Lee (Ed.), *Agricultural economics: New research* (pp. 67–88). New York, NY: Nova Science Publishers.
- Lenth, R. V. (2013). *Lsmeans: Least-squares means. R package version 1.10-2*.
- Meiners, S. J., Pickett, S. T., & Cadenasso, M. L. (2002). Exotic plant invasions over 40 years of old field successions: Community patterns and associations. *Ecography*, *25*, 215–223.
- Meyer, A. H., & Schmid, B. (1999). Experimental demography of the old field perennial *Solidago altissima*: The dynamics of the shoot population. *Journal of Ecology*, *87*, 17–27.
- Michener, C. (2007). *The bees of the world* (1st ed.). Baltimore, MD: Johns Hopkins University Press.
- Moroń, D., Lenda, M., Skórka, P., Szentgyörgyi, H., Settele, J., & Woyciechowski, M. (2009). Wild pollinator communities are negatively affected by invasion of alien goldenrods in grassland landscapes. *Biological Conservation*, *142*, 1322–1332.
- Nakagawa, S., & Cuthill, I. C. (2007). Effect size, confidence interval and statistical significance: A practical guide for biologists. *Biological Reviews*, *82*(4), 591–605.
- Pickett, S. T. A. (1989). Space-for-time substitution as an alternative to long-term studies. In *Long-term studies in ecology*. New York, NY: Springer.
- Pickett, S. T. A., Cadenasso, M. L., & Barthia, S. (2001). Implications from Buell-Small Succession Study for vegetation restoration. *Applied Vegetation Science*, *4*, 41–52.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Development Core Team. (2013). *nlme: Linear and nonlinear mixed effects models. R package version* (vol. 3).
- R Core Team. (2013). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. (<http://www.R-project.org/>).
- Rogerson, P. A. (2001). *Statistical methods for geography*. London: Sage.
- Ruprecht, E. (2006). Successfully recovered grassland: A promising example from Romanian old-fields. *Restoration Ecology*, *14*, 473–480.
- Sanda, V., Popescu, A., Doltu, M. I., & Doniță, N. (1983). Caracterizarea ecologică și fitocenologică a speciilor spontane din flora României [Ecological and fitosociological characteristics of the native flora of Romania]. *Studii și Comunicări*, *25*(Suppl.), 5–126.
- Standish, R. J., Cramer, V. A., & Hobbs, R. J. (2008). Land-use legacy and the persistence of invasive *Avena barbata* on abandoned farmland. *Journal of Applied Ecology*, *45*, 1576–1583.
- Stoate, C., Báldi, A., Beja, P., Boatman, N. D., Herzog, I., van Doorn, A., et al. (2009). Ecological impacts of early 21st century agricultural change in Europe – A review. *Journal of Environmental Management*, *91*, 22–46.
- Stout, J. C., & Morales, C. L. (2009). Ecological impacts of invasive alien species on bees. *Apidologie*, *40*, 388–409.
- Steffan-Dewenter, I., & Tschardt, T. (2001). Succession of bee communities on fallows. *Ecography*, *24*, 83–93.
- Tschardt, T., Batáry, P., & Dormann, C. F. (2011). Set-aside management: How do succession, sowing patterns and landscape context affect biodiversity? *Agriculture, Ecosystems & Environment*, *143*, 37–44.
- 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.
- Zhang, C. B., Wang, J., Qian, B. Y., & Li, W. H. (2009). Effects of the invader *Solidago canadensis* on soil properties. *Applied Soil Ecology*, *43*, 163–169.