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Research Article

Biological invasions threaten crops: Alien Himalayan balsam lures and co-opts floral visitors away from cultivated cherry tomatoes

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Abstract

While it has been demonstrated that invasive alien plants pose a threat to co-occurring wild-growing native plants by attracting their pollinators, we know almost nothing about their impact on crop pollination. Alien plants with attractive flowers sometimes occur close to crops and may influence yields when they share the same pollinators and have overlapping flowering periods. We present the results of an experiment on the impact of alien balsam (*Impatiens glandulifera*) on the pollination of cherry tomato (*Solanum lycopersicum* var. *cerasiforme*). We verified whether balsam decreases the number of insect visits to the tomato flowers or, conversely, whether balsam may have a positive influence on the pollination rate of the crop. We also assessed crop production with and without the insect visitors. The study was conducted in southern Poland under garden and greenhouse experimental conditions simulating small-scale cultivation of the crop with a neighbouring patch of the alien plant. The studied plants were exposed to insects visiting flowers of the following variants: only one of the two species was exposed or both species were exposed together. Moreover, two factors that may influence insect visits in flowers were assessed: the chemical composition of the floral scent that attracts insects and floral pathogens infesting pollinators that may deter them. The number of insect visits (mainly *Bombus pascuorum*) on the tomato flowers decreased significantly when the plants were exposed to the alien balsam. Moreover, alien balsam secreted more flower attractants (mainly fatty acids and their esters) than tomatoes, which could explain more frequent insect visits in balsam flowers. However, the floral pathogens probably had a negligible impact on the number of insect visits to the flowers of the two plants. The level of infestation on both studied species was relatively low (*I. glandulifera*: 5.1% of all pathogen colonies grown in a laboratory, *S. lycopersicum* var. *cerasiforme*: 4.2% and 2.6% of all colonies in the garden and greenhouse, respectively) and we found no pathogens known to infect pollinators. It should be noted, however, that some of these pathogens (e.g. *Botrytis cinerea*, *Fusarium oxysporum* and *Sclerotinia sclerotiorum*) are known to cause severe diseases in many crops. Our results revealed that the presence of attractive invasive alien species near small-scale cultivations may negatively affect crop pollination, resulting in smaller fruit size and irregular shape. The impact of such alien species on crop production and the agricultural economy on a large scale requires further study.

Key words: Agriculture, beta-caryophyllene, biofilm organisms, cerise tomato, economy, eradication near cultivations, floral odours, greenhouse

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Introduction

Nectar- and pollen-rich flowers offer a reward that many pollinators find hard to resist. As invading alien plants attractive for pollinators grow in progressively larger areas and at higher densities, this effect is significantly enhanced. In Europe, examples of this mechanism include invasions of alien goldenrods (*Solidago gigantea* and *S. canadensis*; Moroń et al. (2019)), Japanese knotweed (*Reynoutria japonica*; Johnson et al. (2019)) and Himalayan balsam (*Impatiens glandulifera*; Chittka and Schürkens (2001)). All these species are pollination generalists and are thought to play a dominant role in pollinator network structures (Vilà et al. 2009; Vanbergen et al. 2017). They alter pollinator abundance, richness and pollinator community structure (Fiedler et al. 2012), successfully luring and co-opting pollinators in invaded areas. This may result in a decrease in the number of pollinator visits to flowers of co-occurring wild-growing native plants and, consequently, a decrease in their fitness (Chittka and Schürkens 2001; Brown et al. 2002; Morales and Traveset 2009; Albrecht et al. 2014; Herron-Sweet et al. 2016; Goodell and Parker 2017), even to the point of local extinction of the native species (Kleijn and Raemakers 2008).

Invasion of an alien plant may negatively affect native plants by several mechanisms. First, through an increase in the deposition of heterospecific pollen and, consequently, by limiting their reproductive success of the recipient through reducing fruit and seed set (Malecore et al. 2021) and second, through enhancing the transmission of floral primary pathogens that increase the incidence of plant diseases (Najberek et al. 2023). Moreover, large-scale monospecific floral resources formed by invasive alien species might lead to reduced specialist pollinator performance (Filipiak et al. 2017). For example, the pollen of *I. glandulifera* has lower concentrations of proline, an amino acid important for flight metabolism in bumblebees (Drossart et al. 2017).

The opposite scenario, with the positive influence of flower attractive invasive alien plants on native flora and pollinators, is also possible. For instance, if invaders occur at high densities, they may act as “magnet” species that increase pollination of wild plants through, for instance, pollinator spill-over effects (Charlebois and Sargent 2017). This effect may also play a role in crop pollination; however, only a few studies have explored the influence of alien plant species on pollinator−crop interactions (Vanbergen et al. 2017).

Under experimental conditions, Najberek et al. (2021) revealed that invasive alien balsams, *I. glandulifera* and *I. parviflora*, may decrease the pollination of strawberry plants (*Fragaria ×ananassa*). Cunningham-Minnick et al. (2020) revealed that the invasive alien Amur honeysuckle (*Lonicera maackii*) negatively influenced pollinator diversity and pollination services in adjacent corn or soybean cultivations. However, the removal of Amur honeysuckle led to a decrease in the number of large-bodied generalist bees associated with this alien plant. On the other hand, Russo et al. (2016) reported that the invasive alien thistle (*Carduus acanthoides*) did not influence the visitation of pollinators to cultivated plants, such as sunflower (*Helianthus annuus*), honey clover (*Melilotus albus*) or sweet yellow clover (*M. officinalis*). The beneficial influence of alien plant species on crop pollination was also partially demonstrated by Carvalheiro et al. (2011). This study provided evidence that the presence of wild plants (half of which were alien species) within sunflower fields may enhance crop productivity. On the other hand, “pollinator spill-over" from large crop cultivation to adjacent patches of alien plants cannot be excluded. This may enhance the pollination of such species, particularly because many of them develop flowers later in the vegetative season. To date, this trend has been widely demonstrated in studies with crop fields and co-occurring native wild-growing plants (Hanley et al. 2011; González-Varo and Vilà 2017; Trillo et al. 2020; Harris et al. 2023).

We performed a study in southern Poland to test competition for floral visitors between invasive alien Himalayan balsam (*I. glandulifera*; hereafter: alien species) and cultivated cherry tomato (*Solanum lycopersicum* var. *cerasiforme*; hereafter: crop species). Tomato is a buzz-pollinated crop: the pollen is kept locked inside the poricidal anthers and the most efficient way for pollinators to extract it is "buzzing" (Bowers 1975; Banda and Paxton 1991; Franceschinelli et al. 2013). Buzz-pollination behaviour guarantees the release of high volumes of pollen, which is positively correlated with fruit production. Tomato is pollinated mainly by bumblebees (e.g. Teppner (2005)), which exhibit buzz-pollination behaviour (Mesquita-Neto et al. 2018). Bumblebees are also the main pollinators of *I. glandulifera* in the study area (Najberek et al. 2023). Moreover, both plants have overlapping flowering periods (Najberek et al. 2023, https://www.gardenchic.co.uk/) and both commonly occur close to each other in southern Poland (Najberek, pers. observations).

Bumblebees exploit food sources that are as far as 1500 m from their colonies (Osborne et al. 2008). Therefore, within this radius, patches of nectar-rich *I. glandulifera* (Chittka and Schürkens 2001) around tomato cultivation areas may have a significantly stronger influence upon yields than native wild-growing species that also co-occur with the crop, yet their nectar production is lower. Since pollinator availability determines the quality and volume of tomato production (Velthuis and van Doorn 2006; Franceschinelli et al. 2013; Zhang et al. 2022) and *I. glandulifera* can affect pollinator availability for strawberry plants (Najberek et al. 2021), we assumed that the co-occurrence of cherry tomatoes with *I. glandulifera* should decrease the intensity of insect visits to crop flowers and result in lower fruit production. In Poland, the average total area of cultivated tomato fields calculated for June 2010–2021 was ca. 8,000 ha, which accounted for approximately 5% of the total area of cultivated field vegetables in the country (Statistics Poland 2023). It can, therefore, be assumed that the impact exerted by *I. glandulifera* on crop pollination is meaningful for the country's economy. This effect can be most pronounced in six of the 16 Polish provinces with large productions of tomatoes, including Małopolska (Statistics Poland 2023), where the present study was conducted and where *I. glandulifera* is particularly widespread (Adamowski et al. 2018).

Pollinators can recognise diseased flowers. It was demonstrated that bumblebees can detect the odour of the parasite *Crithidia bombi* (Fouks and Lattorff 2013) and honey bees were found to avoid flowers infected by the fungus *Ascosphaera apis* (Yousefi and Fouks 2019). When primary pathogens are widely dispersed amongst plant individuals at a particular site, disease-retarding pollination may occur. On the other hand, plants exhibit compensatory mechanisms against pathogen infections, for example, by increased flower production that emit different amounts and/or patterns of attractants (Shykoff and Kaltz 1997; Dötterl et al. 2009). This compensation may increase the reproductive efforts of plants; however, it may also intensify intraspecific and interspecific transmission of harmful pathogens (Durrer and Schmid-Hempel 1994; Shykoff and Kaltz 1997; Adler et al. 2018). To account for the effects of flower infestation and attractants, we identified all floral pathogens, with an emphasis on pathogens infesting pollinators (e.g. *Apicystis bombi* infesting bees; Vanderplanck et al. (2019)) and we analysed chemical compounds that lure these insects (e.g. linalool, a strong bee attractant; Williams et al. (1981)); *Impatiens glandulifera* differs from cherry tomatoes in the richness of the floral attractants emitted, which may play a role in intensity of insect visits in their flowers.

Our study primarily tested the hypothesis that the presence of invasive alien *I. glandulifera* alongside cherry tomatoes reduces the frequency of insect visits to crop flowers, leading to lower fruit production. Alternatively, we considered that *I. glandulifera* might cause a pollinator spill-over effect, enhancing the pollination and yield of crops in small-scale cultivations. To test these hypotheses, we evaluated the competition for floral visitors between the alien and crop species, along with analysing their floral pathogens and attractants, as these factors could influence insect visitation to flowers.

Methods

Plant species

The variety of tomatoes that we used was cerise, which is a very popular cherry tomato (*Solanum lycopersicum* var. *cerasiforme* (Alef.) Voss) worldwide. The flowers are hypogynous, regular, pendant and typically six-merous, with short calyx tubes and rotated corollas (Cooper 1927). The flowering phase of cerise tomatoes occurs from June to September (mid-flowering: July). They are visited by pollinators (e.g. *B. pascuorum* and *B. terrestris*; Teppner (2005)) mainly for pollen (Franceschinelli et al. 2013). Moreover, this variety is highly disease-resistant (e.g. https://pomidorlandia.pl/en/, https://www.gardenchic.co.uk/); thus, it is successfully cultivated in both garden and greenhouse cultivation in Poland.

Annual *Impatiens glandulifera* Royle mainly occurs along rivers and streams, which allows for its rapid spread (Najberek et al. 2020). However, the species also prefers roadsides, ruderal areas, wetlands, meadows and forest paths (Helmisaari 2010; Helsen et al. 2021). It has one or more pink or reddish (sometimes white) bell-shaped flowers in axillary racemes; the flowers are bilaterally symmetrical and zygomorphic (Clements et al. 2008). The flowering phase of *I. glandulifera* in Poland largely overlaps with the flowering phase of tomatoes, occurring between July and October (mid-flowering: August/September).

The two studied species, *I. glandulifera* and *S. lycopersicum* var. *cerasiforme*, share the same pollinators (Teppner 2005; Najberek et al. 2021, 2023). However, in contrast to tomatoes, *I. glandulifera* attracts pollinators with extraordinarily high volumes of nectar, amounting to 0.3 mg per flower hourly (Chittka and Schürkens 2001).

Cultivation conditions

The experiment was carried out in 2021 under common garden and greenhouse conditions in a cultivation plot at the Institute of Nature Conservation, Polish Academy of Sciences in Cracow (southern Poland). The seedlings of *I. glandulifera* (n = 100) were transplanted in May 2021 from areas near Cracow: Marcyporęba, Zelczyna, Tyniec and Szczyglice (25 seedlings per locality). These plants were cultivated in a garden in pots (1.1 litre capacity) filled with universal garden soil (pH 5.5–6.5) mixed with sand (a ratio of 3:1). Each plant individual was marked with a unique ID number.

Tomato individuals (n = 122) were germinated in April 2021 from the purchased seeds. The plants were initially cultivated in seedling pots (0.5 litre capacity) under room conditions. On 6 May, the most vigorous plants (n = 80) were transplanted to garden pails (Suppl. material 2: fig. S1) with a 5 litre capacity, which were filled with a standard 100% turf substrate. The plants were marked with unique ID numbers and relocated to a polycarbonate greenhouse (LWH: 405 × 210 × 191 cm). On 8 and 22 July, the substrate was enriched with a biofertiliser.

To avoid frost damage to the cultivated plants, the greenhouse was initially closed at all times and when the day temperature increased, the greenhouse was opened in the morning and closed in the evening. In mid-June, when the day and night temperatures exceeded 16 °C, half of the tomatoes were relocated from the greenhouse to the garden. Since this period, the greenhouse was closed only for the time needed to carry out the tests (see “Ali” treatment in the next subsection) and in the case of weather breakdowns (e.g. windstorms).

The tomatoes were arranged in one patch, ~1.5 m away from the patch of *I. glandulifera*. Such an arrangement simulated a common scenario, where crops are directly adjacent to balsam patches. For example, it occurs when farmers cultivate tomatoes for their own food, as well as *I. glandulifera* – either for ornamental purposes or as a food supply for their apiaries (Najberek, pers. observation).

It should also be noted that polycarbonate disturbs the orientation behaviour of insects, which results in their reduced ability to recognise flowers and the environment in greenhouses (e.g. Blacquière et al. (2006)). Although this approach is a serious disadvantage in commercial cultivation, our experimental setup allowed us to almost completely exclude pollinators from the greenhouse. As a result, it was possible to obtain fruits from self-pollinated flowers and compare their quality with fruits from insect-pollinated garden flowers.

We obtained a permission from the Regional Directorate for Environmental Protection in Cracow, which is required for the use of the invasive alien species of European Union concern (No. OP.672.2.2021. KW) and for studying legally-protected bumblebees (No. OP-1.640 1.81.202l.GZ).

Competition for floral visitors and assessment of crop production

Tests of the activity of insects visiting flowers of the two plant species were carried out under warm and windless weather conditions over eight consecutive days between 26 July and 2 August, when the flowering phases of the two species overlapped.

On each experimental day, we assessed whether insects visited *I. glandulifera* more frequently than they visited tomatoes and whether the invasive alien species co-opted the visiting insects from the crop. The studied plants were exposed to three treatment groups, termed “Ali”, “Cro” and “AliCro”. In the surveys of Ali treatment, only balsams were exposed to insects visiting flowers (simulating a scenario when the balsam is growing alone, not co-occurring with the crop); at that time, all garden individuals of tomato were moved indoors and the greenhouse was closed to isolate tomatoes cultivated inside. In the surveys of Cro treatment, only tomato plants were exposed, both in the garden and in the greenhouse (a scenario when the crop is growing alone in garden or greenhouse); all balsam individuals were moved indoors at that time. In the surveys of AliCro treatment, both balsams and tomatoes (including tomatoes from the garden and from the greenhouse) were exposed together (a scenario when the two plants co-occur). The data collected during the experiment were used to calculate the number of insect visits recorded per plant individual, per survey and per experimental treatment group.

As the activity of particular groups of insects may be determined by day time (Stelzer and Chittka 2010) as well as by the production of pollen/nectar (e.g. Schmidt et al. (2012)), the sequence in which the treatment groups were exposed was randomly selected for each experimental day. Moreover, a similar number of randomly selected flowering plants (ca. 20 per species) was included on each day; although, for each day, the selected set of individuals was different, some of them were used repeatedly (the excessive individuals were closed indoors). In the garden, the numbers of individuals of each species were adjusted to match the number of tomato individuals flowering in the greenhouse. Moreover, the greenhouse tomatoes were not re-arranged between the subsequent surveys. In turn, the selection and spatial arrangement of particular plant individuals in the garden were modified between the surveys, but not between the study treatment groups (Ali, Cro and AliCro).

The tests started between 8:30 and 11:00 h on each study day and ended between 13:00 and 15:00 h. The survey was conducted by the same researcher and with the same sampling effort of 60 minutes per experimental treatment group, with a 30-minute break before the onset of the survey in the next treatment group. Thus, each study day, the experiment lasted for a total of 180 minutes. In the AliCro treatment, each survey transect (visual inspection) started from the balsam individuals, continued with individuals of tomatoes in the garden and finished with tomatoes in the greenhouse. All flowers of the surveyed individuals were monitored to determine their newly-arriving insect visitors; the duration of each survey transect in the AliCro ranged from approximately 3 minutes (in the case of no visitors) to 9 minutes (when visitors were detected). In the Ali and Cro treatments, the survey transect time was shorter (~2–6 minutes) because some of the plants were closed indoors. The flight of each recorded insect visitor was tracked and the IDs of subsequently visited plants were noted. An insect visit was defined as a single contact of the insect with a flower anther or stigma of a particular plant individual. Since we were not able to assess whether a given visit resulted in pollination, we conservatively did not treat floral visitors as pollinators. However, it can be assumed that the majority of the visiting insects that we recorded were *bona fide* pollinators. The maximum distance between the flowers and the observer was 1.5 m, which was sufficient to detect any insects. They were identified without disturbing them (93.3% at the species level, 3.9% at the family level and 2.8% at the superfamily level).

Before each survey, flowers on each individual plant were counted (mean n of flowers: *I. glandulifera* = 2.06 ± 1.04, *S. lycopersicum* var. *cerasiforme* = 2.92 ± 2.51). Air temperature during the survey was monitored using i-Button DS1921G data loggers (with 10-min intervals; Suppl. material 2: fig. S2); wind speed and solar radiation were measured using hand-held environmental meters (Extech 45170CM and SP505). These variables were monitored to include changes in weather conditions that influence pollinator metabolism and activity, for example, an increase or decrease in air temperature during the day (Dixon et al. 2009; Pawlikowski et al. 2020). Notably, the time of day was also included in the analyses because it may impact both the daily patterns of floral resources and the activity of pollinators

(Stelzer and Chittka 2010). During the last survey, the heights of all the plant individuals were measured because taller plants may be more frequently visited by pollinators than shorter plants (Najberek et al. 2021, 2023). In our study, the *I. glandulifera* individuals were taller than the *S. lycopersicum* var. *cerasiforme* individuals (Suppl. material 2: table S1).

In order to assess tomato fruit production involving insect visitors (fruits from the garden) and excluding them (fruits from the greenhouse), size and shape of fruits were measured. Between 27 July and 19 August, 1002 ripe fruits were collected (455 from the garden and 547 from the greenhouse; each of 80 individuals developed fruits; the average number of fruits per single plant was 11.8) and immediately weighed using an analytical balance (Radwag PS 360.R2). Each fruit was classified as healthy (without visible infection symptoms; Suppl. material 2: fig. S3A) or diseased (with major/minor infection symptoms; Suppl. material 2: fig. S4). Diseased fruits with minor disease symptoms were further classified as “saleable” (Suppl. material 2: fig. S4B), whereas fruits with major disease symptoms were further classified as “non-saleable” (Suppl. material 2: fig. S4A). Tomato profiles (n = 856) were photographed against a paper background (Suppl. material 2: fig. S3) and digital images were analysed using ImageJ software (ver. 1.51 k). The fruit area and shape descriptors were calculated (according to Najberek et al. (2020)). The area of one side was assessed for each fruit (Suppl. material 2: table S2), which corresponded to half of the total fruit area. The shape of the tomatoes was assessed using circularity (calculated according to the formula $4\pi \times$ fruit area/fruit perimeter^2) and aspect ratio (the ratio of the major axis of the tomato to its minor axis) data.

Floral chemical attractants

We assumed that the flowers of the two studied plant species differ in terms of the richness of the emitted floral attractants. To investigate this issue, the flowers of *I. glandulifera* (n = 31 from 27 individuals) and *S. lycopersicum* var. *cerasiforme* (n = 87 from 29 individuals) were collected on 26 June and 06 August, respectively. Garden and greenhouse flowers of cherry tomatoes were mixed and analysed without separation because we used this material only for qualitative analysis (Popova et al. 2020; Jakubska-Busse et al. 2022). The samples were placed into 5 ml glass vials filled with 2.5 ml of dichloromethane or hexane (Sigma−Aldrich, 99.9%) at room temperature. These two chemical compounds were used to extract foliar nectar drops. The extracts were stored at -15 °C until they were used for GC/MS analyses. Samples of the extracts of *I. glandulifera* and *S. lycopersicum* var. *cerasiforme* were prepared separately in dichloromethane and hexane (a total of eight samples of *I. glandulifera* and ten samples of *S. lycopersicum* var. *cerasiforme*).

GC/MS was performed on a GCMS-QP2010SE SHIMADZU gas chromatograph equipped with a mass selective detector (MS scan 17–550 m/z) and a Zebron ZB-5 ms (30 m 0.25 mm; Phenomenex) column. The oven temperature at the start of the measurement was 40 °C and then the temperature was increased at a rate of 4 °C/min until it reached 120 °C; afterwards, the temperature was increased to 320 °C at a rate of 40 °C/min and the oven temperature was kept at 320 °C for 5 min. Helium was used as a carrier gas.

Identification of the extract compounds was carried out using the NIST17 Library. For identification of long-chain hydrocarbons, samples of C16–C42 alkanes were analysed by GC/MS using the same oven and column parameters and their spectra and retention times were compared with those obtained from the extracts. Qualitative analysis of *I. glandulifera* samples revealed no differences in the composition of the extracts. Similarly, in the case of *S. lycopersicum* var. *cerasiforme*, the qualitative composition of the extracts was comparable amongst all the tested samples.

Floral pathogens

To explore the possible limiting effect of floral pathogens on the pollination of alien or crop species, the flowers of *I. glandulifera* (n = 115) and *S. lycopersicum* var. *cerasiforme* (n garden = 73, n greenhouse = 210) were collected between 30 July and 3 August on the day following each assessment of insect visitor activity, frozen (-18 °C), transported to the mycological laboratory and inserted into a flask (50 ml capacity) filled with 10 ml of distilled sterile water. The content of each flask was shaken (amplitude = 4 cm, n of cycles = 250 for 10 minutes). Subsequently, 1 ml of the washings was placed directly on a Petri dish and filled with Martin medium (BTL Ltd.) at 49.5 °C (Moszczyńska et al. 2011, 2013). After incubating in the dark for 10–14 days at room temperature (21–22 °C), the fungal colonies were counted (Suppl. material 2: fig. S6) and identified using a Leica DM750 microscope and identification keys (Simmons and Ellis 1972; Sutton 1980; Domsch et al. 1982; Ellis and Ellis 1987; Pitt and Hocking 2009; Watanabe 2011). Based on the available literature, the recorded pathogens were classified as harmful or beneficial – both for the insects visiting flowers and for the plants.

Statistical analysis

The data were analysed in R v. 4.0.3 and RStudio v. 1.4.1103 (R Development Core Team 2015). Data collected during the tests of competition for floral visitors (the main and alternative hypotheses testing) was assessed using a generalised linear mixed model (GLMM) fitted using Maximum Likelihood estimation via the template model builder ‘TMB’ (the glmmTMB package) (Brooks et al. 2017). The number of recorded insect visits calculated per plant individual per survey and per experimental treatment group (n = 1255) was under-dispersed; therefore, the Conway–Maxwell Poisson distribution (‘compois’) of the target variable was used. The main fixed effects in the base model were the treatment group and plant species status, combined into a single variable (Ali - alien species, AliCro - alien crop species, Cro - crop species; details in the Suppl. material 1). These effects allowed for between-species comparisons for the treatment group AliCro, in which the balsam and the tomato were exposed together. Other fixed effects included in the model were the stem height of individual plants and insect species/group (those of *Bombus pascuorum*, *Apis mellifera* and bees from the other groups, as well as syrphids; single flights of *Macroglossum stellatarum* and *B. humilis* were excluded). We also included a weather variable obtained from principal component analysis (PCA), based on air temperature (°C), wind speed (m/s) and solar radiation (w/m^2; Suppl. material 2: table S3). Moreover, two nested random effect structures were included in the model (‘1|Survey No./Plant ID/N minutes’, ‘1|Survey No./Plant ID/N flowers’; Suppl. material 2: table S3). Random effects were applied because of differences between the surveys in terms of: (1) the number of controlled plant individuals per survey, (2) the number of surveys of each controlled plant individual because some of them were controlled more frequently than others and (3) the number of flowers developed by a plant individual, as it influences the number of insect visits per plant individual. Moreover, the time of each visit was included in the structure as the number of minutes since midnight (e.g. 11:52 a.m. was converted using the following formula: ((11 * 60) + 52) = 712).

The base model was reduced by removing particular fixed effects and the model with the lowest Akaike Information Criterion (AIC) was subsequently chosen (Suppl. material 2: table S3). Within-factor comparisons were conducted using the default R treatment contrasts, while the reference groups in particular models were changed using the "relevel" command.

Tomato production was analysed using three different linear models (for weight, surface area and circularity) and one generalised linear model for gamma distribution (for the aspect ratio). In the model for weight, the data for all the collected fruits (n = 1002) were analysed. Three fixed effects were included in the model: cultivation type (garden/greenhouse), disease symptom occurrence (healthy/diseased) and commercial value of the diseased fruit (saleable/non-saleable; Suppl. material 2: fig. S4); two interactions (cultivation type * disease symptom occurrence, cultivation type * sale possibility of diseased fruits) were also included in the model. In turn, the surface area, aspect ratio and circularity of fruits (n = 856) were analysed using models with a single fixed effect—cultivation type. In the model for circularity, the arcsine transformation of the target variable was carried out.

Besides statistical testing of the hypotheses (main and alternative) and parallel crop production assessment, we conducted the quantitative and qualitative analyses of floral pathogens. For pathogen records, two glmmTMB models were constructed, with the number of colonies per plant per dish used as a target variable (n = 201). As over-dispersion was revealed in these models, a negative binomial distribution was used. In the first model, we compared *I. glandulifera* and *S. lycopersicum* var. *cerasiforme* cultivated in the garden using a model with one fixed effect, namely, the plant species. The nested structure of random effects (1|Plant ID/N flowers/Dish ID) was also included because of differences in the number of flowers placed per dish and in the number of dishes used per plant individual. In the second model (n = 132), *S. lycopersicum* var. *cerasiforme* flowers were compared between the garden and greenhouse cultivation conditions. We used a model with one fixed effect (the cultivation type), two nested random effects (1|Plant ID/N flowers) and one crossed random effect (1|Dish ID; the number of dishes was always three per plant individual).

The composition and richness of the recorded pathogens were calculated using three complementary indices: the Shannon–Wiener, Evenness and inverted Simpson indices (Yin et al. 2019; Twardowski et al. 2022). Three GLMMs with a normal distribution were used to compare the three indices (calculated per plant and per dish; n in each model = 165) between *I. glandulifera* and *S. lycopersicum* var. *cerasiforme* cultivated in the garden. In the model for the Simpson index, the data were logged naturally. As in the models for fungal records, each model had one fixed effect (plant species) and one nested random effect structure (1|Plant ID/N flowers/Dish ID). To compare the indices for *S. lycopersicum* var. *cerasiforme* between the garden and greenhouse cultivation conditions, three GLMMs with a normal distribution were used (n in all models = 98). Each model had one fixed effect (cultivation type), two nested random effects (1|Plant ID/N flowers) and one crossed random effect (1|Dish ID).

Results

Competition for floral visitors and assessment of crop production

A total of 1705 insect visits (*I. glandulifera*, n = 1592; *S. lycopersicum* var. *cerasiforme*, n = 114; Fig. 1) during 460 insect flights (*I. glandulifera*, n = 416; *S. lycopersicum* var. *cerasiforme*, n = 44; Fig. 1) were recorded. In both studied plant species, two insect species dominated: the common carder bee *B. pascuorum* and the honey bee *A. mellifera* (Fig. 1). The flowers of *I. glandulifera* were visited 987 times during 131 flights, while the respective values for *S. lycopersicum* var. *cerasiforme* were 91 and 30 (Fig. 1). It should also be stressed that there were two flights of *B. pascuorum* in which both studied plants were visited. The number of flowers visited by *A. mellifera* was lower (n = 593). However, the number of flights was greater (n = 267; Fig. 1). Notably, honey bees visited almost exclusively *I. glandulifera* flowers (99% of visits, 98% of flights; Fig. 1).

Interestingly, while 49% of the individuals of *S. lycopersicum* var. *cerasiforme* exposed during the surveys were visited by insects, in the case of *I. glandulifera*, this value was twice as high, reaching 97% (χ^2 = 545.9, df = 3, p < 2e^{-16}). We revealed that the number of visits to the flowers of *S. lycopersicum* var. *cerasiforme* decreased when this crop was exposed together with the alien species (contrast: estimate = -0.37, SE = 0.03, z = -11.70, p < 2e^{-16}; Fig. 2). The presence of *S. lycopersicum* var. *cerasiforme* had no influence on the insects visiting the flowers of *I. glandulifera* (contrast: estimate = 0.01, SE = 0.01, z = 1.29, p = 0.2; Fig. 2). Therefore, the pollinator spill-over from the crop to the adjacent patch of the alien plants did not occur.

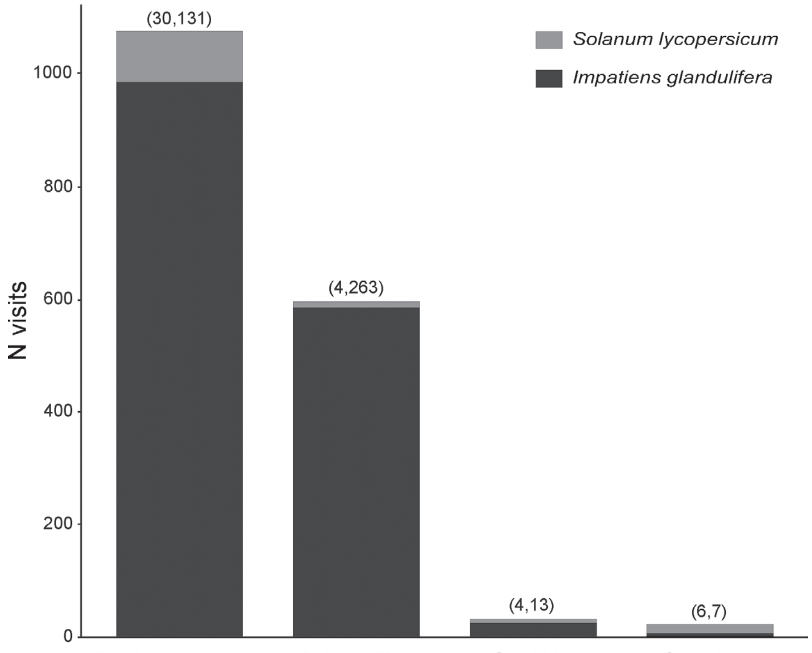

Figure 1. The number of visits by the most common insects visiting flowers of the invasive alien species *Impatiens glandulifera* and cultivated *Solanum lycopersicum* var. *cerasiforme*. The first number in brackets above the bars reflects the number of insect flights to *S. lycopersicum* var. *cerasiforme*, while the second indicates the number of insect flights to *I. glandulifera*. Single flights of *Macroglossum stellatarum* and *Bombus humilis* to *I. glandulifera* are not included in the plot. All insects that had contact with flower anthers or stigmas were accounted for.

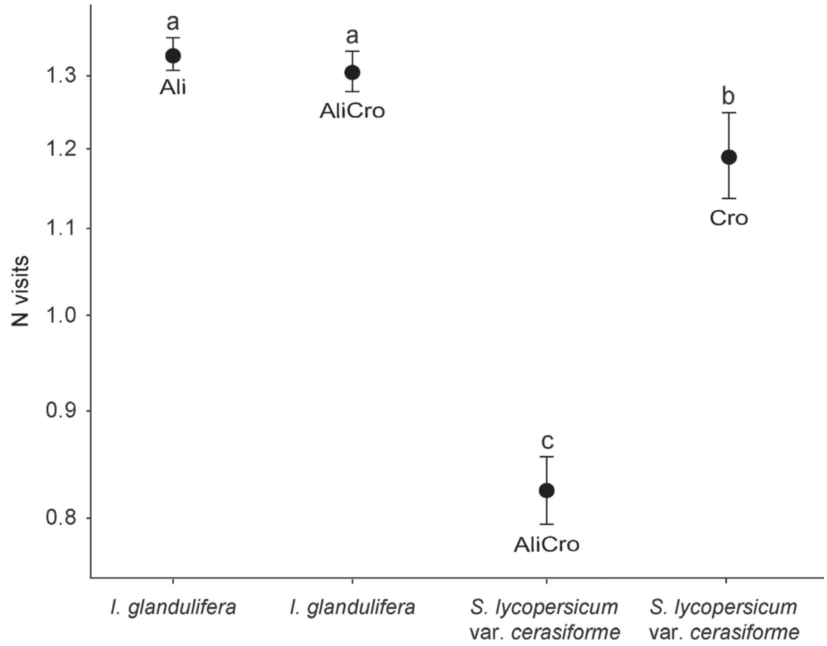

Figure 2. Estimated mean number of insects (± confidence intervals) recorded from the flowers of invasive alien *Impatiens glandulifera* and cultivated *Solanum lycopersicum* var. *cerasiforme* in the three experimental treatment groups: Ali (alien species exposed), AliCro (both species exposed together) and Cro (crop species exposed). Groups with the same letter above the T-bars are not significantly different.

Considering the numbers of visits per particular insect group (see the numbers in Fig. 1; $\chi^2 = 758.7$, df = 3, $p < 2e^{-16}$), we revealed statistically significant domination of *B. pascuorum* over syrphids and the other bees (respective contrasts: estimate = -0.46, SE = 0.02, z = -22.74, $p < 2e^{-16}$; estimate = -0.45, SE = 0.02, z = -18.66, $p = 2e^{-16}$). *Apis mellifera* also dominated these two insect groups (respective contrasts: estimate = -0.46, SE = 0.02, z = -21.87, $p < 2e^{-16}$; estimate = -0.45, SE = 0.02, z = -17.61, $p = 2e^{-16}$). However, there were no differences in the number of visits between *B. pascuorum* and *A. mellifera* (contrast: estimate = 0.0003, SE = 0.002, z = 0.14, p = 0.9) or between syrphids and the other bees (contrast: estimate = 0.01, SE = 0.03, z = 0.37, p = 0.7). Weather conditions had no significant influence on the results ($\chi^2 = 0.06$, df = 1, p = 0.8).

As the polycarbonate effectively prevents insects, we recorded only a single floral visit (of a syrphid species) in the greenhouse, whereas all the remaining insect visit records were from the garden.

Ripe garden tomato fruits were heavier than the fruits from the greenhouse ($\chi^2 = 2129.8$, $F_{1,996} = 129.7$, $p < 2.2e^{-16}$; Fig. 3). The results for fruit weight and area were concordant (Fig. 3): fruits from the garden also had a greater area than those from the greenhouse (sum Sq = 2207949, $F_{1,854} = 82.55$, $p < 2.2e^{-16}$; Fig. 3). Moreover, the analysis of the aspect ratio revealed that the garden fruits were more rounded than those from the greenhouse ($\chi^2 = 12.16$, df = 1, p = 0.0005; Fig. 3). The results for circularity showed a similar trend (sum Sq = 0.001, $F_{1,854} = 2.16$, p = 0.1; Fig. 3). There was a significant interaction between cultivation conditions and the commercial value of the diseased fruits: in the garden, there was no difference between weight of the saleable and non-saleable fruits (contrast: estimate = 0.23, SE = 0.64, t = 0.37, p = 0.7; Fig. 4), whereas in the greenhouse, the saleable fruits were heavier than the non-saleable ones (contrast: estimate = 4.69, SE = 1.05, t = 4.48, $p = 9.02e^{-06}$; Fig. 4).

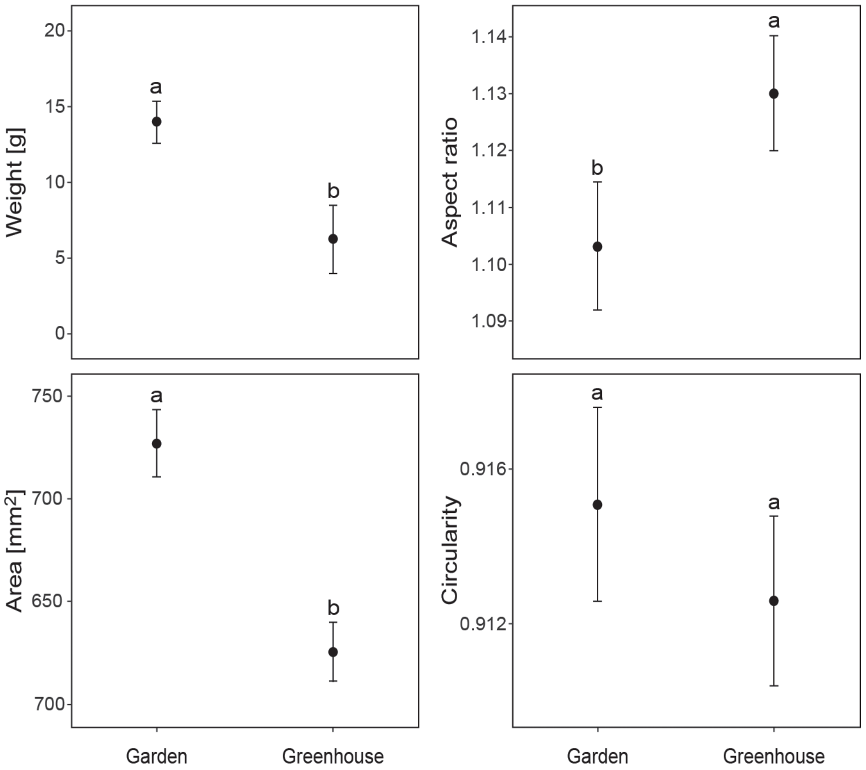

Figure 3. Estimated mean values (± confidence intervals) of the weight, surface area, aspect ratio and circularity of *Solanum lycopersicum* var. *cerasiforme* cultivated under garden and greenhouse conditions. The distribution of letters above the T-bars indicates differences between the two cultivation conditions.

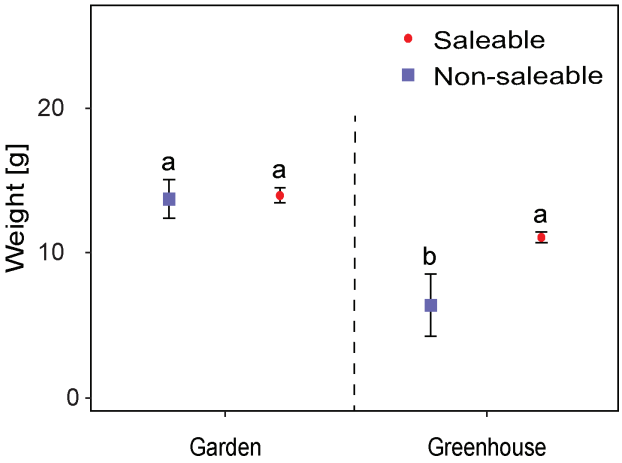

Figure 4. Estimated mean values (± confidence intervals) of the weight of *Solanum lycopersicum* var. *cerasiforme* cultivated in the garden and greenhouse conditions between saleable (healthy and slightly diseased; Figs S3A, S4B) and non-saleable (considerably diseased; Fig. S4/A) fruits. The distribution of letters above the T-bars indicates differences in weight between the saleable and non-saleable fruits within particular cultivation conditions.

Floral chemical attractants

There were considerable differences in the compounds composition between the two plant species. The solvent extract of the *S. lycopersicum* var. *cerasiforme* flowers contained various volatile terpenes, for example, α- and β-pinene (Suppl. material 2: table S4). Oxygen-containing compounds were less abundant in the extract. Amongst them, we identified aromatic alcohols, namely, derivatives of benzyl alcohols, such as methyl salicylate and eugenol. Additionally, two other compounds, dodecyl acetate and hexadecenoic acid, were present in the extract. The extract also contained various saturated long-chain hydrocarbons. Amongst them, long-chain alkanes, which consist of odd carbon atoms (C25–C31), were the most abundant compounds (Suppl. material 2: table S4).

By analysing the GC–MS traces of *I. glandulifera* extracts, we revealed that terpenes were absent in the samples (Suppl. material 2: table S5). The chemical compounds identified in the extracts included a series of aliphatic saturated alcohols, ketones and aldehydes, for example, hexadecanal and nonadecanol. Amongst oxygen-containing compounds, various fatty acids and their esters, for example, palmitic and linoleic acids, were also detected. The *I. glandulifera* samples contained fewer hydrocarbons than the *S. lycopersicum* var. *cerasiforme* samples. However, in contrast to those of the latter species, 1-pentacosene, 9-nonacosene and squalene hydrocarbons were identified solely in the extract of *I. glandulifera* (Suppl. material 2: table S5).

Floral pathogens

In total, 4541 colonies of 43 taxa (mainly fungal) were identified (Suppl. material 2: table S6; details in the Suppl. material 1). We found no pathogens known to infect pollinators. In turn, primary obligatory pathogens, with invariably negative impacts on plants, accounted for 3.6% of all records. These were *Boeremia lycopersici*, *Botrytis cinerea*, *Fusarium avenaceum*, *F. oxysporum*, *F. sporotrichioides*, *Phoma herbarum*, *Rhizoctonia solani*, *Sclerotinia sclerotiorum* and pathogens belonging to the *Pythium* genus. However, the primary pathogens were rarely detected in the flowers of either of the two species. In the case of *I. glandulifera*, only 5.1% of all colonies were identified as primary pathogens. The values for the garden and greenhouse cherry tomatoes were 4.2% and 2.6%, respectively. Less harmful secondary pathogens, whose presence may even be beneficial for plants, were also present in the analysed flowers (e.g. *Alternaria alternata* and *Cladosporium cladosporioides*). We also recorded microorganisms that form biofilms (e.g. *Aureobasidium pullulans* and bacterial colonies) that protect plants from penetration by primary pathogens. Organisms not associated with the surveyed plants were also detected (e.g. the wood-decaying fungus *Dematioscypha dematiicola*, probably associated with the wooden construction of the greenhouse basement), as were parasites of fungi (e.g. *Trichoderma harzianum*; Suppl. material 2: table S6).

The total number of colonies in the garden was more than four times greater for the flowers of *I. glandulifera* than for the flowers of *S. lycopersicum* var. *cerasiforme* (Suppl. material 2: table S6). The dominance of the alien plant species in this respect was confirmed in the GLMM ($\chi^2 = 6.81$, df = 1, p = 0.009; Suppl. material 2: fig. S5A). This result was strongly influenced by the abundant occurrence of a few fungal species and genera (*A. alternata*, *C. cladosporioides*, *Cordyceps fumosorosea*, *D. dematiicola*, *Penicillium sect. chrysogenum*, *Phoma herbarum*, *Ampulliferina* sp., *Basidiomycota* sp., *Exophiala* sp., *Mortierella* sp.) and by the red yeast colony on the flowers of the alien species. Only *T. harzianum* colonies were more abundant in the flowers of *S. lycopersicum* var. *cerasiforme* (Suppl. material 2: table S6).

Amongst the three GLMMs used to compare the composition, richness and diversity of the recorded taxa, models for the Shannon–Wienner and Evenness indices revealed that the taxa detected in *I. glandulifera* occurred significantly more evenly (i.e. without the dominance of a single species) than in the case of

S. lycopersicum var. *cerasiforme* ($\chi^2 = 13.55$, df = 1, $p < 0.001$; Fig. 5A; $\chi^2 = 4.10$, df = 1, $p = 0.043$; Fig. 5B; respectively). Higher values of the two indices reflect more even distributions of pathogen species. In turn, the Simpson index showed that the diversity of taxa was greater in *I. glandulifera* flowers than in *S. lycopersicum* var. *cerasiforme* flowers ($\chi^2 = 11.03$, df = 1, $p = 0.0009$; Fig. 5C); a greater number of taxa in the 1/Simpson analysis indicated a lower diversity of pathogens.

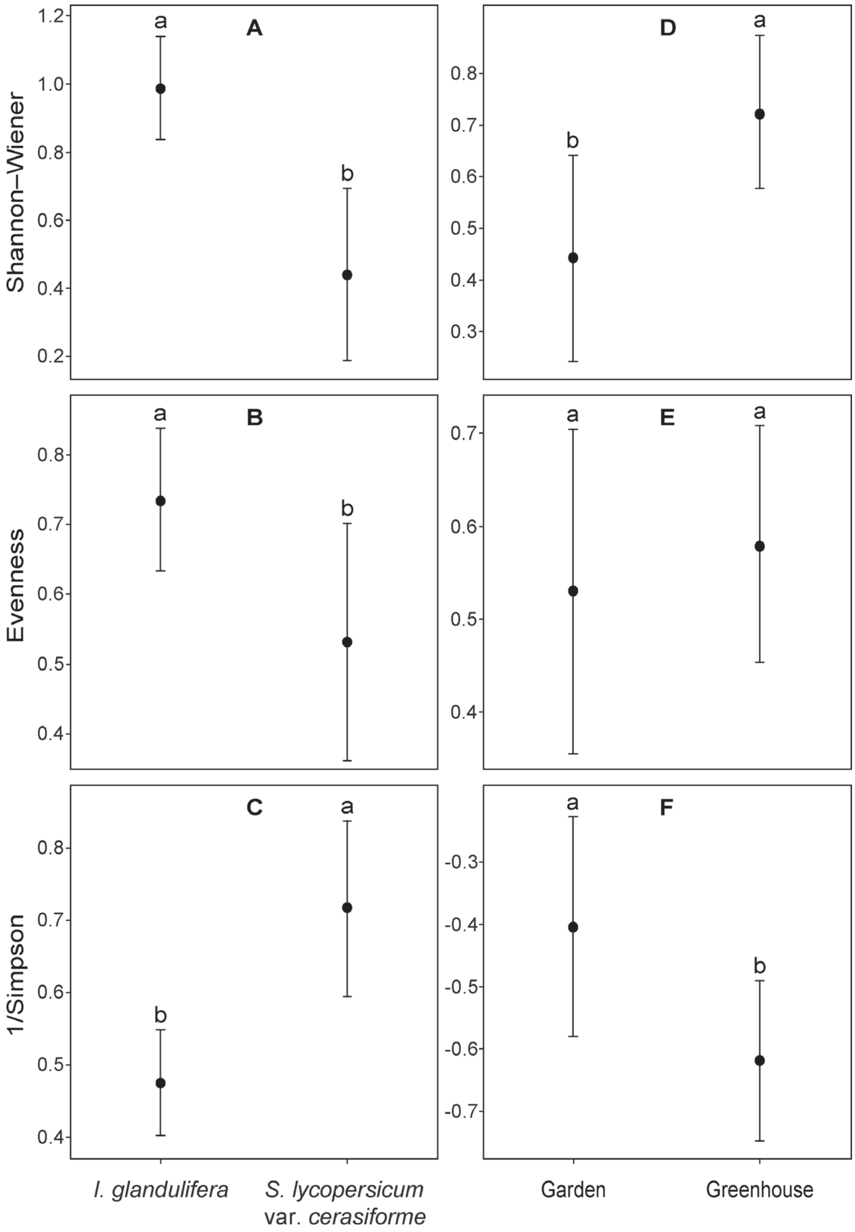

Figure 5. Estimated mean values (± confidence intervals) of the three indices assessing the composition, richness (Shannon–Wiener, Evenness) and diversity (1/Simpson) of the microorganisms recorded from the flowers of the invasive alien species *Impatiens glandulifera* and cultivated *Solanum lycopersicum* var. *cerasiforme*. Comparisons between the two plant species (for each species cultivated under garden conditions) are shown in plots **A–C**. In turn, comparisons between *S. lycopersicum* var. *cerasiforme* cultivated in the garden and in the greenhouse are shown in plots **D–F**. The distributions of the letters above the T-bars indicate differences in the indices between the two plant species/cultivation conditions.

A comparison between the greenhouse and garden tomato flowers was also carried out. In the greenhouse, where the air temperature was higher (Suppl. material 2: fig. S2), the total number of colonies was almost eight times greater than that in the garden (Suppl. material 2: table S6). This dominance was confirmed in the GLMM ($\chi^2 = 5.24$, df = 1, p = 0.022; Suppl. material 2: fig. S5B). This result was driven mainly by the abundant occurrence of the following greenhouse taxa: *A. alternata*, *C. cladosporioides*, *D. dematiicola* and *Penicillium sect. chrysogenum* (Suppl. material 2: table S6). However, abundant colonies of *Aspergillus niger*, *C. herbarum*, *Penicillium commune*, *R. solani*, *S. sclerotiorum*, *Basidiomycota* sp., *Exophiala* sp. and bacteria also played a role (Suppl. material 2: table S6). In turn, the results obtained for the Shannon−Wiener and Evenness indices were not consistent. The result for the former index was significant ($\chi^2 = 5.04$, df = 1, p = 0.02; Fig. 5D), while for the latter, it was non-significant ($\chi^2 = 0.21$, df = 1, p = 0.6; Fig. 5E), which suggests little relevance of the revealed differences in the composition and richness of the taxa. In turn, the Simpson index results were unambiguous, with greater diversity observed for the greenhouse-grown flowers ($\chi^2 = 3.91$, df = 1, p = 0.048; Fig. 5F).

Discussion

Competition for floral visitors and assessment of crop production

The pollination of crops may be negatively influenced by co-occurring alien plant species. To date, this assumption has only rarely been tested (Carvalheiro et al. 2011; Russo et al. 2016; Cunningham-Minnick et al. 2020; Najberek et al. 2021). In the present study, we verified our hypothesis using invasive alien Himalayan balsam (*Impatiens glandulifera*) and a cultivated cherry tomato plant (*Solanum lycopersicum* var. *cerasiforme*). The results showed that the number of insect visits to flowers of tomato significantly decreased when this crop was exposed together with alien balsam. On the other hand, the presence of the crop had no impact on the number of insects visiting the balsam flowers. Thus, insect spill-over from the crop did not enhance the pollination of the alien species. The lower attraction of the crop to pollinators may be due to the fact that *S. lycopersicum* var. *cerasiforme* provides only pollen, whereas *I. glandulifera* offers not only pollen, but also ample amounts of nectar. The most common pollinator species, *Bombus pascuorum*, which visits the flowers of the two species, requires both nectar and pollen to survive. Additionally, in tomato flowers, pollen is locked within the anthers and pollinators must use vibrations to release it ("buzz pollination"; Bowers (1975); Banda and Paxton (1991); Franceschinelli et al. (2013)). Therefore, it is likely that collecting nectar from tomato flowers requires more effort compared to alien species, which may influence the flower choice of pollinators when the two species co-occur.

It should be stressed that the present study was carried out under unique experimental conditions for testing the influence of alien plant species on crop pollination (Najberek et al. 2021). A possible limitation of our study design was that we did not capture the entire community of visiting insects, including visitors active before dawn. There was also some variation in the start and end times of the experiments; thus, we did not have strict control over the differences in the daily phenology of pollen maturation and nectar production, which could bias the obtained results. However, we did not aim to provide absolute numbers of visits of the complete array of floral visitors. The aim of this experiment was to assess the relative differences in visitor assemblages and visit intensities between the two studied plant species under controlled conditions. We included time and weather conditions in our analyses and our experimental design allowed us to reduce the possible confounding effects of multiple additional factors (e.g. the size of the alien species patch or crop field area) or a combination of such factors, which may, in turn, strongly affect the results obtained under field conditions. For example, Carvalheiro et al. (2011) carried out such studies under real-field conditions; half of the flowers within crop fields were alien, while the other half were native. The authors indicated that the alien species had a beneficial effect on crop productivity. However, it cannot be unequivocally estimated whether this result was in fact determined by the alien flora, by the native flora or by combined effects. In turn, in our experiment we excluded the possibility of a confounding effect of native plants by exposing the alien species in combination only with the crop. The two species shared the same floral visitors and occurred in similar numbers. Our study mimics a small-scale cultivation. Similar tests under real-field conditions would provide a complete insight on alien plant-crop interactions mediated by pollinators. The inclusion of reference species, for example, wild-growing native plants, in controlled experimental designs would also be valuable for comparing the luring and co-opting potential of native flora of visitors with those of alien species. Such an approach has not been taken thus far.

The presence of pollinators significantly increases the reproductive success of most wild-growing and cultivated plants (Ollerton et al. 2011). Therefore, alien plants luring and co-opting common pollinators may have a negative impact. In agriculture, pollinator deficiency results in economic losses because the yield and quality of many crops are positively correlated with the availability of pollinators (Stein et al. 2017). This dependence was also revealed for *S. lycopersicum* var. *cerasiforme* (Velthuis and van Doorn 2006). In our tests, the number of insect visits to tomato flowers in the greenhouse was close to zero; as we expected, visitors did not penetrate into the polycarbonate greenhouse used in the experiment. Polycarbonate protects crops from ultraviolet radiation in that it decreases pest and pathogen pressure (e.g. Kittas et al. (2006)). However, ultraviolet radiation also plays a crucial role in the orientation behaviour of bees and bumblebees. The eyes of bees harbour photoreceptors for ultraviolet, green and blue light; hence, a lack of ultraviolet light results in a reduced ability to recognise flowers and the environment (e.g. Blacquière et al. (2006)). Therefore, it can be presumed that floral resources available outside our greenhouse, namely, tomatoes and balsams cultivated in the garden, were much more accessible floral rewards for insects visiting flowers than were greenhouse resources.

In our study, the garden tomatoes were significantly heavier and had a larger surface area than did the greenhouse fruits. In addition, shape, which is an important commercial characteristic, tended to be more circular in gardens. The only parameter that differed between these two groups was the weight of the saleable fruits. The weight of fruits from the garden was even, while in the greenhouse, the share of very light and very heavy fruits was significant. Therefore, the garden tomatoes obtained in our experiments had greater commercial value, as the price of tomato increases with size and when it has a more round shape (Bai and Lindhout 2007).

Other studies reported that the lack of ultraviolet radiation in polycarbonate greenhouses not only protects crops from pests and pathogens, but also increases their quantity and quality (Kittas et al. 2006). In our study, the result was the opposite: in polycarbonate greenhouse, with no ultraviolet radiation, the yields were lower than in the garden. Other studies have also revealed a smaller and more heterogeneous fruit size and irregular shape associated with low pollinator activity (Velthuis and van Doorn 2006). It is, therefore, likely that the close-to-zero intensity of visits to the greenhouse tomato flowers resulted in a lower level of pollination by insects.

Importantly, the obtained results are essential in the context of the main problem explored in this study: the possibility of luring and co-opting insects visiting flowers of tomatoes induced by the attractive invasive alien *I. glandulifera*. Co-occurrence with alien species may produce a similar effect of decreasing numbers of pollinators, as was demonstrated in our polycarbonate greenhouse. Additionally, with climate warming, *I. glandulifera* begins flowering increasingly earlier in the season, potentially disrupting crop pollination for a longer duration. For instance, in 2024 in Zakopane (a mountainous region in southern Poland), the first bloom of this species was observed on 20 June (Najberek, personal observation).

Our results indicate that the eradication of *I. glandulifera* with co-occurring tomatoes should be recommended. This approach would not only be beneficial for farmers, but also comply with regulatory frameworks. The European Union law was tightened to limit the impact of several dozens of invasive alien species, including *I. glandulifera* (European Commission 2017). It should also be stressed that tomatoes are valued worldwide (Anwar et al. 2019) and the invasion of *I. glandulifera* has been recorded in countries with the greatest tomato production (e.g. Netherlands, Russia, United States; Anwar et al. (2019); Helsen et al. (2021)). The results of our experiment may, therefore, have economic significance at the global scale.

Floral chemical attractants

The chemical composition of the floral extracts of the two studied species certainly had an impact on the results of the tests of competition for floral visitors. We found considerable differences between the two plant species, suggesting that they use different strategies to chemically attract the same groups of insects (mainly bumblebees and bees) that visit their flowers.

The predominant aroma compound of the *S. lycopersicum* var. *cerasiforme* fragrance was beta-caryophyllene, a strong universal attractant for many groups of insects, including bees. Moreover, we found that the flowers of *S. lycopersicum* var. *cerasiforme* secreted numerous specific attractants, such as docosane, tricosane, pentacosane, hexacosane, heptacosane, octacosane, nonacosane and derivatives. These compounds are long-chain hydrocarbons and are known to attract *B. pascuorum* and *A. mellifera* (Cahlíková et al. 2004; Ferreira-Caliman et al. 2012) — the most abundant tomato and balsam floral visitors in our study. We also detected the presence of dodecyl (lauryl) acetate, which is an attractant for several bumblebee species (Coppée et al. 2008) and methyl salicylate, a floral attractant for Syrphidae (Rodriguez-Saona et al. 2011), which were found to attract these insects to the tomato flowers in this study.

Although we cultivated *I. glandulifera* in pots under garden conditions, it emitted chemical compounds similar to those of *I. glandulifera* in natural habitats (Jakubska-Busse et al. 2023). *Impatiens glandulifera* produces numerous attractants, based on fatty acids and their esters. Amongst them, acids (linoleic, stearic, palmitic, myristic and lauric) and methyl esters (palmitic acid and methyl linolenate) are well-known attractants for *A. mellifera* and *B. pascuorum* (Le Conte et al. 1990; Cahlíková et al. 2004). Interestingly, in the extracts of *I. glandulifera*, we detected fewer long-chain hydrocarbons (e.g. tricosane, pentacosane, heptacosane and nonacosane) than in the *S. lycopersicum* var. *cerasiforme* extracts. However, some of them (1-pentacosene, 9-nonacosene and squalene) were detected only from the alien balsam. As previously mentioned, long-chain hydrocarbons are well known attractants of *A. mellifera* and *B. pascuorum* (Cahlíková et al. 2004; Ferreira-Caliman et al. 2012). Moreover, alcohols and aldehydes were also identified from *I. glandulifera*. Amongst them, hexadecanal deserves particular attention because it is an attractant for bumblebees (Coppée et al. 2008). Although we did not study all known floral signals that may attract insects (visual, gustatory, tactile or thermal; Raguso (2004); Leonard et al. (2011)), it can be assumed that the attractants secreted by *I. glandulifera* (mainly fatty acids and their esters) are more efficient at attracting insects than the aroma compounds of *S. lycopersicum* var. *cerasiforme* flowers (mainly beta-caryophyllene).

Floral pathogens

We did not find pathogens reported as harmful to pollinators. However, we did record primary pathogens threatening plants. They were more abundant in the flowers of *I. glandulifera* than on tomatoes, albeit the total number of colonies of these pathogens was relatively low (3.6% of all pathogen records in both studied plants). Notably, the low number of primary pathogens could be a result of the abundant co-occurrence of secondary pathogens (e.g. numerous recorded *Alternaria alternata* and *Cladosporium cladosporioides*). These secondary pathogens may even be beneficial to the host plant by reducing infestations by more harmful pathogens (Liggitt et al. 1997). In addition, in our flower attractant analyses, we found that *I. glandulifera* produces two compounds with antifungal activity, 1,4-naphthalenedione 2-hydroxy and 1,4-naphthalenedione 2-methoxy (PubChem 2022). These compounds may be produced in response to infection by the detected pathogens.

Although the recorded primary pathogens probably had only a minor impact on pollinating insects, they may be transmitted to other plant species that share the same pollinators and grow in proximity (Durrer and Schmid-Hempel 1994; Adler et al. 2018). In this study, we identified the primary pathogens of the crops *Botrytis cinerea* and *Fusarium oxysporum*. These species are included in the list of the top ten fungal pathogens identified in molecular plant pathology on the basis of their scientific and economic importance (Dean et al. 2012). *Botrytis cinerea* was found in the flowers of both studied plants, while *F. oxysporum* was found only in the greenhouse tomato plants. Two other *Fusarium* species (*F. avenaceum* and *F. sporotrichioides*) were also detected in the flowers of *I. glandulifera*. *Fusarium* species cause a devastating disease, fusarium head blight (Timmusk et al. 2020). Other primary pathogens that we detected were *Boeremia lycopersici* and *Phoma herbarum*. The former was isolated from tomato samples collected in the garden. This pathogen causes leaf spot disease and ascochyta blight in tomato plants (Horst 2013). *Phoma herbarum*, recorded mainly from *I. glandulifera*, is known to cause leaf spot disease (Thangaraj et al. 2018). We also detected *Rhizoctonia solani* and *Sclerotinia sclerotiorum* in both species. *Rhizoctonia solani* is one of the most common factors that destroy many plant seedlings (Horst 2013), while Sclerotinia stem rot is one of the most devastating diseases in tomato plants (Mazumdar 2021). Thus, if the recorded primary pathogens are transmitted to other neighbouring plant species, the progressive invasion of *I. glandulifera* may play a role as a hub in pathogen transmission between plants. Such new hosts may include *S. lycopersicum* var. *cerasiforme*, as we found that insects visited flowers of both studied species interchangeably. Nevertheless, further studies are needed to confirm our supposition.

We also recorded biofilm organisms and mycoparasitic fungi that increase the resistance of plants to primary pathogens. The former group comprises numerous recorded bacteria, yeasts and fungi (e.g. *Exophiala* species, *Epicoccum nigrum* and *Aureobasidium pullulans*), while the latter includes rarely recorded *Trichoderma* species. Importantly, more than 80% of the biofilm organisms were detected on the flowers of *I. glandulifera*. It can, therefore, be assumed that the flowers of this alien species are more resistant to primary pathogens than those of *S. lycopersicum* var. *cerasiforme* and that this factor contributes to the extraordinary ability of *I. glandulifera* to attract insects visiting flowers and to its invasion ability in general.

Conclusions

We demonstrated the negative influence of the invasive alien species *Impatiens glandulifera* on the intensity of insect visits to flowers of cherry tomato (*Solanum lycopersicum* var. *cerasiforme*), which aligns to our earlier findings on the adverse effects of alien balsam invasions on the pollination of strawberry plants (*Fragaria ×ananassa*; Najberek et al. (2021)). In both crop species, the yield and fruit quality increase with the availability of pollinators (Velthuis and van Doorn 2006; Dimou et al. 2008). Therefore, pollinator shortage due to competition with this alien species has a negative impact on crop production. Although we found no pathogen species known to infect pollinators, we recorded pathogens that may pose serious threats to crops (primarily *Botrytis cinerea* and *Fusarium oxysporum*). These pathogens may be transmitted between flowers of co-occurring alien and crop plants by visiting insects (Durrer and Schmid-Hempel 1994). The European Union has tightened the law to limit new introductions and spread of *I. glandulifera* (European Commission 2017). The level of control of this species is still insufficient in Poland. Our study indicates that efforts to control this alien plant species should be intensified near crops which require insect pollinators.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Research idea: KN; study design: KN, AJ-B, KP, IC, WS, MH; surveys and insect identification: KN; microbiological analyses: KP, AK-P; flower attractant analyses: AJ-B, IC, MH; statistical analyses: KN; writing - original draft preparation: KN, AJ-B, IC; writing - review and editing: KN, WS, AJ-B, IC, KP; funding acquisition: KN, AJ-B, IC, KP, WS.

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Data availability

The raw data used to perform the statistical analyses are provided in the Suppl. material 1.

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Supplementary material 1

Raw data used to perform statistical analyses

Authors: Kamil Najberek, Katarzyna Patejuk, Izabela Czeluśniak, Wojciech Solarz, Marek Hojniak, Agata Kaczmarek-Pieńczewska, Anna Jakubska-Busse

Data type: xls

Explanation note: The file includes raw data on recorded floral visitors and fungal pathogens (number of colonies and composition).

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.95.134168.suppl1

Supplementary material 2

Experiment on invasive alien species *Impatiens glandulifera*, cultivated species *Solanum lycopersicum* var. *cerasiforme*, insect visitors of their flowers and floral pathogens

Authors: Kamil Najberek, Katarzyna Patejuk, Izabela Czeluśniak, Wojciech Solarz, Marek Hojniak, Agata Kaczmarek-Pieńczewska, Anna Jakubska-Busse

Data type: pdf

Explanation note: Supporting tables contain data on stem height of the surveyed plants and data on size/shape of their fruits. In addition, details of model selection in statistical analysis are also provided. Supporting figures include data on tomato cultivation and cherry tomato fruits. Weather conditions recorded during the study are also presented, as well as the culture of fungal pathogens from *Impatiens glandulifera* flowers.

Link: https://doi.org/10.3897/neobiota.95.134168.suppl2