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RESEARCH ARTICLE

The golden threat—*Solidago* invasion alters native plant–pollinator interactions by vegetative crowding

Marie Charlotte Grange[1] | François Munoz[1,2] | Marco Moretti[3] | Sylvain Varona-Y-Varona[1] | Julien Renaud[1] | Marie-Pascale Colace[1] | Maya Guéguen[1] | Axel Ssymank[4] | Laure Gallien[1]

[1]Laboratoire d'Ecologie Alpine, UMR 5553 CNRS—Univ. Grenoble Alpes, Grenoble, France

[2]Laboratoire Interdisciplinaire de Physique, UMR 5588 CNRS—Univ. Grenoble Alpes, Grenoble, France

[3]Biodiversity and Conservation Biology, Swiss Federal Research Institute WSL, Birmensdorf-Zurich, Switzerland

[4]Bundesamt für Naturschutz, Bonn, Germany

Correspondence
Laure Gallien
Email: laure.gallien@univ-grenoble-alpes.fr

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Abstract

1. Pollination, a vital biological process, faces potential disruption from invading alien plants. Here, we investigate whether the abundance of an invader enhances or hinders native plants' pollination success. Using a functional trait-based approach, we examine how floral traits and pollinator behaviour mediate the effects of a major invader of Eurasian wetlands (*Solidago canadensis* L.) on native pollination.
2. To study the impacts of our invader, we conducted plant–pollinator surveys along a gradient of invasion for an entire flowering season (720 transects in total), in a protected wetland of the French Alps. We then used structural equation models to (i) determine whether the impacts of *S. canadensis* on the pollination of native plants depend on their floral traits and (ii) whether these impacts are due to changes in insect behaviour, the insect species pool and/or the plant species pool. We specifically distinguished the effect of vegetative density from that of floral density of *S. canadensis*.
3. Our findings reveal cumulative effects of the invader on three main components of native plant pollination success: altered flower production, insect visits and insect fidelity. All these effects tend to benefit native plants with flowers similar to those of *Solidago* and to cost plants with flowers that are dissimilar. Unexpectedly, the vegetative density of *Solidago*, rather than its floral density, primarily drives these differences in impact between flower types.
4. *Synthesis*. Our results highlight the importance of 3D vegetation structure in pollinator foraging choices and advocate for its incorporation into the sampling design of pollination studies.

KEYWORDS
facilitation, flower morphotype, foraging behaviour, indirect effects, invasive plant, plant-insect interactions, pollination success, pollinator competition, structural equation models

1 | INTRODUCTION

Pollination, a vital biological process, faces potential disruption due to invasions by alien plants. Most flowering plants depend on insect pollination (87.5% of angiosperms, Ollerton et al., 2011), and a wide variety of insects feed on nectar and pollen produced by plants. Since invasive plants often originate from ornamental or horticultural introductions (about 80% in Europe; Arianoutsou et al., 2021), many of them produce showy flowers that are particularly attractive to local pollinators (Morales & Traveset, 2009). This makes invasive plant species particularly good competitors regarding pollination. Despite the pivotal role of plant–pollinator networks in terrestrial biodiversity, we still know little about how invasive plants modify native plant–pollinator interactions (Mitchell et al., 2009).

In the context of biodiversity preservation, an open question is whether the presence of invasive plants favours or hampers the pollination of native plants (Bjerknes et al., 2007; Morales & Traveset, 2009). Initially, invasive plants were thought to have negative effects on the reproduction of native plants due to competition for resources and/or pollinators, especially when the invaders are abundant (Bartomeus et al., 2008; Bjerknes et al., 2007; Dietzsch et al., 2011; Morales & Traveset, 2009). Recent studies show more ambiguous results, suggesting that invader effects can also be beneficial for some native species, for instance if they increase attraction to the site ('magnet effect') or modify insect preferences for their flower type (Iler & Goodell, 2014; Parra-Tabla & Arceo-Gómez, 2021). Yet the nature of the impacts (negative or positive) of invaders on the pollination of native plants, and their underlying mechanisms remain largely unknown.

The nature and mechanisms of invaders' impact on the pollination of native plants can vary from species to species. The pollination success of a plant species corresponds to the successful fertilization of its ovules and is thus tightly linked to three main elements: (i) flower production, (ii) the number of insect visits per flower ('visitation rate') and (iii) the fidelity of the visiting insects ('fidelity received') (Figure 1b; Mitchell et al., 2009; Morales & Traveset, 2008; Parra et al., 2022). Invaders can thus reduce (or improve) native plant pollination success if they decrease (or increase) these factors. Flower production of a focal native species can decrease if the invader competes for resources with the species, or increase if the invader facilitates the species (e.g. by outcompeting a local dominant; Rodriguez, 2006). The visitation rate and the fidelity of the visiting insects on a focal native flower can decrease or increase if the presence of the invader modifies (i) the insect behaviour or the network composition by (ii) selecting for insect species with different preferences (change in insect species pool) or by (iii) selecting for plant species with different levels of attractiveness (change

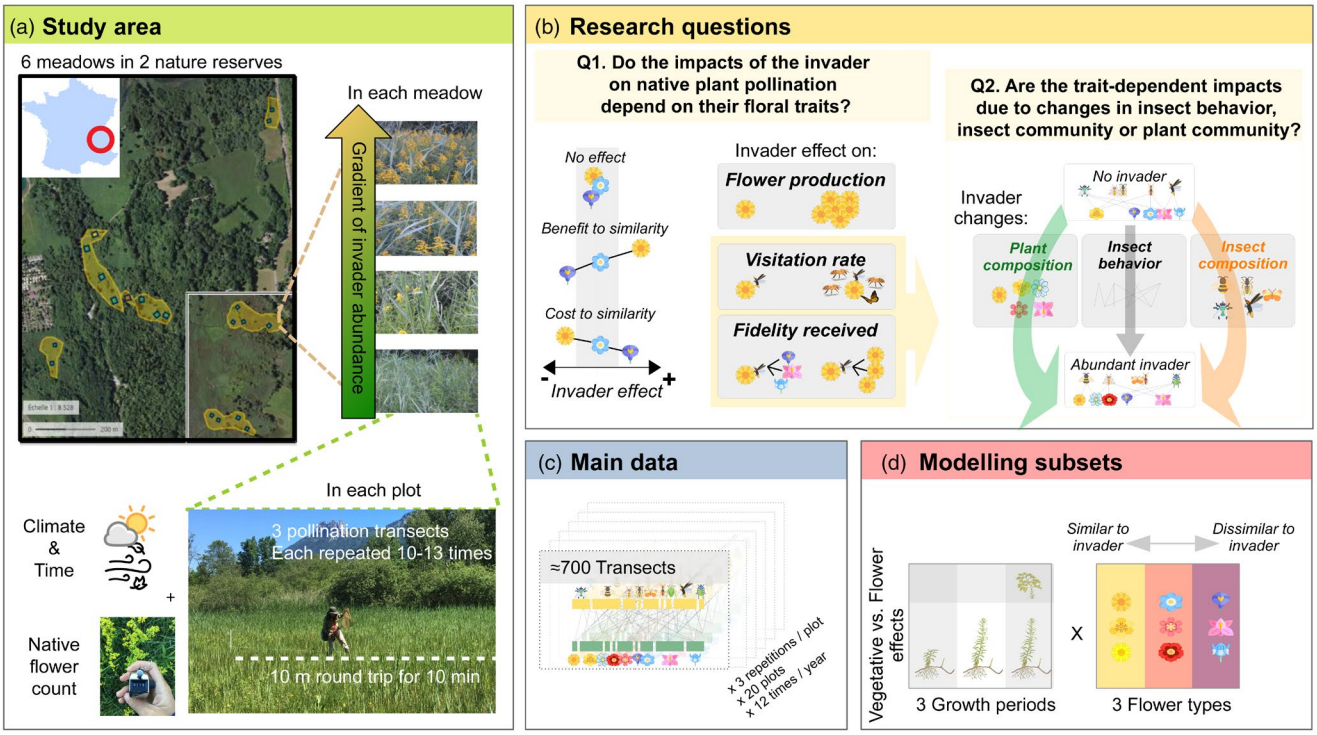

FIGURE 1 Study area and research questions overview. (a) The study area comprises six wet meadows and a total of 20 plots located in two nearby French Alps nature reserves. (b) The study system addresses two main research questions on (Q1) the nature and (Q2) the mechanisms of *Solidago* impacts on native plant pollination (all flower and insect icons represent native species). (c) To answer them, we conducted 720 transects settled across 20 plots spread along a gradient of *Solidago* density, with each plot being resampled 10–13 times (with three replicates per plot per sampling time). (d) These data allowed us to build a series of models that can account for three growth periods of *Solidago* ('Growing', 'Dominance', 'Flowering') and for three native species morphotypes (ranging from native flowers similar to that of *Solidago*, to flowers dissimilar to *Solidago*; details in section *Solidago developmental stages and native plant morphotypes*).

in plant species pool). For instance, invaders can modify insect behaviour if their showy flowers attract most of the pollinators that usually visit the co-occurring native species (Waters et al., 2020). Indeed, greater competition for pollinators, leads to lower visitation rates and lower fidelity received by the native plants, which represent a cost due to the dilution of pollen on the insects' bodies (Albrecht et al., 2016; Baskett et al., 2011; Thijs et al., 2012). Invaders can also modify the insect species pool if their flowers attract new insect species to prospect on the site and repel others, thereby changing the probability for co-occurring native plants to be visited (Albrecht et al., 2016; Fenesi et al., 2015; Moroń et al., 2019; Sun et al., 2013). Invaders can also alter pollination by modifying the native plant community composition (i.e. the resources available for pollinators; Flacher et al., 2020; Sampson & Cane, 1999). Some of these effects are not necessarily dependent on the attractiveness of invader flowers, as by modifying the vegetation spatial structure invaders can also influence flower detection and visitation by insects (McKinney & Goodell, 2010). For instance, a tall and leafy invader can hide the flowers of short native plants from pollinators and favour some insect predators, thereby concentrating pollinators on the flowers of tall native plants.

A functional approach is now needed to understand which native species see their pollination success increase or decrease in the presence of invaders and by what mechanism. In the context of pollination, the simplest approach is to test whether one invasive plant has beneficial and/or detrimental effects on different native plants depending on the similarity of their floral traits (Waser, 1983). Natives with similar floral morphologies as the invaders may benefit (e.g. magnet effect) or suffer (e.g. competition for pollinators) more than natives with dissimilar flowers. Corolla colour and flower symmetry (radial vs. bilateral) are two of the most important morphological traits that allow pollinators to discriminate among flowers (inflorescence shape, flower scent and nutritional reward are likely important but difficult to measure; Hemingway et al., 2024; Menzel & Shmida, 1993; Neal et al., 1998; Pioltelli et al., 2024). It is thus important to evaluate how the similarity in floral traits between alien and native co-flowering species influences the impact of the alien on native pollination. Additionally, as invaders can alter pollination independently of their flower morphology (e.g. by modifying the native plant community composition and altering the vegetation spatial structure), it seems important to disentangle their vegetative versus floral effects. To do so, one should not only consider the period of bloom of the invader, but also the period before bloom, when the invader is tall and dense, but not in flower.

Here we focus on a major invader in Europe (*Solidago canadensis* L.) and determine whether it has positive or negative effects on native plant pollination, the mechanisms underlying these effects and whether they vary with invader-native floral similarity. To do so, we use plant–pollinator surveys along a gradient of invasion by *S. canadensis* in a protected wetland, resampled during a whole flowering season (720 transects in total). Our study area has the benefit of hosting both pristine and invaded patches in virtually identical local environmental conditions prior to the invasion, which allows us to quantify the effects of the invader on the system (rather than the factors that led to its establishment). The repeated surveys across the whole flowering season also allow us to disentangle the effects of the invader due to its vegetative versus flower parts. With these advantages at hand, we focus on two key questions: (Q1) Do the impacts of *S. canadensis* on native plant pollination depend on their floral traits? (Q2) Are the trait-dependent impacts of *S. canadensis* driven by a change in insect behaviour, insect species pool and/or plant species pool?

2 | MATERIALS AND METHODS

2.1 | Study system

Solidago canadensis (L., 1753; hereafter *Solidago*) is a rhizomatous Asteraceae from North America that was introduced to Europe as an ornamental species in the 17th–18th century. It is one of the most invasive plants in Eurasian wetlands, where it forms tall and dense patches (ca. 2 m high). *Solidago* competes with native plants for resources (Grange et al., 2023) and may further impact pollinators by producing abundant, nectar- and pollen-rich flowers (late bloom between mid-July and early fall; Fenesi et al., 2015; Moroń et al., 2019).

Our study sites cover six nearby wet meadows in a protected area of the French Alps (Figure 1a; Fieldwork permits n°DDT-2019-430 delivered by *Le préfet de la Haute-Savoie*). All meadows have a homogeneous vegetation and management regime (late mowing with export), and each contains multiple patches of *Solidago* at different densities (from 0 to 117 stems/m^2). To study plant–pollinator interactions, we selected a total of 20 homogeneous 'plots' (10 m × 10 m) along a gradient of *Solidago* densities (density estimated as the number of shoots per m^2, quantified in each plot by 12 randomly placed quadrats of 0.5 m × 0.5 m).

2.2 | Plant–pollinator sampling

To quantify and understand the impacts of *Solidago* on native plant pollination, we estimated plant–pollinator interactions in each plot. To do so, we performed standardized transects along which we sampled insects visiting native flowers, and quantified the local biotic and abiotic conditions that may also influence pollination (native flower pool, meteorology).

In each 10 m × 10 m plot, we set 3 permanent transects (10 m-long each). Each transect was sampled 10–13 times from mid-May to mid-August (pre-mowing). Within each plot, all three transects were sampled simultaneously by three observers. All plots in a meadow were sampled within a half-day session, with session order randomized (720 transects in total; Figure 1c; Data S1 and Grange et al., 2021). We sampled only under meteorological conditions favourable for insects to flight (temperature >15°C, wind <13 km/h, cloud coverage <70%). Sampling a transect consisted of making a single round trip along a 10 m line for 10 min, observing up to 1 m on each side of the line, capturing all insects seen in contact with the stamens of entomophilous plants using a net (or directly using

a sampling vial for species with dropping or death feigning strategies; timing interrupted during capture, after Gibson et al., 2012) and recording the identity of the plant species visited (see Grange et al., 2021). We captured all insects, except for the easily identifiable *Apis mellifera*, regardless of their taxonomic group, as the importance of non-Apidae and non-Syrphidae taxa in pollination is increasingly recognized (Orford et al., 2015; Ssymank et al., 2008). Captured insects were identified to the species by expert entomologists for most of hymenoptera and diptera (see *Acknowledgements*), or morphospecies level (non-lethal identification methods remain to be developed for such a wide range of taxa; Lövei & Ferrante, 2024; van Klink et al., 2022).

Before walking each transect we estimated the number of open inflorescences of each native entomophilous plant species, to quantify species floral cover per transect (number of open inflorescences × average surface area of an inflorescence). We also recorded the local abiotic conditions influencing pollination: date, hour (corrected for variations in day length and centred on 12:00), temperature, wind speed and cloud cover (in % of covered sky).

As we captured all the insects for identification, we were unable to follow the sequences of their visit from flower to flower. Therefore, to estimate the general properties of the plant–pollinator network in the study area, we built a meta-network that contains all plant–pollinator interactions recorded in all transects. This meta-network will be used to estimate several indices representing average insect preferences and flower attractiveness in the study area (see below).

2.3 | *Solidago* developmental stages and native plant morphotypes

This study aimed to disentangle the effects of *Solidago* on native vegetation via its vegetative versus floral structures and to assess whether these effects depend on native species' floral similarity to *Solidago*. To do so, we divided the sampling season into three time periods corresponding to characteristic growth stages of *Solidago*: (i) the *growing phase* when its height is inferior or equal to the native vegetation (mid-May to end of June; 303 transects), (ii) the *vegetative dominance phase* when it accumulates vegetative biomass and reaches its maximum height (from July 1st to its first open flower on the meadow; 276 transects) and (iii) the *flowering phase* (from the first flowering event until mowing in mid-August, i.e. the first ca. 3 weeks of the *Solidago* flowering season which usually ends in late September in our study area; 141 transects).

Additionally, we estimated the similarity between the native species and the invader based on their flower colour and symmetry (radial vs. bilateral; Data S2), and created three flower morphotypes: (i) yellow & radial (similar to *Solidago*), (ii) not-yellow & radial (partially dissimilar to *Solidago*) or (iii) not-yellow & not-radial (completely dissimilar to *Solidago*). We could not use the fourth morphotype (yellow & not-radial flowers) as it was borne by seven native species with too few occurrences in the transects to reliably parameterize models.

2.4 | Statistical analyses of the impacts of *S. Canadensis* on the pollination of native plant, depending on their floral traits (Q1)

We assessed the impact of the invader on the pollination success of each flower morpho-group in two steps. First, we measured three components of pollination success: flower production, visitation rate and visiting insect fidelity. Second, we quantified the relative importance of direct and indirect effects of the invader on these components of pollination success with structural equation models (SEM; Lefcheck, 2016; Shipley, 2000).

2.4.1 | Components of pollination success

Three components of pollination success were estimated per plant species and transect. (i) Flower production was measured as the number of open floral units on the transect. (ii) Visitation rate—an indicator of the total amount of pollen received (de Santiago-Hernández et al., 2019)—was measured as the number of visits received per floral unit. (iii) The fidelity of the insects visiting a flower (from the plant species perspective), called '*fidelity received*'—an indicator of the proportion of conspecific pollen received—was defined as the average fidelity of insects that visit a floral unit of the focal species, given the floral composition of the transect. As we could not track insects during their foraging sequences, we estimated the fidelity received by a focal plant species as the proportion of interactions that an insect species could have with the focal plant, expected from the meta-network subsampled to represent the floral composition of the transect, averaged over all insects visiting the focal plant on the transect and weighted by their number of visits. The fidelity received index ranges from 0 to 1 and represents the probability of an insect visiting the flower species to have previously visited another flower of the same species in the transect (and thus to carry conspecific pollen). To ensure that the effects of *Solidago* were not confounded with the effects of intrinsic differences between native plants in terms of maximum abundance and attractiveness, each index was rescaled between 0 and 1 for each plant species (at the scale of the whole dataset). Note that these indicators are only indirect measures of pollination success, as we did not directly measure pollen deposition, pollen germination, pollen tube growth and ovule fertilization for each native plant of each transect.

2.4.2 | Statistical model

We used piecewise SEMs to examine the effects of *Solidago* density on our three indicators of pollination success, considering separately each developmental stage of *Solidago* and each native floral morphotype (i.e. 3 stages × 3 morphotypes = 9 models, Figure 1d; details in Data S4). Each model had the same structure, where we hypothesized that native pollination success can be directly influenced by *Solidago* density (via vegetative cover and/or flower abundance) or

indirectly by *Solidago*-mediated changes in native floral context (native richness and total flower cover). We also hypothesized that the temporal and meteorological contexts of the observations could influence native and invasive flower abundances, as well as plant–pollinator interactions (CaraDonna et al., 2017; Grange et al., 2021) and integrated them in the model structure (Figure 2a).

We included plant species with at least two observed interactions at different densities of *Solidago* within the same meadow and at least 10 visits in the meta-network. In the 9 models (Figure 2b), the number of observations in the models varied between 63 and 536 (mean = 238), depending on the number of flowering species in each transect considered (which changed across morphotypes and *Solidago* developmental stages).

Each SEM followed a three-step fitting process. Step 1, define the model initial structure following our ecological hypotheses (Figure 2a), and identify a list of *authorized* causal links that could be added to the initial structure (those that make sense biologically but that we did not expect to be important a priori). Step 2, estimate the initial models with the data. Step 3, simplify and improve the models until stabilization of the selected variables (details in Figure S4).

In each model, we quantified both direct and indirect effects of *Solidago* on: flower production, visitation rate and fidelity received (i.e. the response variables of the models; see details in the previous section *Components of pollination success*). A direct effect was measured as the standardized effect size of the corresponding direct link in the model. The indirect effects were calculated as the sum of the effects of all indirect paths between *Solidago* density and the focal response variable in the model (the effect of an indirect path being the product of all standardized estimates on that path).

2.5 | Statistical analyses to determine whether the impacts of *S. Canadensis* are driven by changes in the insect species pool, insect preference or plant species pool (Q2)

Solidago may influence the interactions between pollinators and each flower morphotype through three non-exclusive mechanisms. It can change (i) the community of insects attracted to the plot (e.g. attracting species feeding on yellow & radial flowers), (ii) the behaviour of the pollinators on the plot (e.g. increasing visitation and fidelity of insects on yellow & radial flowers) and/or (iii) the floral resources available (e.g. favouring the most attractive yellow & radial flowers). To disentangle these three mechanisms, we propose

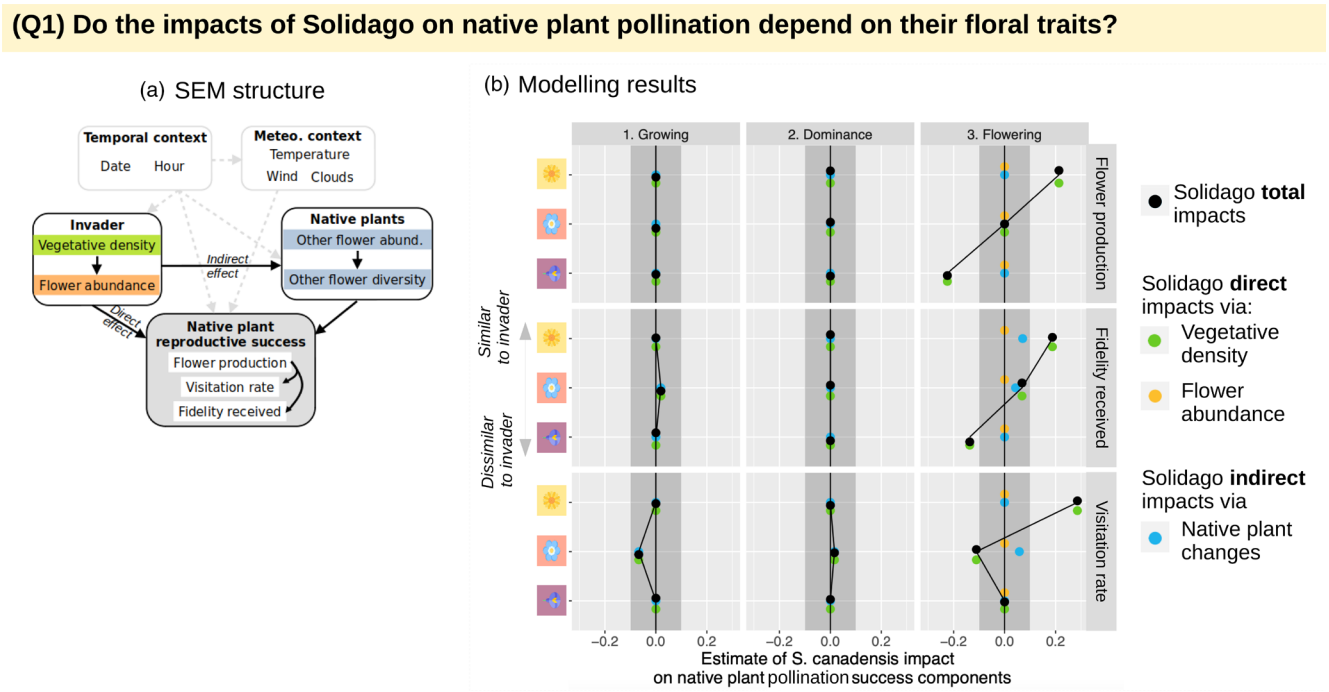

FIGURE 2 *Solidago* direct and indirect effects on the pollination success of native plants. (a) The structural equation models (SEMs) used followed the same general structure and were applied over nine modalities: 3 time periods × 3 native morphotypes. All explanatory variables retained in the final model had a significant effect on the response variables (p-value <0.05; see Data S4 for details on the selection procedure). (b) The results of each model show the standardized effect size of *Solidago* on the three pollination success components: Native flower production (top row), fidelity received (middle row) and visitation rates (bottom row), while separating direct effects via its own vegetative density (green dots) and flower density (orange dots), from indirect effects via modifications of the native plant composition (blue dots). The overall effect of *Solidago* is indicated with black dots; the black lines connecting these total effects are simply there to make the results easier to read. The vertical black line at zero indicates null effect, and the vertical grey bands represent areas of non-significant deviation from the null effects. Standardized effect sizes can be interpreted directly in terms of the average change in the response variable (e.g. if *Solidago* has an estimated total effect on flower production of 0.2, this means that its presence at highest abundance increases flower production by 20%).

a method based on new indices and SEMs. The idea is simply to calculate for each transect (i) the *mean observed insect preference* for a flower morphotype and then test with a SEM whether increasing *Solidago* density has a direct effect on this observed preference (i.e. change in insect behaviour) or whether the effect is indirect and mediated via modification of (ii) the insect species pool (measured, for the same flower morphotype, as the *mean insect preference expected from the observed insect species composition*) and/or (iii) the plant species pool (measured, for the same flower morphotype, as the *mean flower attractiveness expected from the observed plant species composition*; see Box 1 for details).

2.5.1 | Statistical model

We built one piecewise SEM for each of the three developmental stages of *Solidago* (in contrast to Q1, here the insect preference indices for each native morphotype are fitted simultaneously in the SEMs, as they are not entirely independent of each other). Each model had the same general structure as in Q1, including the temporal and meteorological covariates, and possible direct and indirect effects of *Solidago* on each insect preference index (Figure 3a). Note that indirect *Solidago* effects via changes in the local native plant context (total cover and richness) could only affect the observed insect preference (as expected preferences are related to meta-network properties). This SEM structure could be used to determine whether increasing *Solidago* density impacts the observed insect preference for each morphotype, and if it is due to (i) a direct change in insect behaviour (i.e. direct path) or (ii) an indirect effect via modification of the insect species pool (i.e. indirect path via expected insect preference) or (iii) an indirect effect via modification of the plant species pool (i.e. indirect path via expected flower attractiveness). We followed the same methodology as for Q1 to optimize each SEM and to quantify all direct and indirect effects of *Solidago* (Data S4).

All statistical analyses were performed using the software R (R Core Team, 2024) and the packages: *piecewiseSEM* (Lefcheck, 2016), *lme4* (Bates et al., 2015) and *MuMIn* (Bartoń, 2023).

3 | RESULTS

We recorded a total of 9679 plant–pollinator interactions across 720 transects: 1610 during the growing phase, 967 during the dominance phase and 7102 during the flowering phase of *Solidago*. These interactions involved 91 native plant species, mainly Apiaceae (29%), Lamiaceae (28%) and Asteraceae (23%). The pollinators comprised 373 insect taxa (256 species, 117 morphospecies; Table S3.1; Figure S7.2) in the Hymenoptera (31% honeybees, 19% wild Hymenoptera), Diptera (22%), Coleoptera (19%) and Hemiptera orders (9%).

BOX 1 Indices of insect preference and flower attractivity.

We propose three indices of insect preference and flower attractivity that can be estimated for a given flower morphotype in one transect (see illustration in Data S5).

- The *mean observed insect preference* is the observed preference of an insect species for the focal floral morphotype in a transect (observed preference of an insect species = proportion of its visits observed on the focal morphotype, minus the prevalence of the morphotype in the transect), averaged across all insect species recorded in this transect (weighted by their relative abundances). It varies between 1 and −1, where a value of 1 indicates a very strong preference for the focal morphotype given its abundance, 0 indicates the expected preference of a perfect generalist species (preference perfectly matches the abundance of the morphotype), and −1 indicates a very strong avoidance of the focal morphotype. It depends on the attractiveness of the flowers present on the transect, the a priori preferences of the insects prospecting on the transect and the local variations of their behaviour.
- *Mean insect preference expected from the observed insect species composition* is calculated as the expected preference of an insect species for a focal morphotype in the transect given the meta-network (expected preference of an insect species = proportion interactions with the focal morphotype in the meta-network), and averaged across all insect species recorded in this transect (weighted by their relative abundances). It varies between 0 and 1, where values going towards 0 indicate that the insects are not observed interacting with the focal morphotype in the study area, and values tending towards 1 indicate that the insects observed are preferentially feeding on the focal morphotype in the study area.
- *Mean flower attractiveness expected from the observed plant species composition* is calculated as the expected preference—for a focal morphotype—of an insect of the transect given the observed local floral composition and the meta-network (expected attractiveness of a plant species = proportion interactions that occur with the plant species in the meta-network), and averaged across all plant species recorded in this transect (weighted by their relative abundances). This index represents the potential attractiveness of each morphotype in the floral patch (independently from the insect identity). It varies between 0 and 1, where values tending towards 0 indicate that the flowers observed are usually not visited in the study area, and values tending towards 1 indicate that the flowers are very attractive in the study area.

3.1 | (Q1) *Solidago* favours the pollination of similar native species and reduces that of dissimilar species

Model results indicate that *Solidago* density has a significant positive effect on all three components of pollination success for native plants with similar flowers (yellow and radial symmetry). On average these plants produce more flowers (+21%), which attract more insects (+19%), and these insects are more loyal to the species (+29%). For native plants whose flowers are partly similar to those of the *Solidago*, there is only a moderate decrease (−11%) in pollinator fidelity. For native plants whose flowers are fully dissimilar (not-yellow and not-radial), *Solidago* has a significant negative effect on two components of pollination success. On average, these native plants produce fewer flowers (−23%) and the insects that visit them are less loyal (−14%). These effects of invader density are only visible during the flowering phase of *Solidago* and are mainly determined by its vegetative density (stems per m^2). In fact, neither the flower density of *Solidago* (the effect flower abundance being calculated independently of vegetative density), nor the indirect effects via changes in the native plant community have a significant effect on pollination success (Figure 2b). Results for each insect group follow a similar pattern, though with high variability between groups (Figure S6.1). All final model structures were valid (p-value of the Fisher C test >0.05) and included only explanatory variables with significant effects on the response variables (p-value <0.05 for each predictor) and the proportion of the variables of interest explained by the models during *Solidago* flowering phase ranged from 3% (e.g. for the models of the 'Growing' and 'Dominance' periods) to 63% (mean $R^2 = 0.26$).

3.2 | (Q2) *Solidago* impacts are mostly due to changes in insect behaviours, not changes in network composition

The models indicate that (i) higher *Solidago* vegetative density increases insect preference for native plants with similar flowers (yellow and with radial symmetry), whereas (ii) at a given vegetative density, further increasing *Solidago* flower abundance has the opposite (negative) effect on insect preference for these native plants. (iii) Both effects occur only during *Solidago*'s flowering period and (iv) are primarily driven by direct changes in insect behaviour

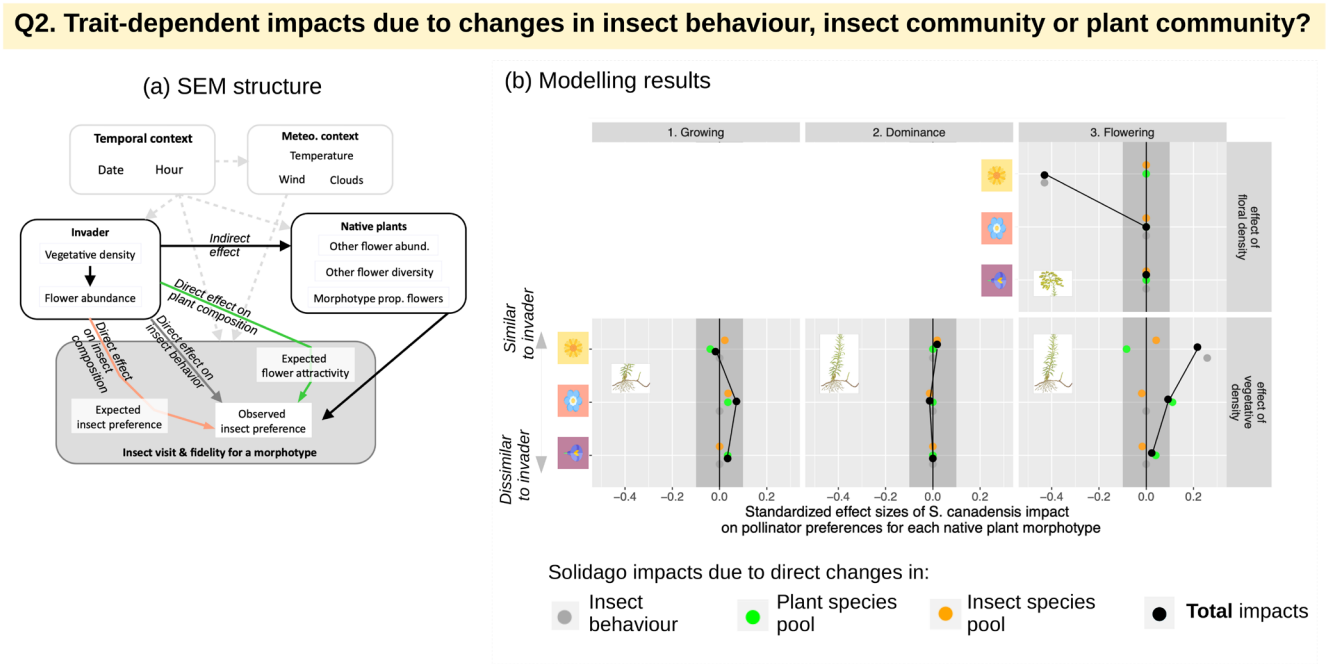

FIGURE 3 *Solidago* effects on insect preferences for each native flower morphotype. (a) The structural equation models (SEMs) used followed the same general structure and were declined over nine modalities: 3 time periods × 3 native morphotypes. All explanatory variables retained in the final model had a significant effect on the response variables (p-value <0.05; see Data S4 for details on the selection procedure). (b) The results of each model shows the standardized effect size of *Solidago* on insect preferences for each morphotype. The total effect of *Solidago* (black dots) can be decomposed into three different mechanisms: Impacts due to the modification of insect behaviours (grey dots), impacts due to modification of the insect species pool prospecting on the site (orange dots) and impacts due to modifications of the plant species pool present in the site (green dots). The effects of *Solidago* can also be separated according to the abundance of its stems versus the abundance of its flowers (bottom vs. top row). The sum of *Solidago*'s effects is indicated by black dots; the black lines connecting these total effects are simply shown for greater readability. The vertical black line at zero indicates null effect, and the vertical grey bands represent areas of non-significant deviation from the null effects. Standardized effect sizes can be interpreted directly in terms of the average change in the response variable (e.g. if *Solidago* has an estimated total effect on insect preference of 0.2, this means that its presence at highest abundance increases insect preference for the native morphotype by 20%).

rather than shifts in plant or insect community composition (indirect *Solidago* effects; Figure 3b).

All model final structures were statistically valid (Fisher's *C* test, *p*-value >0.05) and included only explanatory variables with significant effects on the response variables (*p*-value <0.05 for each predictor). The models explained 2% to 62% of the variance in the variable of interest (mean $R^2 = 0.28$). Results by insect group tend to follow the same pattern, but with high variability between groups (Figure S6.1).

4 | DISCUSSION

Overall our results suggest that native plants whose flowers are similar to those of the invader gain pollination success with the invasion, while dissimilar natives lose in pollination success. These effects appear to be primarily due to changes in insect foraging behaviour (rather than changes in the insect or plant community composition) and in response to the density of *Solidago* vegetative parts (rather than its flowers) at the end of the growing season.

4.1 | Pollination: Floral similarity with the invader benefits the natives, dissimilarity costs them

Our results suggest that *Solidago's* effects on pollination can be positive or negative depending on the native flower morphotype. The invasion of *Solidago* favours the pollination of native plants with flowers similar to its own. These native plants tend to produce more flowers, these flowers are more often visited, and the insects that visit them are more likely to carry pollen of the same species. Conversely, *Solidago* invasion decreases several components of the pollination success of native plants with dissimilar flowers. The magnitude of this impact increases with this dissimilarity: partially dissimilar flowers only experience a slight decrease in visitation rate, while fully dissimilar flowers experience a decrease in both flower abundance and in the proportion of conspecific pollen they can receive (i.e. increased pollen competition).

These results confirm that *Solidago* competes with some native plants (e.g. lower flower production for dissimilar natives), but that it also facilitates others (e.g. higher flower productions for similar natives). *Solidago* can compete with certain native plants for soil nutrient, light interception and/or pollinators (Grange et al., 2023; Zhu et al., 2022). However, it can also facilitate other native species by attracting new pollinators or by regulating the abundance of otherwise dominant native species. These competitive and facilitative interactions can typically influence flower production on the transect by affecting population sizes (number of individuals) and/or by modifying individual investment in sexual reproduction (e.g. favouring or not flower production vs. clonal growth when possible).

Interestingly, the trait-dependent impacts of the invader are essentially driven by its vegetative parts, at the end of the growing season when the invader biomass is at its maximum. This suggests that, in our study system and for our indicators of pollination success (visitation rate and fidelity received), the colourful and fragrant *Solidago* flowers do not disturb the general floral offer enough to be detected as a significant insect attractor or pollinator monopolizer (the same models built with only *Solidago* flower abundances do not find significant results either). The importance of *Solidago* vegetative parts on pollination now represents an additional underlying mechanism.

4.2 | Mechanisms of impacts: The invader changes insect behaviours, not species pools

Our results suggest that the invasion of *Solidago* modifies the preference of foraging insects for native plants with flowers similar to those of the invader, but only during its flowering period. As the density of the invader increases, the insects prospecting on the site change their behaviour to visit more often native flowers similar to *Solidago*. However, if we consider a given vegetative density of *Solidago*, the more *Solidago* flowers there are, the less the insects are visiting yellow-symmetric flowers compared to the other morphotypes (i.e. yellow-symmetric flowers are less visited than expected given their prevalence on the transect).

A high density of *Solidago* stems (at maturity) seems to increase insect preferences for native plants with similar flowers. This effect may be caused by its modification of the vegetation structure (McKinney & Goodell, 2010), which directly alters plant–pollinator interactions by hiding some native flowers more than others (as insects' ability to perceive flowers can vary between morphotypes, and for instance pink or blue flowers are more difficult to detect between stems than yellow ones; Klecka et al., 2018; McCall & Primack, 1992). In fact, mature *Solidago* stems can reach up to 2 m height, while the native community has a weighted mean of ca. 1.2 m. *Solidago* may also indirectly alter plant–pollinator interactions by changing predation patterns. Indeed, *Solidago* has been shown to favour insect predators such as spiders (Bauer et al., 2021; Dudek et al., 2016), making it more dangerous for pollinators to visit flowers within the vegetation patch (lower flowers). On the other hand, for a given stem density of *Solidago*, increasing its number of flowers seems to decrease insect preferences for native flowers of the same morphotype. This effect may be caused by direct competition for pollinators between *Solidago* showy flowers and the native species, competition being the strongest with the most similar flowers (Sun et al., 2013).

Interestingly, the balance between these two mechanisms—benefits from enhanced flower detection versus costs from competition for pollinators—varies among native morphotypes. Flowers similar to those of *Solidago* may particularly benefit from the presence of the invader as some insects optimize their foraging towards their flowers, but they will also be more directly in competition with the invader's flowers (Sun et al., 2013). This suggests that both competition and facilitation occur between

Solidago and native plants with similar flowers, even though overall we found that facilitation was the predominant mechanism for native pollination success. This facilitation is mainly determined by the invader vegetative density (a result consistent for both plant pollination success and insect preferences). Regarding the other mechanisms that can affect insect preferences, we found no strong evidence for modifications of plant-insect interactions due to changes in the plant species community (e.g. selecting native plants with more attractive flowers) or changes in the insect species community (e.g. attracting new insects with different foraging preferences). Overall, the effects of Solidago on the pollination patterns of native plants may lead to changes in the fitness of their populations. To confirm this hypothesis, however, specific studies on the growth, fecundity and survival of these native plants are needed.

4.3 | Limits and perspectives

Four methodological constraints limited our analyses, and we discuss here how they might be mitigated in future studies. First, field constraints (management by mowing) prevented us from continuing our observations after mid-August, which is when most *Solidago* flowers open. This may be partly responsible for the limited effects of flower density in the models. Nevertheless, full flowering of *Solidago* was reached in four of the six meadows before the end of the studies, and peak flowering of native vegetation was already over for almost all native flowers (Figure S7.1). The impact of *Solidago* on the pollination of native plants after our fieldwork session is therefore probably marginal compared with the impacts we quantified.

Second, we considered only species (plants and insects) observed in at least two densities per meadow per period to ensure statistical robustness. As a result, our conclusions might be biased towards the response of the most abundant species in the system. The abundant species are potentially more resistant to invasion, while the rare species may be more vulnerable to invasion. Yet, the dynamics of rare species remain difficult to study, especially in the case of insects.

Third, our indicators of pollination success and insect preferences are indirect as they are based on data from visitation networks. A better approach to quantify pollination and reproduction successes would have been, for instance, to follow in situ pollen tube growth and seed production for all plant species during the whole growing season. Similarly, a better approach to quantify insect preferences would have been to identify and quantify the pollen carried per sampled insect, in order to have a direct measure of its recent pollination circuit (instead of an average preference for the year; Cirtwill et al., 2024). At the moment, these two approaches are extremely time consuming and costly, but future developments in image recognition should make them more accessible in the future (e.g. Olsson et al., 2021).

Finally, our study system is composed of relatively small invaded patches (ca. 300 m^2) within globally pristine environments, and taking into account larger invaded plots (e.g. complete grassland coverage) may modify the results. Typically, it is possible that the observed beneficial effects of *Solidago* on similar native flowers becomes lost if the invaded patch area increases enough to generate strong losses in the plant and/or insect species pool (Moroń et al., 2019). A better understanding of these dynamics will be gained by repeating such study in diverse environments and across broader invasion gradients.

5 | CONCLUSIONS

Our work shows that invasive plants can rewire the local web of interactions by modifying the foraging behaviours of local pollinators. The consequences of plant invasions therefore extend beyond the well-described plant–plant interactions to include mutualistic pollination networks, potentially initiating cascading interaction chains that propagate throughout native multi-trophic networks.

Invasion impacts are mediated by complex mechanisms with negative impacts on some species but also positive impacts on others (Vimercati et al., 2022). Our relatively simple approach allows to better understand pollination at the community scale and may be transferred to other invaded systems. In our study, the different impacts of invasion across flower types seem dominantly driven by the vegetative density of *Solidago* and not the density of its flowers. These results highlight the importance of the 3D vegetation structure on pollinators foraging choices (e.g. due to navigation difficulties, increased predation or decreased detection of flowers) and thus suggests that even wind-pollinated plants can be important to understand pollination network dynamics.

AUTHOR CONTRIBUTIONS

Marie Charlotte Grange, Laure Gallien, Marco Moretti and François Munoz designed the study. Marie Charlotte Grange, Sylvain Varona-Y-Varona, Laure Gallien, Maya Guéguen, Julien Renaud, Marie-Pascale Colace, Marco Moretti and François Munoz collected data in the field, Axel Ssymank performed half of Syrphidae identification. Marie Charlotte Grange performed the statistical analyses. Marie Charlotte Grange, Laure Gallien and François Munoz interpreted the results. Laure Gallien and Marie Charlotte Grange led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

None of the authors have a conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data and R code used in this manuscript are available on Zenodo at https://doi.org/10.5281/zenodo.17199121 (Gallien et al., 2025).

ORCID

Marie Charlotte Grange https://orcid.org/0000-0003-1900-0126
François Munoz https://orcid.org/0000-0001-8776-4705
Marco Moretti https://orcid.org/0000-0002-5845-3198
Julien Renaud https://orcid.org/0000-0001-5991-4657
Marie-Pascale Colace https://orcid.org/0009-0007-7951-1514
Maya Guéguen https://orcid.org/0000-0002-1045-2997
Axel Ssymank https://orcid.org/0000-0002-8285-5429
Laure Gallien https://orcid.org/0000-0003-4882-1580

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SUPPORTING INFORMATION

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

Details on (S1) the transect sampling design, (S2) the floral trait data, (S3) the insect species sampled, (S4) the structural equation modeling, (S5) the pollination indices, (S6) the results when considering separately the different insect orders, and (S7) the phenology of native flowers and insects.

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