

Research article

Attractiveness of exotic invasive plants can disconnect native plants from their floral visitors

Clément Tourbez^{ID}✉, Natasha de Manincor^{ID}, Guillaume Ghisbain^{ID} and Denis Michez^{ID}

Laboratory of Zoology, Research Institute for Biosciences, University of Mons, Mons, Belgium

Correspondence: Clément Tourbez (clement.tourbez@umons.ac.be)

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Exotic invasive plant species (EIP) threaten ecosystem diversity and stability through competition for abiotic resources with native plant species. They can also compete for pollinators, as native floral visitors can incorporate EIP floral resources (i.e. pollen and nectar) in their diets, potentially shifting their foraging behaviour away from the native flora. To decipher how EIP attract native floral visitors and the potential competition between EIP and native plants for pollinators, we focused on five major exotic invasive plant species in Europe: *Buddleja davidii*, *Impatiens glandulifera*, *Reynoutria japonica*, *Robinia pseudoacacia* and *Senecio inaequidens*. We recorded in 16 sites in Belgium: 1) EIP floral visitors, 2) EIP pollen carried by these visitors and 3) pollen from native plant species on these visitors. We showed that bees were the dominant visitors and pollen vectors for *Impatiens glandulifera*, *Robinia pseudoacacia* and *Buddleja davidii*; hoverflies were the primary visitors for *Senecio inaequidens*; and non-hoverfly flies, alongside bees, were the most frequent visitors for *Reynoutria japonica*. *Senecio inaequidens* exhibited the highest species richness of floral visitors, species richness of pollen vectors, and shared interactions with native plant species. *Impatiens glandulifera* exhibited the highest pollen transfer efficiency, with nearly 90% of its floral visitors carrying its pollen. While floral visitors of the other four studied species also interacted with numerous native plants, those of *I. glandulifera* carried its pollen almost exclusively, potentially substituting native species. These findings highlight how widely introduced exotic invasive plant species can integrate native pollinator networks to the point of disconnecting local pollinators from their original resources.

Keywords: alien species, global changes, palynological analysis, pollinators

Introduction

Biological invasions are major ecological disturbances acting as drivers of biodiversity loss (Jaureguiberry et al. 2022, Roy et al. 2024). With over 37 000 plant species introduced worldwide, exotic plant species are main invaders and can cause profound changes to ecosystem services and biodiversity (Roy et al. 2023). The rate of these introductions drastically increased with recent globalisation, driven by expanded trade networks and human mobility, contributing to an increase in plant invasions

worldwide (Seebens et al. 2015, Roy et al. 2023). A major impact of these exotic invasive plants (EIP) is their competition with the native flora for both resources and space, which can lead to drastic shifts in plant community composition (Crystal-Ornelas and Lockwood 2020, Xu et al. 2022). Through their own attractivity and the alteration of native plant communities, EIP may also disrupt pollinator communities and subsequent plant-pollinator interactions (Stout and Tiedeken 2017).

Pollinators are globally recognised as essential for the sexual reproduction of nearly 90% of angiosperms, with pollination constituting an ecosystem service of high economic and ecological value (Porto et al. 2020, Tong et al. 2023). Nevertheless, pollinator populations are declining at an alarming rate due to anthropogenic threats, often in combination, including climate change, pesticide use, chemical and light pollution and habitat destruction (Dicks et al. 2021, Wagner et al. 2021, Nath et al. 2023). Additionally, the rise of EIP poses well-established risks to pollinator diversity and pollination (Vanbergen et al. 2018, Kovács-Hostyánszki et al. 2022). One primary impact of EIP is the displacement of the native flora, which threatens the primary food resources of many pollinators (Crystal-Ornelas and Lockwood 2020). By outcompeting native flora, EIP can act as ecological filters, disadvantaging pollinators that cannot benefit from these novel floral resources (Kleijn and Raemakers 2008). As a result, native pollinators now face an increased risk of extirpation as native floral diversity declines under invasion pressure.

Most EIP are entomophilous and produce abundant flowers, offering profuse resources for native floral visitors (Goodell and Parker 2017, Stout and Tiedeken 2017, but see Traveset and Richardson 2020). Although some exotic invasive plants reproduce vegetatively, pollination by native floral visitors often enhances their reproductive success and accelerates their expansion (Traveset and Richardson 2020). Species with floral traits that align with the requirements and traits of native floral visitors may establish more successfully (Szigeti et al. 2023, Lopresti et al. 2024). By visiting the EIP, native floral visitors may interact with the reproductive structures of the plants and act as pollen vectors (i.e. a floral visitor carrying pollen of the visited plant species on its body; Morón et al. 2021, Wang et al. 2023). As not all floral visitors are pollen vectors and contribute to pollination (Page et al. 2021, Tourbez et al. 2023), it is critical to identify which floral visitors function as effective pollen vectors to unravel their role in the spread of invasive species.

To explore the impact of exotic invasive species on plant-pollinator interactions, the use of networks has been proven to be particularly useful (Daniels and Arceo-Gómez 2020, Parra-Talba et al. 2021, Emer and Memmott 2023). EIP tend to occupy a central position within networks thanks to their abundant floral resources, which can in turn affect the stability of plant-pollinator networks (Parra-Talba and Arceo-Gómez 2021, Wang et al. 2023, but see Simla et al. 2022). Most importantly, invasion can lead to depressed visitation rates to native plants (Goodell and Parker 2017), increase heterospecific pollen deposition on native plant species (Daniels

and Arceo-Gómez 2020, Parra-Talba et al. 2021, Wang et al. 2023) and ultimately reduce their fitness (Parra-Talba et al. 2021). To elucidate how invasive species integrate into pollen networks and affect community dynamics, it is essential to quantify whether native pollinators continue interacting with native plants in invaded areas, potentially acting as connectors between native and invasive species, or whether the native plants are substituted from the network (Stouffer et al. 2014, Parra-Talba and Arceo-Gómez 2021).

Given the growing challenges posed by the rapid spread of exotic invasive species, understanding how they interact with the pollinator communities has become ever more critical. Therefore, through a study combining visitor sampling in field conditions and palynological analyses, we investigated five major European exotic and highly invasive plant species to address the following questions: 1) Which floral visitors exploit their floral resources? 2) Which of these floral visitors act as pollen vectors of these invasive species? 3) Do these floral visitors still forage on native plant species?

Material and methods

Model species

We selected five model exotic plant species ranked amongst the most invasive in Europe: *Buddleja davidii*, *Impatiens glandulifera*, *Reynoutria japonica*, *Robinia pseudoacacia* and *Senecio inaequidens*. This selection was based on 1) their widespread distribution across European countries (Roy et al. 2020), 2) their demonstrated impact on native biodiversity (Weber and Gut 2004, Tallent-Halsell and Watt 2009), 3) their documented entomophily (Vanparys et al. 2008, Bartomeus et al. 2010, Giovanetti and Aronne 2013, Chen et al. 2014, Johnson et al. 2019), and 4) the availability of extensive populations in the study regions.

1) The butterfly bush *Buddleja davidii* (Scrophulariaceae), is a perennial shrub native to China, introduced to Europe in the 19th century through horticulture (Tallent-Halsell and Watt 2009). It rapidly colonises disturbed areas, forming monospecific patches by outcompeting native plant species (Starr et al. 2003, Tallent-Halsell and Watt 2009). *Buddleja davidii* produces large, fragrant, purplish inflorescences that are highly attractive to butterflies (Chen et al. 2011, 2014). 2) The Himalayan balsam *Impatiens glandulifera* (Balsaminaceae), is an annual herb native to the Himalayas, introduced to European gardens as an ornamental species in the 19th century (Beerling 1993, Bartomeus et al. 2010). It thrives along riverbanks and in wetlands, where it competes with native species for soil resources, contributing to increased bank erosion (Bartomeus et al. 2010, Coakley and Petti 2021). The plant produces white to pink, zygomorphic, summer-blooming flowers that are highly attractive for bumble bees (Emer et al. 2015). 3) The Japanese knotweed *Reynoutria japonica* (Polygonaceae), is a perennial herb native to East Asia, introduced in the 19th century as an ornamental (Beerling 1993). It spreads vigorously in moist soils across various habitats, forming extensive stands through

vegetative reproduction that displace native flora (Saad et al. 2009, Johnson et al. 2019). Its small white flowers bloom in late summer and are visited by Diptera (Del Tredici 2017, Johnson et al. 2019). (4) The black locust *Robinia pseudoacacia* (Fabaceae), is a tree species native to North America, introduced to Europe in the early 17th century for forestry, nitrogen fixation and ornamental purposes (Huntley 1990). This heliophilous pioneer species can also spread vegetatively, readily colonising disturbed areas (Huntley 1990, Cierjacks et al. 2013). *Robinia pseudoacacia* produces numerous zygomorphic white flowers that bloom in late spring. Pollen is released only when large pollinators, such as bumble bees, trigger a floral mechanism (Giovanetti and Aronne 2013). (5) The South African ragwort *Senecio inaequidens* (Asteraceae), is a perennial herb native to South Africa, accidentally introduced to Europe in the late 19th century through the transport of goods (Ernst 1998). It spreads prolifically in disturbed, low-competition dry grasslands (Lachmuth et al. 2018). The plant bears yellow flower heads that bloom in summer, attracting numerous hoverfly and bee species (Vanparys et al. 2008, Lachmuth et al. 2018).

Study and sampling design

Sampling of floral visitors was conducted across 16 sites in the Hainaut province, Belgium, from early June to late September 2023 (Fig. 1). All EIP were sampled on heavily disturbed, invasive species-rich slag heaps, except for *I. glandulifera*, which was collected along riverbanks. All sites consisted of native species-rich habitats, providing floral visitors with potential access to native floral resources. Five sites

per EIP were sampled, each comprising isolated slag heaps or riverbanks, with a minimum distance of 2.55 km between sites to limit floral visitor population overlaps in accordance with insect flight distance (Zurbuchen et al. 2010). Sampling was conducted twice per site to maximise records of insect diversity. The time between the two sampling events was maximised and adjusted to the local flowering periods, thereby covering the full blooming season of the focal EIP (details in the Supporting information). Each sampling session focused on a single exotic invasive plant species and consisted of a 1.5 hour period (total per species = 15 h) during which all insects entering flowers were captured using an entomological net. Sampling occurred under insect activity conditions (10:00–17:00, low wind, cloud cover $\leq 40\%$, and minimum temperature of 17°C, or 13°C in full sunshine; Barkmann et al. 2023). To minimise floral visitor disruption, a single observer sampled within a defined 3 m² patch that corresponds to an area easily accessible without movement. To avoid pollen contamination, all captured insects were immediately isolated in Eppendorf tubes or small plastic bags (for larger insects, including Lepidoptera) and euthanised via freezing directly in the field. Although honey bees *Apis mellifera* were frequently observed on *B. davidii*, *R. japonica* and *R. pseudoacacia* (but were nearly absent on *I. glandulifera* [4 individuals] and *S. inaequidens* [18 individuals]), they were excluded from the analyses. Their abundance was drastically influenced by the presence or absence of nearby beekeeping activity, which could introduce significant bias and obscure the response of wild pollinators to EIP. We therefore focused our study exclusively on wild floral visitors.

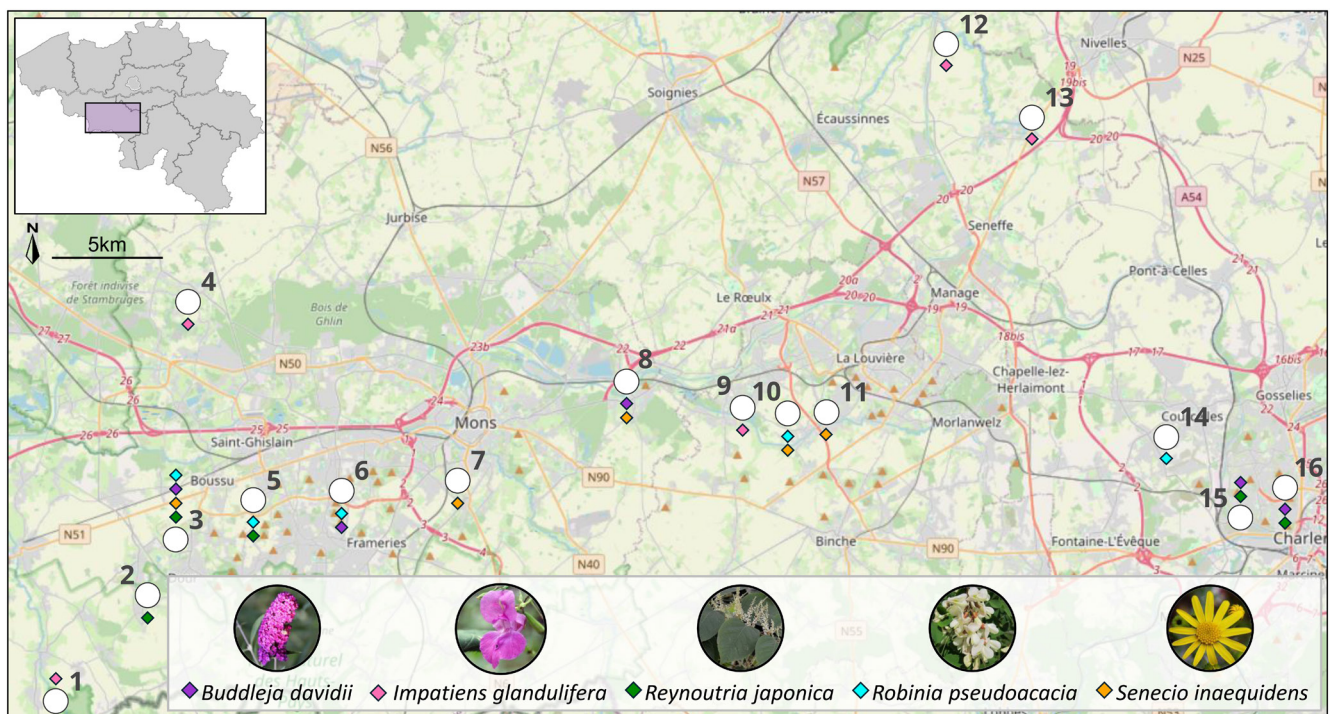


Figure 1. Map of the 16 sampled sites (details in the Supporting information). The inset shows the geographical region studied within Belgium. Map created using QGIS ver. 3.28 with an OpenStreetMap background layer. Pictures: pixabay.com.

Palynological analysis

Palynological analyses were conducted on all floral visitors to examine: 1) if they transported pollen of the EIP from which they were sampled (considered therefore as EIP pollen vectors) and 2) additional interactions with other plant species in the habitat. Each insect was identified to species (Anthophila, Syrphidae and Rhopalocera) or morphospecies level with the assistance of taxonomists (Acknowledgements). Pollen grains were sampled by gently touching the insect body with a gel cube containing fuchsin (pollen stain), which was then melted and mounted on a slide (following Dafni et al. 2005, Tourbez et al. 2023). Since the pollen gathered by non-parasitic female bees in their scopa (i.e. their pollen-carrying apparatus) is considered unavailable for pollination because it is aggregated and mixed with nectar, pollen sampling excluded the scopa and adjacent areas (i.e. mesothoracic legs and abdomen sides; Tourbez et al. 2023). All specimen preparation and pollen sampling were conducted with gloves, and equipment was routinely cleaned to avoid pollen contamination. Pollen slides were examined under an optical microscope at 400× magnification. Identification was based on pollen morphology, mainly at the species-level but extended to genus or morphogroup-level for cryptic groups, as commonly done in palynological studies (Zhao et al. 2019, see the Supporting information for morphogroup lists and potential associated species). Identifications were aided by a reference pollen collection, a plant survey of sampling sites, and online databases (<https://pollen.tsteblar.ch>, accessed April 2024). Broken or immature pollen grains, as well as pollen from non-entomophilous species (e.g. *Pinus* sp., *Betula* sp., Poaceae), were excluded. To mitigate potential contamination from handling (e.g. pollen in the net) or environmental sources (e.g. heterospecific pollen previously deposited in flowers), pollen transport as associated interaction was only considered when a minimum of 20 grains were detected on the pollen slide (Zhao et al. 2019). Given these precautions, any remaining contamination was expected to be minimal. Specimens and pollen slides are conserved in the collection of the Laboratory of Zoology at the University of Mons, Belgium. Based on the palynological data, a quantitative pollen network was constructed for each exotic plant species, with interaction weight based on the number of times a visitor (morpho-)species carried pollen of a given plant species. Because insect sampling was centred on individual EIP, these networks are plant species-centred and do not represent comprehensive pollen networks of the habitat. However, they provide valuable insight into the plant species which the floral visitors interact with.

Data analysis

All data analyses were conducted with R studio using R ver. 4.3.1 (www.r-project.org). Figures were plotted using the 'ggplot2' package ver. 3.4.4 (Wickham 2016) and networks constructed using the 'igraph' package ver. 2.0.3 (Csárdi et al. 2024). Statistical analyses were performed using generalised linear models (GLMs) with *glmmTMB* from the package 'glmmTMB' ver. 1.1.8 (Brooks et al. 2017). First, to compare

the proportion of floral visitors acting as pollen vectors across EIP, we applied a GLM with a binomial distribution (logit link). The presence or absence of EIP pollen on each floral visitor individual was set as the response variable, with plant species as the explanatory variable. Second, to analyse interspecific variation in 1) visitor richness and 2) pollen vector richness across sites, we constructed two GLMs with negative binomial and Poisson distributions, respectively. In both models, visitor or pollen vector richness were used as response variables, with plant species as the explanatory variable. Third, to assess interspecific variation in the pollen network in 1) plant species richness and 2) interaction richness across sites, we developed two additional GLMs, applying Poisson and negative binomial distributions, respectively. In both models, plant species richness or interaction richness were used as response variables, with plant species as the explanatory variable. Due to the sparse distribution of EIP across sites, the variable site could not be included as a random factor in the models. The limited within-site EIP replication resulted in convergence issues and unreliable variance estimates (Harrison et al. 2018). Therefore, to account for potential site-level effects, data from both sampling rounds were pooled by site for each EIP. All model assumptions were checked using the 'DHARMA' package ver. 0.4.6 (Hartig 2022). Statistical metrics were obtained with the *Anova* function from the R-package 'car' ver. 3.1-2 on our models (Fox and Weisberg 2019). Post hoc tests were realised for all analyses using the *emmeans* function with Tukey's adjustment method, from the R-package 'emmeans' ver. 1.10.0 (Lenth 2024).

Results

Visitor and pollen vector diversity

A total of 1070 floral visitors were collected, representing 156 morpho-species (with 74% of the specimens identified at the species level) including 33 bee, 19 hoverfly and 8 butterfly/moth species (Supporting information). Bumble bees were the predominant floral visitors of *I. glandulifera* (84%) and *R. pseudoacacia* (82%). *Buddleja davidii* was mainly visited by hoverflies (36%) and bumble bees (40%), while *S. inaequidens* attracted mostly hoverflies (53%) and solitary bees (18%). The primary visitors of *R. japonica* were non-hoverfly Diptera (46%), followed by hoverflies (15%) and wasps (13%; Fig. 2A).

Among these floral visitors, 523 individuals (49%, 56 morpho-species) were pollen vectors of the EIP. The main pollen vectors were among the dominant visitors (Supporting information), with a more prominent representation of bumble bees (*I. glandulifera*: 95%, *R. pseudoacacia*: 86%; *B. davidii*: 64% and *R. japonica*: 28%) and solitary bees (*S. inaequidens*: 25%), while non-hoverfly Diptera decreased (34%). Collectively, Hymenoptera and Diptera comprised 99% of all the pollen vectors. The proportion of pollen vectors among visitors differed significantly across exotic invasive plant species (GLM, $\chi^2 = 211.0$, $df = 4$, $p < 0.0001$, Fig. 2B).

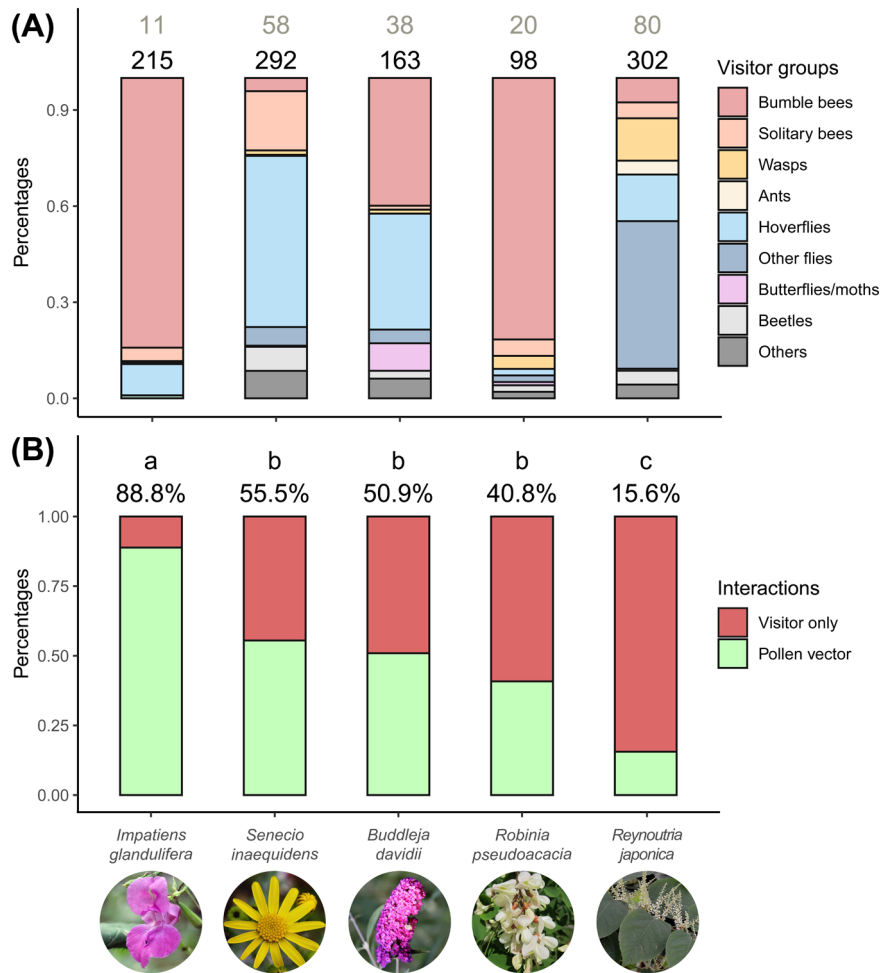


Figure 2. (A) Floral visitors of five major exotic invasive plant species in Europe. Black and grey numbers above the bars indicate the number of individuals sampled and the number of different morphospecies identified, respectively. (B) Proportion of floral visitors (red) acting as pollen vectors (green) for the five exotic invasive plant species. Different letters indicate significant differences based on post hoc tests.

Floral visitors of *I. glandulifera* showed the highest proportion of pollen vectors (88.8%), followed by *S. inaequidens*, *B. davidii* and *R. pseudoacacia* (55.5%, 50.9% and 40.8%, respectively) while *R. japonica* visitors had notably less pollen vectors (15.6%).

EIP exhibited significant variation in both visitor species richness (GLM, $\chi^2=55.4$, $df=4$, $p < 0.0001$, Fig. 3A) and pollen vector species richness (GLM, $\chi^2=45.7$, $df=4$, $p < 0.0001$, Fig. 3B). *Reynoutria japonica* attracted the highest species richness of floral visitors (mean \pm SE: 27.6 ± 4.12), followed by *S. inaequidens* (19.4 ± 1.96), *B. davidii* (11.4 ± 2.88), with the lowest species richness observed in *R. pseudoacacia* (6.2 ± 1.28) and *I. glandulifera* (4 ± 0.55). Conversely, *S. inaequidens* exhibited the highest species richness of pollen vectors (11.4 ± 2.86), surpassing all other species (*B. davidii*: 4 ± 1.18 , *I. glandulifera*: 2.8 ± 0.37 , *R. pseudoacacia*: 2.8 ± 0.8 , and *R. japonica*: 4.2 ± 3.29).

Pollen networks

The palynological analyses identified 831 insect–plant interactions, encompassing 227 unique interactions (i.e. one

floral visitor species carrying the pollen of one plant species). Among these, 154 interactions involved plant species other than the focal EIP. *Impatiens glandulifera* pollen-network exhibited minimal interactions with other plant species, with only a single interaction recorded (Fig. 4A). In contrast, the pollen-networks of the other four exotic invasive species were highly connected to native plant species through their floral visitors (Fig. 4B, Supporting information). Key connectors to alternative species varied by invasive plant: hoverflies (76%) and solitary bees (15%) for *S. inaequidens*; bumble bees (94%) for *R. pseudoacacia*; hoverflies (57%) and bumble bees (40%) for *B. davidii*; and hoverflies (48%) and bumble bees (24%) for *R. japonica*. Pollen-network of EIP exhibited significant differences across species in both plant species richness (GLM, $\chi^2=17.1$, $df=4$, $p=0.0018$, Supporting information) and interaction richness (GLM, $\chi^2=11.2$, $df=4$, $p=0.0243$, Supporting information). Plant species richness was significantly lower for *I. glandulifera* (mean \pm SE: 0.2 ± 0.2) compared to the other species (*B. davidii*: 7 ± 1.64 , *R. pseudoacacia*: 4 ± 0.95 , *R. japonica*: 5 ± 1 , and *S. inaequidens*: 7 ± 2.21 ; Supporting information). Similarly,

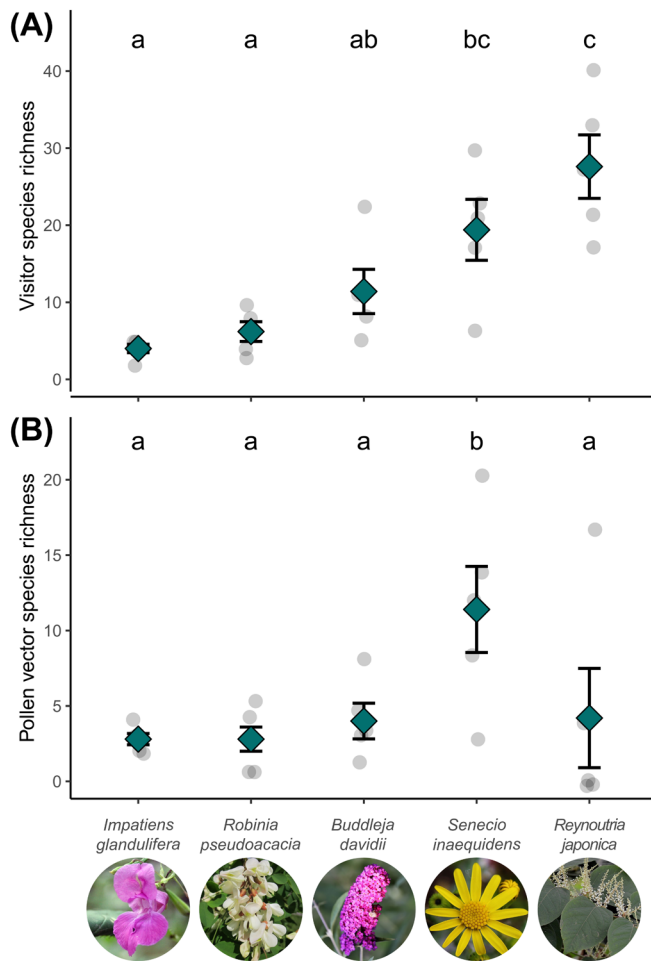


Figure 3. Comparison of the (A) floral visitor species richness and (B) pollen vector species richness of five major exotic invasive plant species in Europe. Dots represent the mean species richness ($n = 5$), with error bars indicating the associated standard errors. Different letters indicate significant differences based on post hoc tests.

interaction richness between the floral visitors of exotic invasive species and alternative plant species was significantly higher for *S. inaequidens* (15.8 ± 5.79) and *B. davidii* (11 ± 3.02) than for *I. glandulifera* (0.2 ± 0.2), with intermediate levels observed for *R. pseudoacacia* (5 ± 1.22) and *R. japonica* (7.2 ± 1.5 ; Supporting information).

Discussion

Floral visitors

With invasion rates rising globally, exotic invasive plant species are increasingly coexisting with native floral visitors (Roy et al. 2023). When these invaders provide floral resources, they may constitute a substantial portion of the nectar and pollen supplies available to native floral visitors (Goodell and Parker 2017). Among five of the most prominent EIP in Europe tested in this study, all demonstrated high interactions with the native floral visitor community, attracting abundant and

diverse floral visitors, albeit with variations in dominant floral visitor groups. Major floral visitors of *I. glandulifera* and *R. pseudoacacia* were bumble bees, consistent with previous findings (Nienhuis and Stout 2009, Bartomeus et al. 2010, Emer et al. 2015, Najberek et al. 2023). Despite their high nectar and pollen production (Coakley and Petti 2021), both species attracted the lowest floral visitor richness, likely due to their complex floral morphologies. Indeed, while they do not fully prevent small insect visits, complex flowers tend to be mainly visited by large floral visitors, especially larger bees (Krishna and Keasar 2018). In addition to zygomorphic flowers, both species feature floral traits that favour large, long-tongued bees such as bumble bees: *I. glandulifera* conceals nectar in corolla spurs accessible only to long-tongued species (Kostrakiewicz-Gierałt 2015), while *R. pseudoacacia* emits bumble bee-attracting scents (Dekebo et al. 2022) and exhibits papilionaceous flowers with strength-dependent pollen release mechanisms likely only activated by bumble bees (Giovannetti and Aronne 2013). Regarding *B. davidii*, while butterflies were expected to dominate as floral visitors (Ebeling et al. 2012, Chen et al. 2014), bumble bees and hoverflies appeared more prominent in our sites. Its deep, tubular flowers with narrow entrances restrict nectar access primarily to long-tongued bees and butterflies (Ebeling et al. 2012). Other *Buddleja* species are also known to attract bumble bees (Gong et al. 2015), and *B. davidii* emits a floral scent appealing to both butterflies and bees, explaining these results (Gong et al. 2015). Hoverflies, unable to access nectar, likely only collected pollen, the stamen being positioned at the corolla entrance (Chapelin-Viscardi et al. 2015). Finally, *S. inaequidens* and *R. japonica* attracted the highest richness of floral visitors, consisting respectively mainly of hoverflies and solitary bees, and Diptera and wasps, confirming previous findings (Vanparys et al. 2008, Johnson et al. 2019). Their open flowers with easily accessible rewards favour short-proboscis visitors and may facilitate their interactions with these native floral visitors. Notably, the invasive Asian hornet *Vespa velutina* was a frequent visitor of *R. japonica*, suggesting a potential co-invader mutualism that could facilitate both species' expansion (Devenish et al. 2025). The integration success of these five species into native pollinator diets, along with their abundant floral resource availability (Chittka and Schürkens 2001, Cierjacks et al. 2013), may stem from their specific phenology (Wolkovich and Cleland 2011). While *R. pseudoacacia* blooms in late spring, the others bloom in summer, with some continuing into autumn (Tallent-Halsell and Watt 2009, Emer et al. 2015, Lachmuth et al. 2018, Johnson et al. 2019). Given that native flowering peaks in spring or early summer, these late-flowering invaders provide substantial foraging opportunities for pollinators in these resource-scarce periods (Wolkovich and Cleland 2011, Zaninotto et al. 2023).

Pollen vectors

By foraging on EIP floral resources, native floral visitors may charge pollen on their body and potentially act as pollen vectors, which can promote EIP pollination, sexual reproduction,

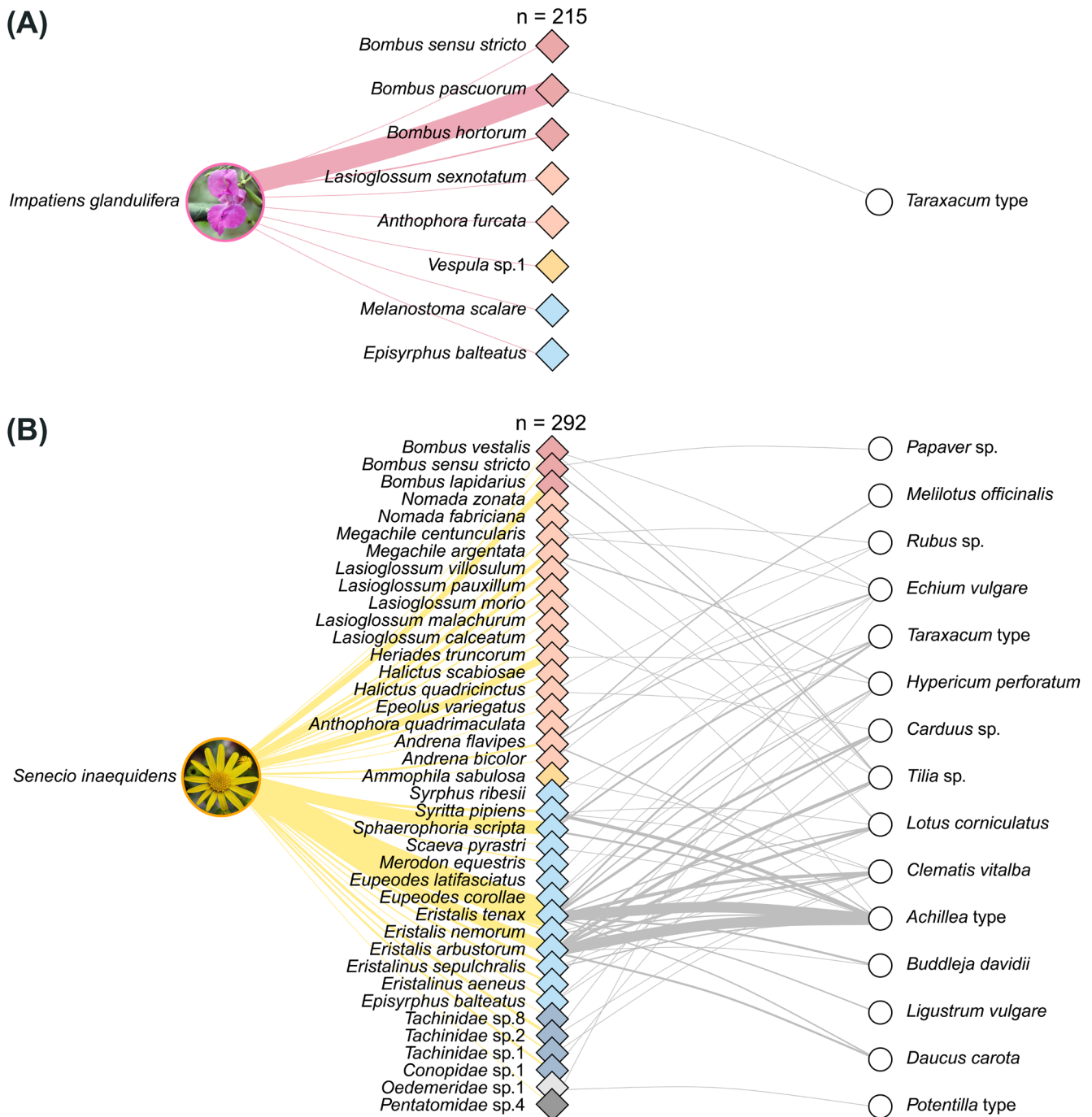


Figure 4. Species-centred pollen interaction networks for two major exotic invasive plant species in Europe, (A) *I. glandulifera* and (B) *S. inaequidens*. Floral visitor species are shown at the centre and coloured by insect groups as in Figure 2. Interactions with the exotic focal species are displayed on the left (pink for *I. glandulifera* and yellow for *S. inaequidens*) while interactions with native plant morphogroups are coloured in grey and displayed on the right. Interactions are weighted based on the number of times a particular floral visitor species was found carrying the pollen of a particular plant species. Pollen analysis was conducted on all sampled visitors, with the total number of visitors indicated at the top of the graph.

and spread (Titze 2000, Morón et al. 2021, Wang et al. 2023). The five studied species varied in the efficacy of transferring pollen on their floral visitors. With nearly 90% of its floral visitors being pollen vectors, *I. glandulifera* exhibits the highest pollen transfer efficiency in our study, aligning with

previous observations (Titze 2000). However, this species has the lowest species richness of pollen vectors, with the pollen being virtually only carried by highly efficient bumble bees, particularly *B. pascuorum*, as previously observed (Titze 2000, Nienhuis and Stout 2009, Vanderplanck et al. 2019). The

pollen deposition mechanism of *I. glandulifera* is remarkably adapted to bumble bees, which fit the floral morphology and collect maximum pollen/nectar per visit, leading to a 100% seed set according to earlier studies (Titze 2000, Nienhuis and Stout 2009). Conversely, despite having a similar flower morphology and bumble bees as primary visitors, *R. pseudoacacia* had, in our study, only 41% of its floral visitors carrying its pollen. In its native range, up to two-thirds of the ovules remain unfertilised due to pollen limitation, a trend therefore likely to be similar in Europe (Susko 2006). This reduced pollen transfer could be attributed to the pollen release mechanism, which is triggered only when larger bee species visit to collect nectar (Giovanetti and Aronne 2013). For instance, honey bees are too small to activate this mechanism, and among bumble bees, smaller individuals may not always be able to activate it, thus limiting pollen transfer (Giovanetti and Aronne 2013). In addition, some individuals circumvent that constraint by piercing the corolla base to obtain nectar, a form of nectar robbing already documented for honey bees and observed frequently among bumble bees during our surveys (Giovanetti and Aronne 2013). Such robbing behaviour further reduces legitimate pollen transfer which may explain our results. With its long nectar spur, a comparable nectar robbing, while not observed, is also likely in *I. glandulifera* as seen in other *Impatiens* species (Rewicz et al. 2024).

Although *B. davidii* was previously thought to be primarily butterfly-visited (Ebeling et al. 2012, Chen et al. 2014), our results reveal that bumble bees and hoverflies are its primary pollen vectors. The limited role of butterflies in effective pollen transfer has been demonstrated in other studies (Alarcón et al. 2010, Zhao et al. 2019). Similarly, bumble bees are known, as bees in general, to be particularly efficient as pollen vectors due to their high morphological and behavioural adaptations, which maximise pollen transfer (Danforth et al. 2019, Zhao et al. 2019, Tourbez et al. 2023). Furthermore, while hoverflies may be less effective than bees, their role as pollinators remains important, largely due to their abundance, aligning with our results (Klecka et al. 2018, Dunn et al. 2020).

Regarding *S. inaequidens*, its diverse floral visitors also serve as pollen vectors, including numerous solitary bees and hoverflies. Its easily accessible pollen increases pollen transfer and was even carried by Asteraceae specialists (e.g. *Heriades truncorum*) and rare species (e.g. *Epeolus variegatus*) suggesting strong integration into the native pollen transfer networks (Drossart et al. 2019). In contrast, *R. japonica* exhibited the lowest percentage of pollen vectors among its highly diverse floral visitors, with only about 16% of them carrying pollen. This result aligns with previous findings, which attributed low pollen transfer to non-hoverfly Diptera, the main floral visitors of *R. japonica* (Zhao et al. 2019, but see Orford et al. 2015). Overall, none of these species are capable of self-pollination and are therefore highly reliant on pollen vectors for sexual reproduction (Norman 2000, Titze 2000, Grimsby et al. 2007, Ebeling et al. 2012, Cierjacks et al. 2013, Lachmuth et al. 2018). While *R. japonica* and, to a much lesser extent, *R. pseudoacacia* also reproduce

vegetatively (Bailey 2013, Cierjacks et al. 2013), pollen vectors play a critical role in facilitating the sexual reproduction of these invasive plants, allowing their dissemination. With their abundant and effective pollen vectors, *I. glandulifera*, *B. davidii*, *R. pseudoacacia*, and *S. inaequidens* are likely to easily meet their pollination requirements in their introduced ranges (Titze 2000). Regarding *R. japonica*, its strong asexual dispersal capabilities likely compensate for its lack of efficient pollinators, which may not significantly constrain its spread (Johnson et al. 2019).

Floral visitor interactions with native plant species

With their abundant floral resources, most exotic invasive plant species attract native floral visitors, some of which act as pollen vectors, potentially reducing visits to native plants (Stout and Tiedeken 2017). This shift towards invaders may lower pollination rates for native plants, ultimately impacting their fitness. Highlighting whether native floral visitors maintain interactions with native plants, through pollen analysis, can help elucidate the impact of EIP on native plant species (Parra-Tabla and Arceo-Gómez 2021, Tourbez et al. 2023). Floral visitors of all studied species, except *I. glandulifera*, carried pollen from native plants, indicating that interactions with the native floral community were at least partially maintained. However, only one out of the 215 floral visitors (including 169 *Bombus pascuorum*) sampled on *I. glandulifera*, carried pollen from a native plant species. One explanation for this strong preference observed toward the EIP, may lie in the floral visual signals and their perception by bee vision. *Impatiens glandulifera* flowers display whitish to striking pink colours that are highly salient to bees compared to native plant species, thereby facilitating both detection and associative learning to these nectar-rich flowers, which enhances fidelity (Dessart et al. 2024). By contrast, *B. davidii* and *R. japonica* exhibit floral traits more similar to those of native plant species, promoting interactions with generalised floral visitors that remain connected to native plants (Dessart et al. 2024). Alternatively, the strong affinity of *Bombus pascuorum* for *I. glandulifera* may also be influenced by the floral context of the sampled sites. *I. glandulifera* was the only EIP studied along riverbanks, which generally support lower plant abundance and richness than slag heaps. Although these sites always included abundant native co-flowering alternatives (e.g. *Calystegia sepium*, *Chamaenerion angustifolium*, *Eupatorium cannabinum*, *Lythrum salicaria*, *Rubus* spp. and *Symphytum officinale*), the lower availability of native resources may have limited *B. pascuorum* interactions, in contrast with the slag heaps hosting other EIP, where native alternatives were more abundant. Nevertheless, given the presence of co-flowering alternatives, *B. pascuorum* highly generalist diet, and its large foraging range, these results still suggest a strong preference to *I. glandulifera* (Knight et al. 2005, Casanelles-Abella et al. 2025). Ultimately, out of the five studied EIP, *I. glandulifera* showed the lowest plant species and interaction richness associated with its floral visitors. While this species can increase pollinator abundance in invaded patches due to a strong attraction effect (Bartomeus et al. 2008, Cawoy et al. 2012,

Thijs et al. 2012), our findings suggests that it may drive a set of native pollinators to shift almost exclusively to its abundant floral resources (Bartomeus et al. 2010, Thijs et al. 2012). Such reduced visitation to native plants has also been linked to lower reproductive success of the native plant species in other studies (Chittka and Schürkens 2001).

Regarding the other EIP, *R. pseudoacacia* floral visitors shared substantial interactions with native plants, despite being also primarily visited by generalist bumblebees. Similarly, bumblebees and hoverflies associated with *B. davidii* and most floral visitors of *S. inaequidens* and *R. japonica* interacted extensively with a wide range of native plant species. This resulted in high plant species and interaction richness for their floral visitors, suggesting that these invaders may be well integrated into native networks (Vanparys et al. 2008, Corcos et al. 2020). Considering that these results exclude the highly generalist *A. mellifera*, which is also a visitor of these EIP, integration within native networks are likely even higher in areas near beekeeping activities. These findings are also consistent with a recent global review of exotic plant species visitors, which found that such plants are primarily visited by generalist pollinators, particularly bees and hoverflies (Chittchak et al. 2024). Of the twenty most common floral visitors of exotic species in Europe, fifteen were recorded visiting the EIP studied here and were among their most frequent floral visitors (e.g. *Bombus pascuorum*, *Bombus* sensu stricto, *Episyrphus balteatus* and *Eristalis tenax*; Chittchak et al. 2024). In addition, many of these generalist species were sampled on multiple EIP. In particular, several bumble bee and hoverfly species commonly visited more than one EIP, and two floral visitors (i.e. *Bombus* sensu stricto and *Eristalis tenax*), were even found carrying the pollen of several EIP simultaneously. Although the flowering peaks of the studied EIP show only partial temporal overlap, generalist native floral visitors may therefore benefit from their sequential blooming by switching between species when they co-occur at the same site. By acting as primary visitors and mutual connectors of EIP while also foraging on native plant species, these generalist species play a key role in the integration of exotic plants into native plant–pollinator networks (Chittchak et al. 2024).

While these invaders do not fully substitute native plants in our sites, they are highly attractive and may still compete for pollinators (Davis et al. 2018, Chikowore et al. 2021). For example, a study that compared *R. pseudoacacia* to other plant species (i.e. *Cytisus scoparius* and *Malus domestica*) highlighted its competition for pollinators, potentially outcompeting the natives (Buchholz and Kowarik 2019, Chikowore et al. 2021). Conversely, in another study in Belgium comparing the invasive *S. inaequidens* to its native relative *Jacobaea vulgaris*, showed that the invasive species was less attractive and did not reduce the visitation rate of the native species (Vanparys et al. 2008). In addition, as observed with *B. davidii*, invaders can still attract novel pollinators that subsequently visit co-flowering native species (Corcos et al. 2020). However, maintaining interactions with native plant species does not ensure unaffected pollination quality. As with reduced visitation rates, the fitness of native plant

species can also decline due to significant heterospecific pollen deposition, driven by the abundant pollen produced by invasive plants (Emer et al. 2015). While the effects of heterospecific pollen deposition from exotic invasive species on native plants remain underexplored for the other studied species, they are documented for *I. glandulifera*. This species facilitates substantial pollen transfer to native pollinators, leading to increased deposition of heterospecific pollen on the stigmas of native plants during subsequent visits (Bartomeus et al. 2010, Cawoy et al. 2012, Emer et al. 2015). Such contamination can reduce the reproductive success of natives, though the impact is less severe for highly pollinator-attractive species or self-compatible species (Chittka and Schürkens 2001, Bartomeus et al. 2010, Cawoy et al. 2012). Ultimately, EIP, through the attraction of native pollinators, competition with native plants and inclusion of exotic pollen, may disrupt plant–pollinator interactions, leading to cascading effects that alter the pollen transfer networks (Parra-Tabla et al. 2021). Few studies compared pollination networks in invaded versus uninvaded sites. Despite reports of *I. glandulifera* in the UK and *B. davidii* in the Italian mountains having limited effects on interaction networks, many other invasive species are known to disrupt native networks (Bartomeus et al. 2010, Emer et al. 2015, Corcos et al. 2020). For numerous species such as *S. inaequidens*, *R. pseudoacacia* and *R. japonica*, impacts on pollination network structures remain unexplored, highlighting the need for further research to assess their effects on native plant–pollinator network robustness and stability (Traveset and Richardson 2006, Bartomeus et al. 2008, Stout and Tiedeken 2017, Parra-Tabla et al. 2021).

Conclusion

By attracting native floral visitors, EIP can disrupt native plant–pollinator interactions and potentially compromise ecosystem stability and functionality. Our study on five EIP highlights unambiguous integration into native pollinator diets and their variable efficacy to exploit native floral visitors as pollen vectors, facilitating their reproduction and spread. While most native floral visitors maintained connections to native plant species, the near-exclusive use of *I. glandulifera* by its floral visitors suggests a significant shift from native plants to the invader. While these findings advance our understanding of invasion pathways within plant–pollinator communities, further research remains necessary to assess their long-term effects on native plant–pollinator interactions, their pollination network and fitness.

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Author contributions

Clément Tourbez: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (equal); Investigation (lead); Methodology (lead); Project administration (lead); Resources (lead); Software (lead); Supervision (equal); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Natasha de Manincor:** Conceptualization (supporting); Investigation (supporting); Supervision (supporting); Writing – review and editing (equal). **Guillaume Ghisbain:** Conceptualization (supporting); Supervision (equal); Writing – review and editing (equal). **Denis Michez:** Conceptualization (supporting); Funding acquisition (equal); Supervision (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.wwpzgmsxj> (Tourbez et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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