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Trait-based effects of plant invasion on floral resources, hoverflies and bees

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ORIGINAL ARTICLE

Trait-based effects of plant invasion on floral resources, hoverflies and bees

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Abstract

Plant invasions can lead to homogeneous communities with decreased functional diversity. However, invasive plants, with various morphological and phenological traits, may drive pollinator communities in a less predictable, more complex way. They can promote pollinators compatible with their floral traits, while leaving others without foraging resources. Our observational study on 10 invasive herbaceous species applied a trait-based approach to investigate plant invasion-driven changes in floral resources, hoverfly and bee communities. We sampled invaded and non-invaded (control) sites before and during the flowering of the invasive plants. We analysed the differences in floral traits between invasive and native plants, functional diversity and trait distributions of flower and pollinator communities between the invaded and control sites. Five invasive plant species differed from natives in floral traits. Plant invasion caused species-specific changes in functional diversity and trait distributions of communities. For instance, invaded sites had a decreased functional diversity of hoverflies before flowering of invasive species, and larger hoverflies during flowering of invasive species compared with control sites. Smaller bees were associated with invasive plants with shallow flowers, while larger and long-tongued bees were associated with two invasive species with restricted floral access. Similar to previous studies, pollinator traits showed mixed or neutral responses to plant invasion. This is probably due to the high integration capability of invasive plants into plant-pollinator systems, or limitations in sampling, trait resolution, and unrevealed environmental factors. We provide recommendations for future studies to better understand the trait-based community composition of flowering plants and pollinators.

KEYWORDS
alien species, body size, community assembly via trait-environment interaction, flight phenology, flowering dynamics, functional diversity (RaoQ), plant-pollinator interaction

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INTRODUCTION

Invasive species are one of the most critical anthropogenically driven impacts contributing to global changes in natural systems (Tilman et al., 2017; Vilà et al., 2011). Invasive alien species have been gradually spreading, becoming widespread in all world biomes, and are likely to persist in invaded ecosystems over the long term (Vilà et al., 2011). Invasive species tend to decrease biodiversity, transforming both natural and human-modified environments, thereby affecting ecosystem functions, ecosystem services, and human well-being (IPBES, 2019; Pejchar & Mooney, 2009; Vilà et al., 2011).

Pollination is one of the most important and better understood ecosystem services in the study of invasion ecology (Parra-Tabla et al., 2019; Stout & Tiedeken, 2017; Traveset & Richardson, 2014). Invasive plant species often directly affect pollinators by influencing their diet and behaviour (Chittka & Schürkens, 2001; Goodell & Parker, 2017). Abundant alien species can profoundly modify the vegetation in the recipient ecosystems, tend to decrease the abundance and diversity of native floral resources, and in many cases, they offer more attractive and abundant flowers compared with native species (Fenesi et al., 2015; Vilà et al., 2011). Although there is considerable information on the impacts of invasive plant species on plant-pollinator systems (Chittka & Schürkens, 2001; Fenesi et al., 2015; Hanula & Horn, 2011; Vanbergen et al., 2018), we still lack a deep understanding of the mechanisms and processes underpinning how plant–pollinator communities are invaded, and how they respond to invasion (Charlebois & Sargent, 2017; Gallien & Carboni, 2017; Gibson et al., 2012; Stout & Tiedeken, 2017).

The complex bipartite interactions between plants and pollinators have formed through co-evolutionary processes, entailing morphological (e.g., floral structure and animal mouthpart sizes) and phenological (e.g., flower blooming and animal flight period) adaptations. Hence, their traits are usually more compatible with co-evolved partners than with the unrelated (i.e., alien) species (Ollerton et al., 2009; Pauw et al., 2009; Schiestl & Johnson, 2013; Schleuning et al., 2015). Co-evolved traits of plants and pollinators often explain behavioural patterns (e.g., attracting pollinators and visiting flowers), interactions and services (e.g., resources offered and pollination), individual spatio-temporal co-occurrences, population sizes, and community composition (Fontaine et al., 2006; Fornoff et al., 2017; Ortiz et al., 2021; Schiestl & Johnson, 2013; Schleuning et al., 2015). Multiple connections between plants and pollinators probably result in higher functional diversity and network stability (Fontaine et al., 2006; Fornoff et al., 2017; Wei et al., 2021). However, changing abiotic and biotic conditions can affect the trait distributions of plant–pollinator communities (Carrié et al., 2017; Fontaine et al., 2006; Lázaro et al., 2008; but *see* Fornoff et al., 2017), altering the sensitivity of connections between plants and pollinators, and decreasing their functional diversity (Carrié et al., 2017; Hiraiwa & Ushimaru, 2017; Schleuning et al., 2015).

The functional diversity of plant–pollinator communities has declined rapidly across the globe in the last few decades, with many cascading effects projected for ecosystem functions (Grass et al., 2014; Hiraiwa & Ushimaru, 2017). The human-induced spread of invasive alien species is contributing to this decline through the homogenization of floral resources (Dicks et al., 2021; Potts et al., 2010; Vanbergen et al., 2018). Although the invasion of alien plant species can cause substantial changes in the functional composition of native plant–pollinator communities (Grass et al., 2014; Stout & Tiedeken, 2017), previous studies have shown more or less neutral effects on functional diversity in invaded ecosystems (Charlebois & Sargent, 2017; Gibson et al., 2012; Parra-Tabla et al., 2019). Questions about the general, as well as species-specific, effects of invasive plants on plant–pollinator communities remain unanswered (Daniels & Arceo-Gómez, 2020), in part due to the lack of standard protocol-driven studies (Hulme et al., 2013; but *see* e.g., Davis et al., 2018; Kovács-Hostyánszki et al., 2022). Earlier studies have mostly focused on more developed countries in temperate regions, and so we lack information about the detailed effects of plant invasions at wider geographic scales (e.g., from Eastern Europe with a relatively high pollinator diversity). Moreover, only a few studies have applied trait-based (i.e., mechanism-focused) approaches to investigate the effects of plant invasion on pollinators (Charlebois & Sargent, 2017; Daniels & Arceo-Gómez, 2020; Gibson et al., 2012; Grass et al., 2014; Wong et al., 2019).

Trait-based ecology is a powerful approach which can be used to study the mechanisms underlying community assembly (Bartomeus et al., 2018; Carrié et al., 2017; Hejda & de Bello, 2013; Moretti et al., 2017; Perronne et al., 2017; Wong et al., 2019). Functional diversity may explain ecosystem functioning better than species richness (Schleuning et al., 2015; Schleuter et al., 2010; Song et al., 2014). Trait-based approaches can also help to elucidate the invasion-driven changes in plant–pollinator systems. Since invasive plant species have diverse morphological and phenological traits (e.g., flower structure, shape, colour, flowering period, etc.), they may alter the ecosystem functioning of native communities (including pollinating insects and pollination) in different ways (Davis et al., 2018; Kovács-Hostyánszki et al., 2022; Stout & Tiedeken, 2017; Vilà et al., 2011).

Based on the literature, we have identified a number of important knowledge gaps relating to: (i) how invasive and native plants differ in their floral traits linked to pollination (Gallien & Carboni, 2017; Hejda & de Bello, 2013; Razanajatovo et al., 2022); (ii) how plant invasion can drive functional diversity of floral resources and pollinators (Daniels & Arceo-Gómez, 2020; Gibson et al., 2012; Grass et al., 2014; Parra-Tabla et al., 2019); and (iii) which traits are most influenced by plant invasion (Daniels & Arceo-Gómez, 2020; Martin et al., 2015; ter Braak, 2019). To address these questions, it is necessary to study in tandem the trait set related to floral resources (e.g., flower colour, size, flowering period) and the trait set related to pollinators (e.g., size, flight period), in both invaded and non-invaded habitats. A general assumption is that occurrence of an invasive plant species increases the abundance of those pollinators whose traits are compatible with the invasive species' floral traits (e.g., invasive plants with yellow flowers may promote pollinators preferring yellow flowers; or invasive plants with deep flowers may attract pollinators with longer tongues), while other pollinators may decline as they are incompatible with the traits of the dominant invasive plant. Plant

TABLE 1 Information on the studied invasive plant species.

	Species name	Family	Flowering peak (month)	Flower colour	Flower type	Flower depth, i.e., nectar position	Clusterization and size of flower unit	Flower size (cm)	Insect visitation	Plant height (cm)
	Ambrosia artemisiifolia L.	Asteraceae	8–9	White-yellow and green	Wind flower	Shallow	Clustered small inflorescences	0.30	No, wind pollination, but we have some flower visitation observation (bees, hoverflies)	Medium (10–150)
	Asclepias syriaca L.	Apocynaceae	6	White-pink	Jam trap flower	Moderate	Clustered medium flowers	1.25	Yes, moderate specialist (bees, butterflies, moths, hoverflies, wasps)	Medium–large (50–150)
	Erigeron annuus (L.) Pers.	Asteraceae	7–8	White and yellow	Composite flower head	Shallow	Scarcely-clustered medium inflorescences	1.25	Yes, generalist (bees, beetles, flies, wasps)	Small–medium (40–120)
	Erigeron canadensis L.	Asteraceae	8	White and yellow	Composite flower head	Shallow	More or less clustered small inflorescences	0.30	Mostly self-pollinating, but rarely visited, generalist (bees, beetles, flies, wasps)	Small–medium (20–100)
	Gaillardia aristata Pursh	Asteraceae	6–8	Yellow and red	Composite flower head	Shallow-moderate	Separate large inflorescence	5.10	Yes, moderate generalist (bees, butterflies, hoverflies)	Small (30–45)
	Impatiens glandulifera Royle	Balsaminaceae	7–8	Red	Lip flowers	Deep	Separate large flower	3.25	Yes, moderate specialist (bees, butterflies, wasps)	Large (100–250)
	Reynoutria japonica Houtt.	Polygonaceae	9	White	Bell shaped flowers	Moderate	Clustered small flowers	0.30	Yes, generalist (bees, beetles, butterflies, flies, wasps)	Large (50–300)
	Rudbeckia laciniata L.	Asteraceae	7–8	Yellow	Composite flower head	Moderate	Separate large inflorescence	7.60	Yes, moderate generalist (bees, butterflies, hoverflies)	Large (80–200)
	Solidago gigantea Aiton	Asteraceae	8–9	Yellow	Composite flower head	Shallow	Clustered medium inflorescences	0.65	Yes, generalist (bees, beetles, butterflies, flies, wasps)	Medium-large (40-150)
	Symphyotrichum lanceolatum (Willd.) G.L. Nesom	Asteraceae	9–10	White-pink and yellow	Composite flower head	Shallow	More or less clustered medium inflorescences	1.90	Yes, generalist (bees, butterflies, moths, hoverflies, wasps)	Medium (50-130)

Note: Peak period of flowering (calendar months) were based on the authors observations. Flower colour and type are based on the Biolflor database (Klotz et al., 2002). Flower depth, clusterization, size and insect visitation are based on the available literature, internet resources and the authors expert knowledge. Plant size is based on Király (2009). Grey bar above drawings of flowers indicate 0.5 cm.

TABLE 2 Overview of the range and levels of our analyses.

Analyses Attributes	(i) Floral trait dissimilarities	(ii) Functional diversity		(iii) Multilevel method on community–trait–invasion relationship	
Aim of analysis	To reveal the general dissimilarities among focal invasive and native plant species in their traits	To reveal the differences in the functional diversity of floral, hoverfly and bee communities between invaded and control sites		To reveal how per species abundances (i.e. Communities) of flowering plants, hoverflies and bees are mediated by their traits in interaction with invasion. To reveal the differences in trait distribution of floral, wild bee and hoverfly communities between invaded and control sites	
Levels of traits	Multivariate calculation: all the collected traits together (more univariate and multivariate dissimilarity calculations are in the '*Complementary univariate and multivariate calculations for Floral trait dissimilarities and Functional diversity*' section of the Appendix S1)			All traits were used separately	
Data on invasive species were analysed	Separately	Pooled	Separately	Pooled	Separately
Statistical test	One-tailed, one sample *t*-test	GLMM with Tweedie distribution		ML-ratio test based model selection on GLMM with Poisson distribution and if full model is better extraction of significant model estimation on interaction of explanatory variables	
Response variable	Abundance weighted mean floral trait dissimilarity	Rao's quadratic entropy		Abundances of species of communities	
Explanatory variable	Testing that mean of the distribution of dissimilarities among co-flowering native plants are smaller than mean of dissimilarities among invasive species and natives	Site invasion (i.e., Control vs. Invaded sites)	Focal invasive species, and the interaction of focal invasive species and site invasion	Null model: site invasion and the trait. Full model: site invasion, trait and their interaction	

invasion also disrupts the temporal dynamics of plant-pollinator systems by reducing native floral resources and offering a relatively short-term mass-flowering period (Charlebois & Sargent, 2017; Chittka & Schürkens, 2001; Daniels & Arceo-Gómez, 2020). These mechanisms can lead to a more homogeneous plant-pollinator community, with decreased functional diversity, driven by the attributes of the dominant invasive plant species (Charlebois & Sargent, 2017; Goodell & Parker, 2017; Grass et al., 2014).

In this study, we aim to reveal the trait-based patterns of plant invasions on floral resources and pollinators using 10 case study examples of invasive plant species. We applied a species-level dataset on flowering plants, hoverflies, and bees from a previous field study (Kovács-Hostyánszki et al., 2022), which showed in general a lower abundance and species richness of flowering plants and pollinators before, and higher abundance of both during the flowering of focal invasive plants in the invaded habitats. However, invasive plants also had some species-specific differences. Here, we build upon this dataset with further species-level trait data, using a novel set of analytical approaches, to determine the effect of plant invasions in much more detail. Based on the variability in floral traits of the 10 focal invasive plant species (e.g., flower type, size, colour; see Table 1), we surmised that the functional and mechanistic process behind the effects of plant invasion on pollinators can be better understood. To explore the trait-based patterns, we used novel approaches to analyse: (i) the floral trait dissimilarities between invasive and native plant species; (ii) the differences between invaded and control sites in terms of functional diversity; and (iii) the assembly patterns of floral and pollinator communities mediated by the effect of trait-invasion interaction, to provide insights into the role of plant–pollinator traits in plant invasion (Table 2). We predicted that plant invasion decreases functional diversity in general, as well as drives differences in the trait distributions of plant–pollinator communities. We also expected that these patterns are explained by species-specific attributes and by enhanced or suppressed floral resources before and during the flowering period of the focal invasive species.

METHODS

Invasive plant species

We investigated the trait-based effects of 10 herbaceous invasive alien plant species that are among the most common and most threatening invasives in Eastern Europe (common ragweed, *Ambrosia*

artemisiifolia; common milkweed, *Asclepias syriaca*; annual fleabane, *Erigeron annuus*; horseweed, *Erigeron canadensis*; common blanket-flower, *Gaillardia aristata*; Himalayan balsam, *Impatiens glandulifera*; Asian knotweed, *Reynoutria japonica*; cutleaf coneflower, *Rudbeckia laciniata*; giant goldenrod, *Solidago gigantea*; panicled aster, *Symphyotrichum lanceolatum* agg.; Latin binomials from WFO (2022); see details in Table 1) on floral resources and pollinators, using an observational standardised protocol-driven field dataset (Kovács-Hostyánszki et al., 2022). The 10 invasive plant species were characterised by contrasting phenological and morphological traits regarding their flower characteristics and flowering period (Table 1).

Study sites

We conducted field studies in Hungary and Romania, depending upon the distribution of the focal invasive plant species. For each invasive species, we selected 6–7 pairs of highly invaded (hereafter invaded) versus non-invaded (hereafter control) sites that had broadly similar habitat conditions (vegetation type, native plant species pool, succession status, site history), and were not invaded by any other invasive plant species (Table A1; for site coordinates see Appendix kml files). The studied habitat types varied among the invasive species, but were similar within invasive species. We investigated dry, mesic and wet habitats, including old fields, degraded and semi-natural meadows, and riparian woodlands (see details in Table A1; Kovács-Hostyánszki et al., 2022).

Sampling of pollinators and floral resources

Each invasive plant species was sampled using an identical protocol within a single year (between 2017 and 2019; Table A1), working with three to four invasive species annually. We sampled pollinators and flowers twice during the season to reveal the differences in the effects of plant invasion in different vegetation stages (Tiedeken & Stout, 2015; Vanbergen et al., 2018): before the flowering of the focal invasive plant species and during the peak flowering of the invasive plant species (Table A1). Thereby these two sampling periods in contrasting vegetation phases capture the stark disparity in flower abundance that comes with plant invasion.

We sampled hoverflies (Diptera: Syrphidae) and bees (Hymenoptera: Apoidea: Apiformes), which are widely considered to be the main pollinating taxa in temperate areas. However, we are aware that Lepidoptera, and some additional species of Diptera and Coleoptera can also be pollinators, which were not revealed by the present studies. At each site, we used a standardised transect walk method of 50 or 100 m in length, and 2 m wide, with transects separated by 20 or 30 m, respectively (Table A1). In a few cases, where the sampled habitats were linear (e.g., riparian vegetation along watercourses), we assigned the two transects in a series with a 30 m gap. The observer steadily walked along the transect over a 20-min period, catching hoverflies and wild bees with an insect net, and recording visual counts of honey bees (*Apis mellifera* L.). In the case of *R. japonica*, the dense and high vegetation prevented transect walks. Therefore, we sampled pollinators at five points (2 × 2 m area), for 20 min in total. We conducted all pollinator sampling in sunny conditions at 20°C–30°C, and up to a moderate wind speed (<15 km/h). Specimens were killed with ethyl-acetate, stored in 70% ethanol, and identified to species-level in the laboratory using identification keys and reference collections at the Hungarian Natural History Museum by taxonomic specialists (bees: Zsolt Józan; hoverflies: Zoltán Soltész). Species names follow Ascher and Pickering (2020) and Tóth (2017). Voucher specimens and all the samples are kept at the Centre for Ecological Research, Vácrátót, Hungary.

We counted flowers or inflorescences of each potentially insect-pollinated plant species (based on our prior knowledge from the field and according to the database of Klotz et al., 2002) that was flowering at the time of pollinator sampling in 1 × 1 m quadrats. Quadrats were 10 m apart along each pollinator survey transect (i.e., in 5 quadrats along 50 m transects and 10 quadrats along 100 m transects). In the case of *R. japonica*, we used 2 × 1 m quadrats at each sampling point. In the case of inflorescences, flowers of five individuals were counted, and the number of inflorescences was then multiplied by the mean flower number per inflorescence (except for species that belonged to Asteraceae, where the number of inflorescences was counted). Plant species were identified by expert botanists (Annamária Fenesi, Orsolya Kovács, Zsombor Miholcsa, Csaba Molnár and Dorottya Sándor) based on their prior knowledge and a field guide (Simon, 1994), and we used plant names according to WFO (2022).

Altogether, we recorded 3,241,773 flower units of 352 plant species, we captured 2255 specimens of 76 hoverfly species and 1297 individuals of 172 wild bee species, and we recorded 5556 honey bee individuals.

Trait datasets

We collected species-level trait data for the field-recorded flowering plant, hoverfly, and bee species from established databases and literature. Traits were chosen based on their potential functional explanatory value in plant–pollinator ecosystems (as suggested by Lepš et al., 2006; Wong et al., 2019), and based on their availability for most of the recorded species. We focused primarily on phenological traits and size parameters of floral resources, bees and hoverflies, because these traits are the most important characteristics influencing plant–pollinator communities and their responses to plant invasion (Daniels & Arceo-Gómez, 2020; Grass et al., 2014; Martin et al., 2015). Although it would have been preferable to use quantitative and more specific traits in some cases, for example, floral colour spectral reflectance rather than human-eye based categories (Chittka, 1992), or tongue length in millimetres rather than body sizes (Haverkamp et al., 2016), such trait data were not available for the majority of the species, preventing the use of trait-based analyses in the case of a high proportion of missing values (Kohli & Jarzyna, 2021; Perronne et al., 2017; Wong et al., 2019). At the present time, the traits that we used here were the best

available species-level proxies for functional relationships between plant invasion and plant–pollinator systems.

For insect-pollinated flowering plant species, we assigned the following traits: average of the first and last month of the flowering period, hereafter 'mid-flowering time' (Király, 2009); floral size (converted to centimetres; www.ct-botanical-society.org; www.illinoiswildflowers.info/; www.infoflora.ch; www.luontoportti.com; www.minnesotawildflowers.info; www.wikipedia.org; Heß et al., 2013; Mehlhorn, 2020; Weber et al., 2013); flower colour (assessed by human-eye perception, simplified to nine colours: blue, green or brown, lilac, pink, purple, red, violet, white and yellow; Klotz et al., 2002); and flower type (sensu Kugler, 1970; simplified to nine categories: bell-shaped, disk, flag, funnel, head, lip, pollen, stalk disk, and 'other' [a few species with trap flowers or wind-pollinated but occasionally visited flowers]; Klotz et al., 2002). Missing floral size and colour data were completed by measuring scaled photographs or drawings (from: www.gbif.org; Király, 2009; and by species-specific photographs from the internet).

For hoverfly species, we used the following traits: average of the first and last month of flight period, hereafter 'mid-flight time' (Speight, 2010); and body size (body length in millimetres, as the average of min–max values; Tóth, 2017).

For bee species (similar to some previous studies, e.g., Carrié et al., 2017; Fornoff et al., 2017), we used mid-flight time, body size (mean inter-tegular distance in millimetres; Cane, 1987), guild of tongue length (long: Apidae and Megachilidae; short: other taxa), degree of feeding specialisation or lecty (oligolectic, polylectic or kleptoparasitic, i.e., cuckoo bees), pollen moisture for transport (i.e., how the pollen is carried: dry, moistened with floral oil, moistened with nectar, carried in crop or no transport in the case of kleptoparasites), and sociality (eusocial: raising the offspring together with other females; solitary including communal: building nest and providing food for the offspring alone; parasite: laying eggs in the nests of other wild bees). Most of the data were available from the ALARM project, further developed by Stuart Roberts (Settele et al., 2017). Missing trait data were gathered from the literature (Carrié, 2016; Fortel et al., 2014; Kendall et al., 2019; Kratschmer, 2019) except for a few cases of missing inter-tegular distance data that were measured on scaled photographs from v3.boldsystems.org, www.bwars.com, www.gbif.org, or www.wildbienen.de.

Many indices used in functional ecology are sensitive to missing data. Therefore, imputation of these missing records is highly recommended (Johnson et al., 2021; Penone et al., 2014; Perronne et al., 2017). Hence, in cases where trait data were not available in any databases or literature, we used data of the closest relative species having similar properties, and/or we used the average or most common values in its genus.

Statistical analyses

Floral trait dissimilarities

We tested whether there were significant dissimilarities among the focal invasive and native plant species in their floral traits, since these differences can increase the functional diversity of floral resources (Gallien & Carboni, 2017; Hejda & de Bello, 2013) offering new opportunities for pollinators, and thus changing the pollinator communities (see further analyses). Therefore, we calculated the mean floral trait differences based on all the collected traits together between each focal invasive plant and its co-flowering native species (Gibson et al., 2012; Parra-Tabla et al., 2019). We pooled the species lists of the flowering plant species in the invaded and control sites for the sampling date during the flowering period of the invasive plants, and calculated floral trait dissimilarity indices between each co-flowering plant species pair (invasive–native and native–native). We calculated the per-species mean floral trait dissimilarities weighted by flower abundances, using the 'gawdis' calculation (de Bello et al., 2021). Then, we compared these dissimilarities of co-flowering native plants to the mean floral trait dissimilarity between focal invasive and native plant species, using one-tailed one sample *t*-tests. This means that we tested whether the mean of the distribution of dissimilarities among co-flowering native plants is smaller than the mean of dissimilarities among invasive species and natives. We tested the control and invaded sites, as well as each focal invasive species separately (Table 2). To explore and disentangle the differences in phenology, morphology and a set of key traits together, we presented further univariate and multivariate calculations in the '*Complementary univariate and multivariate calculations for Floral trait dissimilarities and Functional diversity*' section of the Appendix S1.

Functional diversity

We tested the differences in functional diversity of the overall floral, hoverfly and bee communities between invaded and control sites. Functional diversity reflects the difference between species in their functional traits to maximise niche utilisation in the community (see 'diversity hypothesis'; Fornoff et al., 2017; Song et al., 2014). We calculated Rao's quadratic entropy as a measure of functional diversity (hereafter RaoQ; Botta-Dukát, 2005; Lepš et al., 2006), for each site sampled for the 10 invasive plant species on each of the two sampling dates, for flowers, hoverflies and bees separately, if there was at least one specimen recorded or captured in both parts of the site pairs. We used the 'gawdis' dissimilarity calculation (de Bello et al., 2021) for all the collected traits together (Table 2; note: we presented further univariate and multivariate calculations in the '*Complementary univariate and multivariate calculations for Floral trait dissimilarities and Functional diversity*' section of the Appendix S1). We applied generalised linear mixed models (GLMMs) with the Tweedie distribution (Venables & Ripley, 2002; Zuur et al., 2009). To reveal the general effects, we combined data for all 10 studied invasive plant species, and analysed separately for the two sampling dates. Site invasion (control vs. invaded sites) was the explanatory variable, while the focal invasive plant species and the paired sampling structure were treated as nested random factors (1|invasive_species/site_pair_code). To reveal all the differences specific to a given focal invasive species, we fitted similar models that also estimate the differences between invaded and

control sites (i.e., site invasion) for each focal invasive species separately, while handling them in one model, improving standard error estimates and avoiding increased Type I errors due to multiple testing. In these models, the explanatory variables were the 10 focal invasive species with reference to zero, and the interaction between invasive species and site invasion (i.e., ~0 + invasive_species + invasive_species:site_invasion), while the site pairs were specified as a random factor (1|site_pair_code). All analyses were run separately for taxonomic groups and for sampling dates (Table 2).

Multilevel method to assess the effect of invasion on trait-abundance relationships

We were interested in how the community compositions of flowering plant, hoverfly and bee species might be mediated by their traits and their interaction with invasion. We applied the multilevel method of ter Braak (2019; MLM3) to explore how site invasion (as an environmental factor), traits and their interaction, relate to community composition (i.e., relative abundances of species). The approach is equivalent to a random slope GLMM with species abundance as the response variable and species traits, environmental factors and their interactions as explanatory variables. The random factors are the species along with environment factors (i.e., the effect of environment was allowed to vary by species) and sites along with traits (i.e., the effect of traits was allowed to vary among sites). If this type of GLMM fit the data well (i.e., explained the observed abundances), it suggested that community composition was driven by the environment through the trait distribution of the given community.

We applied GLMMs with a Poisson distribution where the response variables were floral, hoverfly, or bee species' abundances recorded at the site level in the invaded or the control site. We assigned a zero value to a missing species in a given site if it was recorded in its site pair. We built two models for each numerical trait where the explanatory (fixed) variables in the null model were second-order polynomials (i.e., linear and quadratic terms) of the centred numerical trait and site invasion, while the full model also included their interaction (i.e., ~poly(trait,2) + site_invasion + poly(trait,2):site_invasion). In the case of categorical traits, the null model included the trait variable and the site invasion, while the full model also included their interaction as an explanatory variable. The null-models hypothesized that abundance depends on traits, and are influenced by invasion, but the effect of invasion does not depend on the traits of recipient species. In the full model the effect of invasion depended on traits of recipient species, thus comparing the two models, we tested the presence of trait specific impacts of invasion. We used random slope models, where the random factors were the (flower, hoverfly, bee) species along with the site invasion (1 + site_invasion|species_name; i.e., the environmental effect, here the invasion, was allowed to vary by species) and the paired sampling structure along with the trait (1 + trait|site_pair_code; i.e., the effect of traits were allowed to vary by sites). Full and null models were compared by ML-ratio test. If this test was significant (i.e., $p < 0.05$), and if p-value of the given interaction was <0.05, we extracted the model estimates for the interaction (i.e., trait explained differences in community composition between invaded and control sites). Note that the full model could be better without any significant interaction, suggesting that there were some trait-based patterns without specific linkage to a given trait. We ran these analyses separately for both the two sampling dates, for the traits, for the 10 focal invasive plant species separately, and also on all focal invasive species together as a pooled analyses (Table 2). Through these analyses, our aim was only an explanatory investigation to reveal the important traits in this system. We were aware that the repeated analyses on the different focal invasive species, on multiple traits and two sampling occasions may increase the Type I error rate. However, we did not aim to use the exact effect sizes from models. These analyses on all the data of invasive plants, sampled guilds, sampling occasions, and traits needed comparable models, therefore, we used the same (Poisson) distribution and model parameters throughout. Note: we had to exclude one outlier (i.e., an extremely high abundance value in the floral data) for *S. lanceolatum* and five outliers (including the previous one) for pooled analyses of samples before flowering of focal invasive species.

During the flowering period of the invasive plants, functional diversity and the multilevel method for the overall floral resources were calculated with and without the focal invasive plant species. In the case of *A. artemisiifolia*, we did not apply analyses of floral trait dissimilarities, as we calculated functional diversity and multilevel method for floral resources only without invasive species, because the flower abundances of this wind-pollinated species were not recorded in the field.

The local abundance of honey bees is usually determined by beekeeper activities, which is not our primary interest here. Hence, we ran separate analyses with honey bees included and excluded from the bee community, to reveal the functional diversity, and the effect of invasion on trait-abundance relationship in bee communities, with and without honey bees. In the main text, we focus mostly on the results of wild bee communities without honey bees, while we also present the results on bee communities including honey bees in the Appendix S1.

The statistical analyses were carried out using R 4.2.1 statistical environment (R Core Team, 2022) using the 'cluster' package ver.2.1.4 and 'gawdis' ver.0.1.3 for trait dissimilarities (de Bello et al., 2021; Maechler et al., 2019), 'FD' ver.1.0–12.1 for calculating RaoQ values (Laliberté et al., 2014; Laliberté & Legendre, 2010), 'lme4' ver.1.1–30 and 'glmmTMB' ver.1.1.5 for GLMMs (Bates et al., 2015; Brooks et al., 2017).

RESULTS

Floral trait dissimilarities

From the nine insect-visited invasive plant species (*A. artemisiifolia* being primarily wind-pollinated), five (*A. syriaca*, *G. aristata*, *I. glandulifera*, *R. laciniata* and *S. lanceolatum* agg.) showed significantly different floral traits compared with co-flowering native species (Figure 1; Table A2; the results on further type of dissimilarity calculation can be found in Appendix S1).

Functional diversity

Before the flowering period of the invasive plants, the functional diversity (i.e., RaoQs) of floral traits was significantly higher in sites invaded by *A. artemisiifolia*, the RaoQs of hoverflies were lower in sites invaded by *E. canadensis*, *R. japonica* and for pooled analysis, and the RaoQs of wild bees were lower in sites invaded by *S. lanceolatum* (Figure 1; Table A3). During the flowering period of the invasive

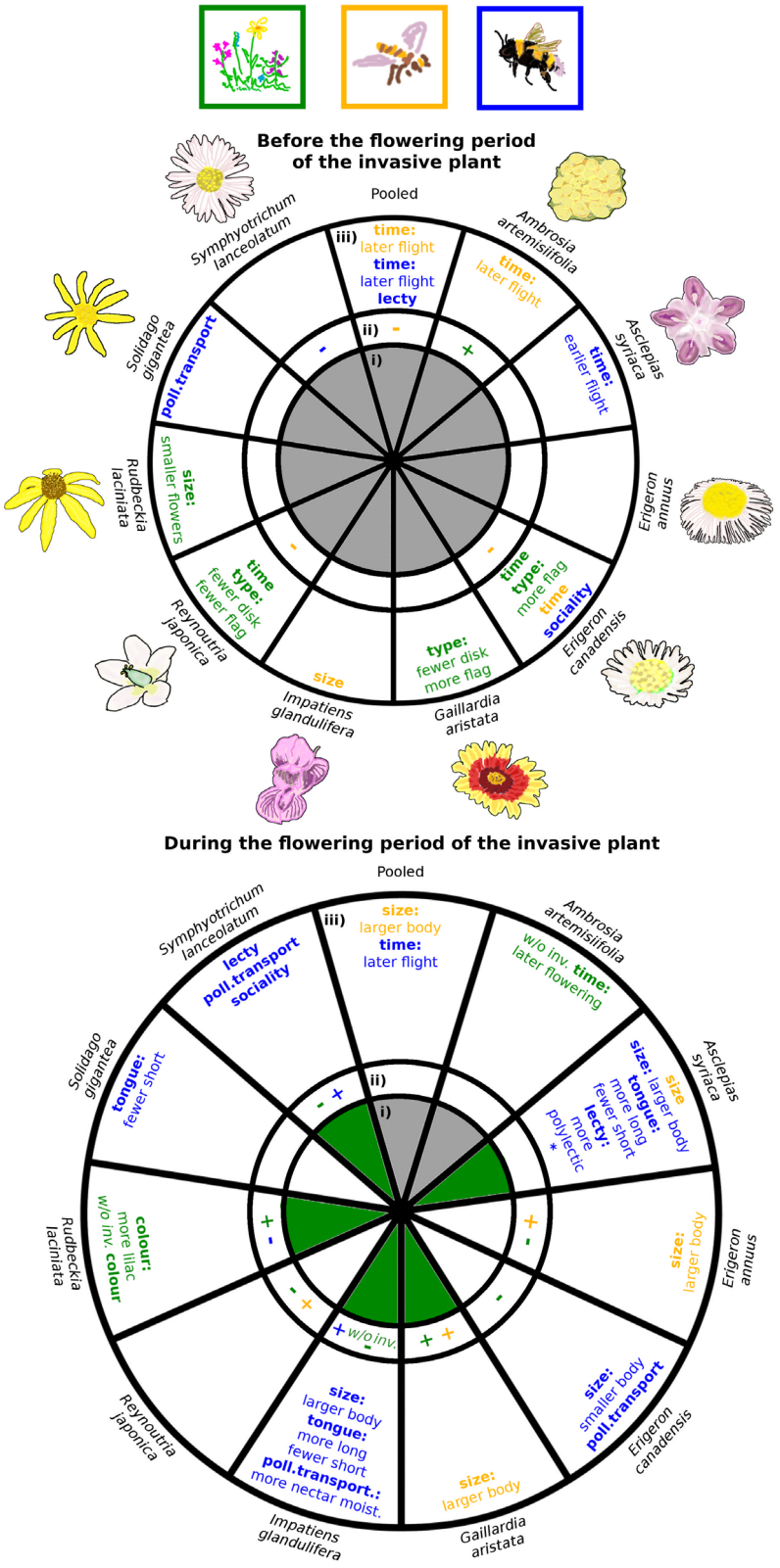

FIGURE 1 Legend on next page.

plants, the RaoQs of floral traits were higher in sites invaded by *G. aristata* and *R. laciniata*, but lower in sites invaded by *E. annuus*, *E. canadensis*, *R. japonica*, *S. lanceolatum* and in analysis without focal invasive species in sites invaded by *I. glandulifera* (Figure 1; Table A3). The RaoQs of hoverflies were higher in sites invaded by *E. annuus*, *G. aristata* and *R. japonica*, while the RaoQs of wild bees were lower in sites invaded by *R. laciniata*, and higher in sites invaded by *I. glandulifera* and *S. lanceolatum*, as well as at the sampling carried out during the flowering period of the invasive plants (Figure 1; Table A3). The RaoQs of bees including the traits of honey bees were significantly lower in sites invaded by *S. lanceolatum* at the sampling carried out before the flowering period of the invasive plants, and in the case of *G. aristata*, *R. laciniata* and *S. gigantea*, at the sampling carried out during the flowering period of the invasive plants (Table A7).

Multilevel method to assess the effect of invasion on trait-abundance relationships

In 15.5% of the cases, the full model was the best model, suggesting that the effect of invasion on abundance depends on the traits of recipient species (Figure 1; Tables A8–A10). We found that the best explanatory traits (i.e., size and time) significantly explained the effects of invasion on communities. For example, in invaded sites, we found larger hoverflies in general, smaller bees (in the case of *E. canadensis*; a plant with shallow flowers), larger and long-tongued bees (in the case of *A. syriaca* and *I. glandulifera*; plants with deep flowers), as well as hoverflies and wild bees with a later mid-flight time.

Specifically, for the pooled dataset, the full model was the best in the case of mid-flight time of hoverflies, wild bees, and lecty (i.e., feeding specialisation) of wild bees at the sampling carried out before the flowering period of the invasive plants, as well as body size of hoverflies and mid-flight time of wild bees at the sampling carried out during the flowering period of the invasive plants (see details in Figure 1; Tables A8–A10). For the species-level analyses, we also found that the full models were the best in some cases, but the traits that were associated with invasion (i.e., demonstrating significant interaction effects) differed among the focal invasive species (Figure 1; Tables A8–A10). For the sampling conducted before the flowering period of the invasive plants, we found more flag flowers in sites invaded by *E. canadensis* compared with control sites, fewer disk and more flag flowers in invaded vs. control sites for *G. aristata*, fewer disk and flag flowers in sites invaded by *R. japonica*, smaller flowers in sites invaded by *R. laciniata*, hoverflies with later mid-flight time in sites invaded by *A. artemisiifolia*, and wild bees with earlier mid-flight time in sites invaded by *A. syriaca* (Figure 1; Tables A8–A10). During the flowering period of the invasive plants, we found more lilac flowers in sites invaded by *R. laciniata*, plants with later mid-flowering time in sites invaded by *A. artemisiifolia* (according to the analyses without focal invasive species) compared with the control sites (Figure 1; Table A8). We found larger hoverflies in sites invaded by *E. annuus* and *G. aristata*, larger and long-tongued wild bees in *A. syriaca* and *I. glandulifera*, smaller bees in *E. canadensis*, and fewer short-tongued bees in sites invaded by *S. gigantea* compared with the control sites (Figure 1; Tables A9 and A10). In the case of further bee traits, during the flowering period of the invasive plants, we found also more wild bees that transport pollen moistened with nectar in sites invaded by *A. syriaca* and *I. glandulifera*, but fewer wild bees that transport dry pollen without moistening, fewer solitary, more primitively eusocial species, and more polylectic bees, in sites invaded by *A. syriaca*, compared with the control sites (Figure 1; Table A10). There were fewer changes between analyses on bees including honey bees compared with analyses only on wild bees for the sampling carried out before the flowering period of the invasive plants, while more for the sampling conducted during the flowering period of the invasive plants (Table A11). For example, including honey bees, we found larger bees in sites invaded by *S. gigantea* and *S. lanceolatum*, but lost the similar patterns for *A. syriaca* and *I. glandulifera* during the flowering period of the invasive plants (see details in Table A11).

DISCUSSION

Across our case studies on the 10 invasive plant species, we found some dissimilarities in floral traits among the invasive and native flowering plant species, and also some differences in functional diversity and trait distribution between the invaded and uninvaded plant–pollinator communities. The species-level effects on plant–pollinator

FIGURE 1 Results of (i) floral trait dissimilarity (inner sector of the circle), (ii) functional diversity (middle sector), and (iii) multilevel method, assessing the invasion–trait–community relationships (outer sector) for floral resources (green), hoverflies (orange) and wild bees (blue), separately for the two sampling periods. The filled cells (floral trait dissimilarity), symbols (functional diversity) or texts (multilevel method) in cells of circles at the intersection of analyses type and focal invasive species show the significant ($p < 0.05$) differences. For (i), cells indicate that native and invasive species are significantly more different than co-flowering natives (details in Table A2). For (ii), cells with '−' symbol show lower, while '+' show higher functional diversity (RaoQ) on invaded sites (details in Table A3). For (iii), cells show the traits (with bold) where the full model of multilevel method is better ($p < 0.05$) and show the variables of a given trait (with normal font) if the interaction in the model was significant ($p < 0.05$; but note the full model could be the best model without any significant interactions, in which case we present only the trait; see details in Tables A8–A10). We indicate that a given variable was more or fewer (categorical traits), earlier or later (mid-flowering time, mid-flight time) and smaller or larger (size) on invaded sites compared with control sites. Empty cells mean no significant differences. Abbreviations: poll. transport, pollen moisture for transport; w/o inv., calculation without invasive plant species. Blue* is an addition for wild bee traits in *Asclepias syriaca* at sampling during the flowering period of the invasive plants: pollen moisture for transport: fewer dry and more moistened with nectar; sociality: more eusocial and fewer solitary. Floral trait dissimilarity and floral resources without focal invasive species are only interpretable for floral resources at sampling during the flowering period of the invasive plants. Drawings of flowers are not scaled.

communities differed among the focal invasive plants with different traits. For example, smaller bees were found on sites invaded by plant species with shallow flowers, while larger and long-tongued bees were found at sites invaded by species with restricted floral access. These results suggest that the invasive plants may also affect pollinator communities through the compatibility or incompatibility of their floral traits with the local pollinators.

The significant differences in floral morphology and phenology between the invasive and native plant species, and the changed functional diversity of floral resources suggest that some of the invasive plant species offer new opportunities for pollinators. These floral trait differences from native species might facilitate the successful establishment and spread of alien plant species (Grass et al., 2014; Hejda & de Bello, 2013; Stout & Tiedeken, 2017). For example, floral size as a signal to pollinators often reflects resource (nectar and pollen) availability (Ortiz et al., 2021). Hence, different floral size of invasive plants is expected to affect pollinators through their resource requirements and mouthpart sizes (i.e., nectar access capability; Daniels & Arceo-Gómez, 2020; Grass et al., 2014; Pauw et al., 2009). In this study, during the flowering period of focal invasive plants, we found larger hoverflies in invaded sites in the case of the pooled analyses, for *E. annuus*, and *G. aristata* invasion specifically. We also found smaller bees in sites invaded by *E. canadensis* which has shallow flowers, and larger and long-tongued wild bees in sites invaded by *A. syriaca* and *I. glandulifera* which have large, deep flowers (see Table 1), aligning with the previously shown higher abundance of *Bombus* spp. in sites invaded by *A. syriaca* and *I. glandulifera* (Kovács-Hostyánszki et al., 2022; Szigeti et al., 2020). The phenology of the three summer-flowering (*G. aristata*, *I. glandulifera*, *R. laciniata*) and one autumn-flowering (*S. lanceolatum*) invasive species (Table 1), that showed floral trait dissimilarities, compared with the average phenology of the native floral communities (see the univariate calculation on mid-flowering time, in the Table A2), may explain the dominance of hoverflies and wild bees with later mid-flight time in invaded sites. These results suggest that some of the invasive plant species fill gaps in the morphological and phenological niche space (as already shown for gardens by Tew et al., 2022).

Despite the above-mentioned results, many of the tested trait variables and applied analyses suggested species-specific, mixed or neutral trait-based effects of plant invasion. Thus, our hypotheses about strong trait-based differences in floral and pollinator community caused by plant invasion, and lower functional diversity in invaded habitats were only partly supported. Similarly, previous studies also found mostly neutral and highly contradicting trait-based effects of invasion on plant–pollinator systems (Charlebois & Sargent, 2017; Martin et al., 2015; Parra-Tabla et al., 2019). Despite these results, we still suggest that invasive plants can have a significant effect on some of the basic characteristics of pollinator communities (e.g., abundance and diversity, Bezemer et al., 2014; Davis et al., 2018) by changing the functional diversity of floral resources. This impact should be especially strong, if the traits of invasive species differ substantially from the traits of native species, thereby filling in unused functional space, offering new types of resources for pollinators, and dominating the 'floral market' (Chittka & Schürkens, 2001; Fenesi et al., 2015; Goodell & Parker, 2017; Hejda & de Bello, 2013). Therefore, in the next section, we propose some of the potential causes, uncertainties and problems related to these neutral results and potential approaches that could be considered in future studies.

Explanation of neutral results and recommendations for further studies

There are at least two basic explanations for the neutral effects of plant invasion on trait-based pollinator community assembly: (1) invasive plants genuinely do not change the pollinator communities through their functional composition and invasion may cause lower effects in pristine than in more degraded habitats, or (2) limitations of the datasets themselves may mask trait-based effects, in spite of the various approaches used here.

The first explanation could be plausible, if there is a relatively easy integration capability of invasive plant species into the native plant-pollinator networks with few changes in native pollinator communities, coupled with the dynamic adaptation ability of the plant–pollinator interactions (Hiraiwa & Ushimaru, 2017; Traveset & Richardson, 2014). This could be fostered by similar floral traits of the alien plants to the natives (Parra-Tabla et al., 2019). However, the opposite could also occur, and pollinator communities could be persistent and robust against the introduction of invasive alien species through niche and behavioural flexibility (or complementarity) within pollinator species or functional groups, or through the different responses of functionally similar species (Hiraiwa & Ushimaru, 2017; Schleuning et al., 2015; Zhang et al., 2020). Furthermore, the different pollinator guilds might show distinct changes in the same type of traits under plant invasion (Grass et al., 2014). In addition, a less degraded, more natural and genuinely heterogeneous landscape could be a substantial source of pollinators (Garibaldi et al., 2022; Gill et al., 2016; but see also Lázaro & Gómez-Martínez, 2022), which may also be the case for adjacent invaded sites (Charlebois & Sargent, 2017), and so mask the local effect of invasion. Furthermore, if the alien plant species differs markedly from the native species, its presence may increase functional diversity initially. But when it becomes abundant, it could potentially reduce functional diversity. This hypothesized, but unrevealed pattern could also cause mixed effects among invasive species.

For the second (data limitation) explanation, we highlight some factors that might mask the results. Pollinator communities can be shaped by several environmental factors besides plant invasion (Carrié et al., 2017; Martin et al., 2015). For example, invasive plants can influence pollinators, not only through their floral attributes, but also the structural changes of the vegetation (Fenesi et al., 2015; Hejda & de Bello, 2013; Vilà et al., 2011). A high abundance of managed honey bees might also drive the relationship between invasive plants and wild pollinator communities (e.g., by facilitating invasion, Parra-Tabla et al., 2019), especially during the flowering period of particular invasive plants that are intensively used by beekeepers as bee pastures (Botta-Dukát & Balogh, 2008). Our results are in line with this explanation; honey bees decreased the functional diversity and changed

the trait-community mostly during the flowering period of the invasive species, when they were relatively abundant in the invaded sites (Kovács-Hostyánszki et al., 2022). Other masking factors, such as the sampling intensity, the studied organisational, trophic, and spatio-temporal scales, or the resolution of trait measurement, could be limited compared with the complexity needed in a study with trait-based aims and focal systems (Perronne et al., 2017). For example, floral colours based on human-eye perception may have less explanatory power than standardised perceptual colour distance values fitted to the perception of the investigated pollinator taxa (including even the ultraviolet spectrum, Chittka, 1992). Trait-based analyses are still under rapid development, and the results of analyses may partially depend on the type of traits selected, and the indices and analytical methods used (de Bello et al., 2021; Hejda & de Bello, 2013; Mammola et al., 2021; ter Braak, 2019). Whereas a single type of calculation method could mask potential functional effects (Grass et al., 2014; Hejda & de Bello, 2013; Perronne et al., 2017; Schleuning et al., 2015; Song et al., 2014). Therefore, we recommend that future functional-based studies on plant–pollinator systems should consider increasing sampling over greater spatio-temporal scales and different levels of organisation, from individual behaviours (e.g., flower visitation and pollination success) to monitoring whole networks, including additional traits of the wider insect community. Ideally, such studies should also be undertaken over the long-term, and across various habitat types along disturbance gradients (e.g., from pristine to degraded landscapes; Charlebois & Sargent, 2017; Perronne et al., 2017; Song et al., 2014; Stout & Tiedeken, 2017; Vanbergen et al., 2018). Trait resolution should be maximised (Kohli & Jarzyna, 2021), using more relevant and continuous traits, considering that the different traits have different biological importance, measurability, usability, availability, quality and resolution (Bartomeus et al., 2018; Carrié et al., 2017; Daniels & Arceo-Gómez, 2020; Fornoff et al., 2017). Traits should be measured in situ, using standardised methods (Bartomeus et al., 2018; Wong et al., 2019) that aim to capture intraspecific trait variation wherever possible (e.g., due to ontogenetic plasticity, Perronne et al., 2017; Zhang et al., 2020). Environmental changes can have a direct effect on individuals, influencing the trait distribution of populations, and therefore the whole community assembly (Moretti et al., 2017; Perronne et al., 2017; Wong et al., 2019). The currently available trait databases are developing rapidly and represent many years of data harvesting and validation, but they could still be refined further (e.g., measuring more and more direct, relevant traits by standard protocols, such as dispersal ability, hairiness, fecundity, flower handling behaviour of pollinators, as well as detailed nectar and pollen data on insect-pollinated plants) and be available as open-access resources (Bartomeus et al., 2018; Kendall et al., 2019; Kohli & Jarzyna, 2021; Parreño et al., 2021). Finally, as suggested by Song et al. (2014), the correct, fine-scale measurement of a few traits on all the sampled individuals simultaneously is often challenging, but there are situations, when it can be more effective, and offers more information on functional relations, than the coarse-scale measurement of trait-mean values for species in the community. Although not all the available traits, indices, and analytical approaches can be used simultaneously, we suggest that widely used, well-planned and standardised indices, as well as some complementary analytical approaches should be applied in parallel to help disentangle the complexities of the mechanistic impact of invasion on plant–pollinator system in future studies.

Although trait-based ecology is a potentially powerful approach to investigate mechanisms underlying community assembly (Bartomeus et al., 2018; Carrié et al., 2017; Hejda & de Bello, 2013; Moretti et al., 2017; Perronne et al., 2017; Wong et al., 2019), it is still open to further improvements (de Bello et al., 2021; Kohli & Jarzyna, 2021; ter Braak, 2019). For instance, the set of methodological choices (i.e., designing, sampling, measuring, analysing) strongly influences the key ecological conclusions of a study (Charlebois & Sargent, 2017; Mammola et al., 2021; Perronne et al., 2017). Thus further detailed studies are needed to fill key knowledge gaps in the functional ecology of interactions between plants, pollinators, and environment, using recent recommendations on trait-based approaches (Kohli & Jarzyna, 2021; Moretti et al., 2017; Perronne et al., 2017; Schleuter et al., 2010; Song et al., 2014; Wong et al., 2019).

CONCLUSIONS

Plant invasion alters both ecological patterns and processes. However, like a number of previous studies, we found several species-specific, but also neutral effects of plant invasion on functional diversity and trait distributions of plant–pollinator communities. The differences in floral morphological and phenological characteristics between the invasive and native species seem to influence functional diversity, size and flight time of pollinators in invaded sites. In a few cases, the trait-based relation is more invasive species specific and obvious, such as smaller bees in communities invaded by plants with shallow flowers, and larger, long-tongued bees in communities invaded by plants with deeper flowers. However, our results support only a part of our hypotheses, and several questions remain unanswered. To understand trait-based effects of invasive species, we need more case studies on a wider scale of invasive plants, more effort in data gathering and analysis, as well as meta-analytical syntheses. Since functional diversity of plant–pollinator communities may be rapidly declining in some regions across the globe, it is particularly important to understand the full range of factors structuring pollinator communities (including human-induced environmental changes) from local to global scales, as well as the consequent ecological and evolutionary processes. Better knowledge of the functional diversity of pollinator communities can help inform decision-making on the conservation of wild flowers and their pollinators as well as the management of agro-ecosystems to ensure the availability of important crop pollinators.

AUTHOR CONTRIBUTIONS

Viktor Szigeti: Conceptualization (lead); data curation (lead); formal analysis (lead); investigation (lead); methodology (equal); project administration (equal); resources (equal); validation (equal); visualization (lead); writing – original draft (lead); writing – review and editing

(lead). **Annamaria Fenesi:** Conceptualization (equal); data curation (equal); investigation (equal); methodology (equal); resources (equal); supervision (equal); validation (equal); writing – original draft (equal). **Zoltán Botta-Dukát:** Conceptualization (equal); formal analysis (equal); validation (equal); writing – review and editing (equal). **Michael Kuhlmann:** Data curation (equal); writing – review and editing (equal). **Simon Potts:** Data curation (equal); writing – review and editing (lead). **Stuart Roberts:** Data curation (equal); writing – review and editing (equal). **Zoltán Soltész:** Data curation (equal); investigation (equal); validation (equal); writing – review and editing (equal). **Edina Török:** Data curation (equal); investigation (equal); validation (equal); writing – review and editing (equal). **Anikó Kovács-Hostyánszki:** Conceptualization (lead); data curation (equal); formal analysis (equal); funding acquisition (lead); investigation (equal); methodology (equal); project administration (lead); resources (lead); supervision (lead); validation (equal); visualization (supporting); writing – original draft (lead); writing – review and editing (lead).

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CONFLICT OF INTEREST STATEMENT

There are no conflicts of interest to be declared among the authors of the manuscript.

DATA AVAILABILITY STATEMENT

The original field data of floral resources, bees and hoverflies, as well as the coordinates of the sampling sites are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.05qfttf76.

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SUPPORTING INFORMATION

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

Data S1. Supporting Information.

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