



HAL
open science

Predator and pollinator? An invasive hornet alters the pollination dynamics of a native plant

Sandra V Rojas-Nossa, Thomas A O'Shea-Wheller, Juliette Poidatz,
Salustiano Mato, Juliet Osborne, Josefina Garrido

► **To cite this version:**

Sandra V Rojas-Nossa, Thomas A O'Shea-Wheller, Juliette Poidatz, Salustiano Mato, Juliet Osborne, et al.. Predator and pollinator? An invasive hornet alters the pollination dynamics of a native plant. Basic and Applied Ecology, 2023, 71, pp.119 - 128. 10.1016/j.baae.2023.07.005 . hal-04180700

HAL Id: hal-04180700

<https://hal.inrae.fr/hal-04180700>

Submitted on 13 Aug 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial - NoDerivatives 4.0 International License



RESEARCH PAPER

Predator and pollinator? An invasive hornet alters the pollination dynamics of a native plant

Sandra V. Rojas-Nossa^{a,*}, Thomas A. O'Shea-Wheller^b, Juliette Poidatz^{b,c}, Salustiano Mato^a, Juliet Osborne^{b,*}, Josefina Garrido^a

^a Department of Ecology and Animal Biology, Faculty of Sciences, University of Vigo, 36310, Vigo, Pontevedra, Spain

^b Environment and Sustainability Institute, University of Exeter, Penryn, Cornwall, TR10 9FE, UK

^c UMR PVBMT Peuplements Végétaux et Bioagresseurs en Milieu Tropical, CIRAD, 97 410 Saint Pierre, La Réunion, France



ARTICLE INFO

Keywords:

Asian hornet
Competition
Hedera hibernica
Invasive species
Pollination
Predation
Social wasp
Vespa velutina

ABSTRACT

Invasive vespids are able to disrupt native species assemblages, modify ecological dynamics, and degrade ecosystem services. However, it is often difficult to quantify such effects within invaded ranges, principally due to the complexity of interactions, and a lack of comparative pre-invasion controls. In this study, we thus examine the effects of an invasive hornet, *Vespa velutina*, upon native species densities and pollination in a major food plant, *Hedera hibernica*. Using the highly heterogeneous distribution of *V. velutina* in a coastal area of the northwestern Iberian Peninsula, we assessed the impact of differing hornet abundance on insect diversity, flower visitation frequency, and predator-prey interactions. We then examined resultant effects upon the pollination success of *H. hibernica*, in the form of fruit and seed set. Our results demonstrated that in areas with high *V. velutina* abundance, the floral visitation frequencies and durations of insect pollinators were significantly altered. Effects varied widely across insect families, reflected in the differing predation success rates of *V. velutina* upon various native pollinators, in tandem with competitive exclusion. Interestingly, *V. velutina* was itself a frequent floral visitor, becoming the most common nectar forager in areas where it was abundant. In spite of this, *H. hibernica* reproductive success was significantly degraded in these areas, resulting in reduced seed set. As such, *V. velutina* appears to have multidirectional effects upon pollination services, first as an insect predator, and second as a nectar competitor and pollinator. Crucially, our findings suggest that *V. velutina* is an inferior pollinator when compared to the native species that it displaces, resulting in a net reduction in pollination efficacy, and hence reproductive success in *H. hibernica*. This study thus reveals the profound effects of an invasive vespid on native species through both competitive and predatory interactions.

Introduction

European pollination systems are currently experiencing the invasion of *Vespa velutina*; a social vespid requiring large quantities of carbohydrate and protein across an extended foraging period (Monceau et al., 2013). This has the potential to disrupt the mutualistic interactions of plants and insect pollinators, raising concern over potential impacts upon pollination services, and concordant effects on the native species that rely on entomophilic seeds and fruit (Traveset & Richardson, 2006). When hunting in the vicinity of blooming plants, *V. velutina* can diminish the floral visitation rate and duration of certain pollinating insects, thus influencing the pollination dynamics of wild plant species (Rojas-Nossa & Calviño-Cancela, 2020). Notably however, *V. velutina* is

both a floral visitor and an insect predator, suggesting that its presence may result in existing pollination services either increasing (via additional *V. velutina*-mediated pollination) or decreasing (via predation of other pollinators and competition for nectar). The directionalities of such effects depend upon the relative impact of each function in the overall plant-pollinator community, and thus are complex to untangle.

Whilst the appearance of *V. velutina* in Europe is relatively recent (Monceau et al., 2014), social vespid invasions are an ongoing global concern, impacting ecosystems via resource exploitation and predation (Beggs et al., 2011; Rankin, 2021). Carbohydrates, in the form of nectar, fruit, and honeydew, are keenly consumed, often resulting in cascading effects for native ecosystems (Richter, 2000). For example, in the southern beech (*Nothofagus* spp.) forests of New Zealand, the

* Corresponding authors.

E-mail addresses: rojas@uvigo.es (S.V. Rojas-Nossa), J.L.Osborne@exeter.ac.uk (J. Osborne).

<https://doi.org/10.1016/j.baae.2023.07.005>

Received 14 July 2022; Accepted 15 July 2023

Available online 17 July 2023

1439-1791/© 2023 The Author(s). Published by Elsevier GmbH on behalf of Gesellschaft für Ökologie. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

consumption of honeydew by invasive wasps (*Vespula* spp.) impacts native community assemblages and dynamics, including birds, insects, and soil biota, with consequences spanning trophic levels (Wardle et al., 2010). By consuming floral nectar, vespids reduce overall nectar availability for other pollinators, consequently altering pollination services and decreasing the fruit set of plants (Hanna et al., 2014). Further, the exponential population growth of vespid colonies is maintained by a substantial protein intake, obtained from both the hunting of insects, and by scavenging (Monceau et al., 2014).

A common visible impact of the ingression of vespids into an area, and particularly of hornets (*Vespa* spp.), is the predation of managed honey bees (*Apis* spp.) (Laurino et al., 2020). However, a variety of other pollinator groups are also common prey, especially those visiting patches of flowers at which hornets hunt (Rojas-Nossa & Calviño-Cancela, 2020; Rome et al., 2021). As such, pollination services may be broadly affected (Beggs et al., 2011; Liang et al., 2022), with specific concern for wild pollinators. *Vespa velutina* is known to hunt insect pollinators of mint (*Mentha* spp.), disrupting and modifying pollen transfer (Rojas-Nossa & Calviño-Cancela, 2020), yet there is a paucity of data relating to effects upon other plant-pollinator assemblages, many of which constitute keystone species (Bond, 1994). The ivies (*Hedera* spp.) are one such example, being valuable floral nectar sources for pollinators, common in both rural and urban areas, and blooming in the autumn when very few other plants are available (Garbuzov & Ratnieks, 2014). Additionally, ivy fruits are an important food source for birds and mammals in the winter (Jacobs et al., 2010), hence changes in pollination efficacy may have impacts across trophic levels.

Prior evidence indicates that exploitative competition for resources modifies assemblages of native hymenopterans in addition to the direct impacts of predation itself (Wilson & Holway, 2010; Liang et al., 2022). Thus, we wished to investigate the potential effects of *V. velutina* on a system in which it is both a predator, and a pollinator. To achieve this, we focussed on the Atlantic ivy, *Hedera hibernica*, an important but under-studied food source for insect pollinators along the Atlantic coasts of Europe (Grivet & Petit, 2002). We examined whether, as a predator of insect pollinators; or as a pollinator itself, *V. velutina* influences fruit set and seed production at a community scale.

Utilising a range of sites across a gradient of *V. velutina* activity, we assessed whether *V. velutina* has a net “positive” or “negative” effect on *H. hibernica* pollination, through the contrasting behaviours of flower visitation for nectar, and predation of other insects for protein. The specific questions posed were:

- 1) Does predation by *V. velutina* affect the floral visitors of *H. hibernica*?
- 2) Does the abundance of *V. velutina* affect the flower visitation frequency and behaviour of the pollinators of *H. hibernica*?
- 3) Does the abundance of *V. velutina* affect the fruit set and seed production of *H. hibernica*?

Materials and methods

Study system

The Atlantic ivy, *Hedera hibernica*, is a perennial tetraploid liana. It is common in forested, rural, and urban areas of the Atlantic coasts of Europe (Grivet & Petit, 2002). The plant’s climbing or prostrate habit often forms extensive carpets or “patches” consisting of single or multiple individuals (McAllister & Rutherford, 1990). Such patches are able to grow on a diversity of substrates, including tree trunks, cliffs, walls, hedges, and buildings (Melzer et al., 2010). Notably, *Hedera* spp. are dependant on insect pollinators for sexual reproduction, and thus fruit set is significantly reduced when flowers do not receive floral visits (Jacobs et al., 2009).

The reproductive biology of *H. hibernica* is not well understood. In the closely-related species *Hedera helix*, self-pollination is probably absent (Metcalfe, 2005; Jacobs et al., 2009), and studies describing

pollinator assemblages usually report floral visitors for *H. helix* and *H. hibernica* together (Couvillon et al., 2015; Garbuzov & Ratnieks, 2014). This suggests that both ivy species are pollinated by a diversity of dipterans, hymenopterans, lepidopterans, and coleopterans. Additionally, species such as the ivy-bee (*Colletes hederæ*) are oligolectic, obtaining pollen almost exclusively from the flowers of ivy (Bischoff et al., 2005).

The blooming season of *H. hibernica* lasts from August to November. The inflorescences are formed of 5–14 globose umbels (mean = 9 ± 2.6 SD, $n = 41$). Fig. 1A, B), consisting of an apical umbel at the tip of the inflorescence—which is usually the first to bloom—followed by several lateral umbels along the stem. Each umbel has between 2 and 47 flowers (mean = 18.3 ± 6.7 SD, $n = 357$), which progress through two key reproductive stages over time. Immediately after anthesis, both anthers and stigma are present, hence we refer to umbels in this phase as “hermaphrodite” (Fig. 1A). Following this, the petals and anthers fall, and only the ovary and the stigma remain, leaving umbels in a state that we term as “female” (Fig. 1B). Because umbels in the female phase offer only nectar, we aimed to avoid making observations of pollinators during this period. However, to take into account the blooming stage of each site at the time of sampling, we quantified the proportion and number of each flower type for use in further analyses.

Study sites

To test the effect of *V. velutina* activity on pollination dynamics, 19 sites were chosen during July 2019 in a coastal area of northwestern Spain (Pontevedra, Galicia). These sites were located within a patchwork of gardens and orchards, and chosen to encompass a gradient of *V. velutina* activity. At each site, patches of *H. hibernica* measuring approximately 15 m in length and 2 m in height were selected. In order to ensure consistent light conditions between sites, only plants with south-facing flowers were chosen.

Quantification of *Vespa velutina* abundance

We assessed hornet abundance at each site using two complementary methods, these provided a measure of *V. velutina* activity both at the time of sampling, and over the broader period of *H. hibernica* pollination:

- 1) Individuals were captured using baited kill-traps from August to October. Specifically, one VespaCatch trap (Veto-Pharma®) filled with 250 ml of VespaCatch liquid attractant (Veto-Pharma®) was deployed at each site. The traps were hung at a height of 1.50 m, at a maximum distance of 400 mm from the plant. Every 14 days, captured insects were collected and the liquid attractant was renewed (Appendix A: Fig. A.1).
- 2) Visual counts were made of *V. velutina* foraging on *H. hibernica* at each site. Specifically, two counts were taken, each over a period of 15 min, with the first occurring at the beginning of the video recording session (see Video recording section), and the second at the end. The behaviour of individual hornets was characterised as: flying, mating, agonistic behaviour, hunting, or feeding on nectar. When two behaviours occurred for the same individual in a single observation, we utilised the combined categories: ‘nectar foraging and hunting’, or ‘nectar foraging and mating’. When hornets were feeding on nectar, detailed observations of each individual were often possible, and in such cases morphological sex determination was performed. Males were readily distinguished by their rounded abdomen tips, and comparatively longer curved antennae.

These two quantification methods were then compared for parity, to ensure that they were representative of relative *V. velutina* abundance over different timescales (Appendix A: Fig. A.2 and A.3).

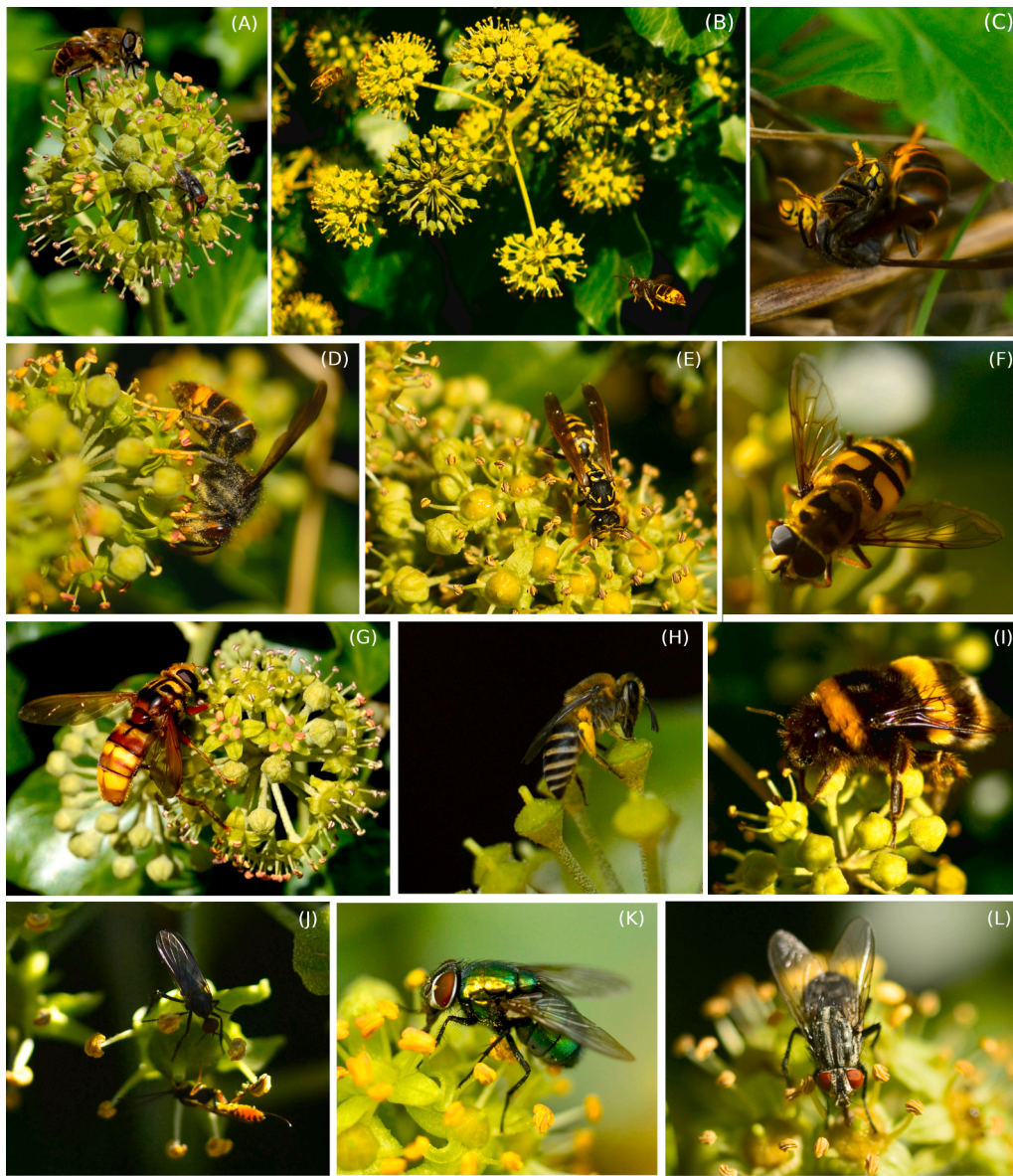


Fig. 1. Blooming phases of the inflorescences of *Hedera hibernica* and examples of the most common insect floral visitors. (A) Hermaphrodite umbel being visited by dipterans. (B) *Vespa velutina* hunting for insects. (C) *Vespa velutina* predating upon a native social wasp of the genus *Vespula*. (D) *Vespa velutina* collecting nectar. (E) *Polistes dominula*. (F) *Myathropa florea*. (G) *Milesia crabroniformis*. (H) *Colletes hederæ*. (I) *Bombus terrestris*. (J) *Empis* and *Ichneumonidae* spp. (K) *Lucilia* spp. (L) *Sarcophaga* spp.

Environmental parameters

To account for environmental conditions and patch characteristics, we quantified the total number of inflorescences in the patch, the proportions of hermaphrodite and female inflorescences, and the number of inflorescences in the sampling frame. We measured ambient climatic conditions at the time of sampling, specifically temperature (°C), wind speed (m/s), illuminance (lx), and relative humidity (%RH) using a PCE-EM 883 portable weather station (PCE Instruments™).

Video recording

From September to October 2019, during the period when both hermaphrodite and female flowers were present on plants, we took video recordings of *H. hibernica* patches at each site. All recordings were made between 10:00 h and 14:00 h, using a GoPro HERO7 camera (GoPro Inc.) placed 400 mm from the plant, thus providing a consistently framed sampling area of 500 × 300 mm. These sampling areas were allocated randomly along the horizontal and vertical planes of each *H. hibernica* patch, to avoid between-site biases.

Predator-prey behaviour

In addition to the video recordings, we conducted separate visual observations of predation behaviour at each site. Observations lasted for 30 min, consisting of 15 min at the beginning of a recording, and 15 min at the end, concordant with the visual counts of *V. velutina* abundance. Specifically, we assessed the identities of insects under attack from *V. velutina* (to the family level), the location of the insect prey at the moment of attack (in flight or on a flower), whether the attack was successful or not, and how the insect reacted if the attack failed (remained on flower, flew to another flower, or left the patch). In cases of successful predation events by *V. velutina*, samples and photos of the predated insects were collected for further identification whenever possible (Fig. 1C).

Floral visitor behaviour

To characterise the behaviour of floral visitors in response to the activity of *V. velutina*, one video sample of 15 min per recording was randomly chosen and analysed. Within this sample, all individual insects appearing in frame were identified to at least the family level, and their

activity over time was recorded using BORIS software (v 7.9.22–2020–11–17, Friard & Gamba, 2016). For each insect, we recorded the time spent in frame, and the number and duration of visits to hermaphrodite and female flowers. To account for variations in flower density across sampling areas, visitation rates were then normalised via the following formula:

$$(\text{Number of flower visits} / \text{number of flowers}) \times 100$$

These observations yielded the subsequent measures: number of insect visits to the observed patch in 15 min (patch visitation rate); number of visits to hermaphrodite and female flowers in 15 min (flower visitation rate); and duration of visits to hermaphrodite and female flowers by individual insects (flower visitation duration). As insects were not marked, we made no assumptions about insect identity when entering or exiting the frame.

Insect pollinators were identified using exemplar specimens preserved in 70% Ethanol, these being captured via a random net sweep of the sampling area following video recordings. Specimens were identified in the laboratory to the most precise taxonomic level possible. Additionally, detailed images of pollinators were collected using an SLR camera (Nikon D3600, with a Nikon Micro Nikkor 55 mm f/2.8 Ai-S lens). All insects appearing in videos were then compared to the exemplar specimens, and cross-referenced with the detailed images, taxonomic keys, field guides (e.g. Willmer, 1985; Chinery, 1986; Leraut, 2007; Aguado et al., 2015), and, where required, were additionally verified by taxonomic experts, to determine identity.

Fruit set and seeds produced per fruit

Before anthesis, two inflorescences per plant were randomly selected, and each was allocated to one of two treatments. The first was a “control” treatment, in which flowers were covered with a tulle bag to prevent insect visits ($n = 20$); and the second was an “open pollination” treatment, in which flowers were left uncovered, thus allowing insect visits across the blooming period ($n = 20$). After blooming, when calyxes began to enlarge and set fruits, inflorescences in the open pollination group were also covered with tulle bags. Consequently, all experimental inflorescences remained covered until the ripening of fruits (December 2019 to January 2020), thus preventing consumption by frugivorous animals.

After fruit ripening, inflorescences were collected and the quantity of fruit produced per umbel was recorded, along with the type of umbel (apical or lateral). This distinction was made due to possible architectural influences on fruit production, as observed in *H. helix* (Metcalfe, 2005). As the calyxes remained on the umbels, revealing the former presence of flowers, it was then possible to determine the total number of flowers per umbel, even in cases where no fruit was produced. Fruit set counts were thus normalised to account for the number of flowers previously present on an umbel (indicating the total quantity of fruit that could have been produced) using the following formula:

$$\text{Number of fruits per umbel} / \text{number of flowers per umbel}$$

Following this, fruits were dissected to quantify the number of seeds produced per fruit.

Range of assessment factors

Analyses were broadly divided into those assessing the effect of *V. velutina* predation and abundance on floral visitor behaviour, and those assessing resultant impacts upon *H. hibernica* fruit set and seed production. In the former case, the influence of environmental conditions was accounted for via the inclusion of local climatic variables.

Summary of floral visitors and predator-prey behaviour

To characterise the range of insect taxa visiting *H. hibernica*, and their

interactions with *V. velutina*, descriptive statistics for species presence and predator-prey interactions (success or failure of *V. velutina* attacks) were calculated (Tables 1 and 2).

Floral visitor behaviour

To assess the impact of *V. velutina* on floral visitor behaviour, we examined the relationship between *V. velutina* abundance and key behavioural dynamics. Specifically, these consisted of insect patch visitation rate, female and hermaphrodite flower visitation rate, and female and hermaphrodite flower visitation duration.

These analyses were conducted across three taxonomic divisions of floral visitors. First, for all insect visitors (excluding *V. velutina*); second, at the order level (excluding *V. velutina*); and third, at the family level (excluding *V. velutina*). To maintain requisite sample sizes at the family level, we included only those families for which total visit counts >40 . All analyses incorporated the local climatic variables of temperature, wind speed, illuminance, and relative humidity, to account for environmental effects at the time of sampling.

Fruit set and seeds produced per fruit

We then assessed the impact of *V. velutina* activity upon resultant *H. hibernica* pollination efficacy. We used trap counts to quantify mean *V. velutina* abundances across sites from August to October, and linked these to subsequent effects on fruit set and seed production per fruit. As analyses consisted of samples from both apical and lateral umbels, we included the effect of umbel type to determine whether this modulated interactions. Additionally, we compared effects across the ‘pollination’ and ‘control’ treatments, to control for other potential effects on fruit set and seed production. Local climatic variables were excluded from these analyses, as pollination occurred over a period of several weeks.

Statistical analyses

For floral visitor analyses including all insects, and those at the order-level; and for assessments of fruit set and seed production per fruit, we employed generalised linear mixed models (GLMMs) to account for the effect of site ID as a random factor. Separate models were generated for each order of floral visitors, and for analyses of the pollination and control treatments. Model selection was based on AIC, beginning with the full model and interactions. In all cases, GLMM model fit was

Table 1
Hedera hibernica flower visitation rates (female and hermaphrodite flowers visited per 15 min) for each insect family. Values indicate medians across sites, and their corresponding 95% confidence intervals.

Family	Median Flower Visitation Rate	Lower 95% CI	Upper 95% CI
Anthomyiidae	2	2	2
Apidae	4	1	15
Calliphoridae	3	1	7
Colletidae	6	4	84
Diptera	3	1	3
Drosophilinae	2	1	3
Empididae	1	1	1
Formicidae	1	1	1
Halictidae	2	2	2
Ichneumonidae	2	2	2
Muscidae	4	1	5
Rhiniidae	2	2	2
Sarcophagidae	2	1	2
Syrphidae	4	3	19
Tachinidae	2	1	5
Vespidae	8	4	13
Vespidae excluding <i>V. Velutina</i>	8	4	18
<i>V. velutina</i>	6	1	25

Table 2

Total floral visits for each insect family and responses to attacks by *Vespa velutina*. Values for successful attacks, behaviour of prey at time of attack, and reaction of prey after an unsuccessful attack, are given as percentages of events within families, while total visits are displayed as a percentage of events across families.

Order	Family	Total visits	Total attacks	Successful attacks	Behaviour of prey at time of attack		Reaction of prey after unsuccessful attack		
					Visiting flower	Flying	No response	Continues foraging	Leaves
Diptera	Calliphoridae	3.4 (46)	6.2 (4)	(0)	50 (2)	50 (2)	(0)	(0)	100 (4)
	Anthomyiidae	0.2 (2)	(0)	(0)	(0)	(0)	(0)	(0)	(0)
	Muscidae	5.9 (80)	1.6 (1)	(0)	100 (1)	(0)	(0)	100 (1)	(0)
	Drosophilinae	0.3 (4)	(0)	(0)	(0)	(0)	(0)	(0)	(0)
	Empididae	4.7 (64)	(0)	(0)	(0)	(0)	(0)	(0)	(0)
	Rhiniidae	0.2 (2)	(0)	(0)	(0)	(0)	(0)	(0)	(0)
	Sarcophagidae	0.7 (9)	(0)	(0)	(0)	(0)	(0)	(0)	(0)
	Syrphidae	26.8 (363)	45.3 (29)	3.4 (1)	27.6 (8)	72.4 (21)	(0)	60.7 (17)	39.3 (11)
Hymenoptera	Tachinidae	1.8 (24)	12.5 (8)	50 (4)	100 (8)	(0)	(0)	100 (4)	(0)
	Unidentified	3.7 (50)	9.4 (6)	(0)	66.7 (4)	33.3 (2)	(0)	66.7 (4)	33.3 (2)
	Apidae	5.3 (72)	3.1 (2)	(0)	100 (2)	(0)	100 (2)	(0)	(0)
	Colletidae	10.0 (136)	12.5 (8)	(0)	100 (8)	(0)	12.5 (1)	25 (2)	62.5 (5)
	Formicidae	0.3 (4)	(0)	(0)	(0)	(0)	(0)	(0)	(0)
	Halictidae	0.2 (2)	(0)	(0)	(0)	(0)	(0)	(0)	(0)
	Ichneumonidae	0.2 (2)	(0)	(0)	(0)	(0)	(0)	(0)	(0)
	Vespidae excluding <i>V. velutina</i>	11.6 (157)	9.4 (6)	50* (3)	66.7 (4)	33.3 (2)	0 (0)	66.7 (2)	33.3 (1)
	<i>V. velutina</i>	24.9 (337)	–	–	–	–	–	–	–
	All	All	(1354)	(64)	(8)	(37)	(27)	(3)	(30)

Values indicate percentages of total events, and brackets indicate corresponding *n*.

validated via analyses of the Pearson residuals.

For floral visitor analyses at the family-level, we used generalised linear models (GLMs) as site ID was redundant, owing to the limited distribution of insect families across sites. Separate models were generated for each family of floral visitors. Model selection was again based on AIC, beginning with the full model and interactions. The fit of all GLMs was validated using omnibus tests, assessment of the deviance to degrees of freedom ratios, and analyses of the Pearson residuals.

Full model structures are detailed in (Appendix B), and the raw data for fruit and seed set are available at (DOI:10.6084/m9.figshare.20110463). All statistical analyses were performed in SPSS (release v. 28.0.1.0).

Summary of floral visitors and predator-prey behaviour

We utilised summary statistics detailing the behaviour of floral visitors at both the family and order levels. These consisted of the number and percentage of patch visits, predation events, predation successes, behaviour at the time of predation, and behaviour following unsuccessful predation attempts.

Floral visitor behaviour

The GLMMs assessing the effect of *V. velutina* abundance on floral visitor behaviour at the order level used patch visitation rate, female and hermaphrodite flower visitation rate, and female and hermaphrodite flower visitation duration as response variables, *V. velutina* counts and local climatic variables as fixed factor predictors, and site ID as a random factor. The GLMMs assessing the effect of *V. velutina* abundance on floral visitor behaviour at the family level used patch visitation rate, female and hermaphrodite flower visitation rate, and female and hermaphrodite flower visitation duration as response variables, with *V. velutina* counts and local climatic variables as fixed factor predictors. Response variable distributions and link functions differed between models, with full details being provided in Appendix B.

Fruit set and seeds produced per fruit

The GLMMs assessing the effect of *V. velutina* abundance on fruit set and seeds produced per fruit used fruits per flower and seeds per fruit as

response variables, *V. velutina* trap counts and umbel type as fixed factor predictors, their two-way interaction, and site ID as a random factor. The GLMMs assessing the effect of pollination treatment on fruit set and seeds produced per fruit used fruits per flower and seeds per fruit as response variables, pollination treatment and umbel type as fixed factor predictors, their two-way interaction, and site ID as a random factor. Response variable distributions and link functions are detailed in (Appendix B).

Results

Summary of floral visitors

Vespa velutina was one of the most common single species visiting flowers of *H. hibernica* (Appendix C: Table C.1; Fig. 1D). Indeed, even when comparing families of visitors with the abundance of *V. velutina*, the latter was the second most frequent visitor to floral patches, after the Syrphidae (Tables 1 and 2). Nectar feeding and hunting were the most common activities that *V. velutina* engaged in, but other behaviours were also present (Fig. 2). Males were also frequent floral visitors, accounting for 40.7% (*n* = 54) of the individuals observed consuming nectar. They regularly copulated in front of the plant by coupling in the air at a height of 1.2 m (\pm 0.7 SD, *n* = 28), before falling to the ground to mate. amongst native insects, the most common floral visitors belonged to the families Syrphidae, Vespidae and Colletidae (Table 1 and 2; Fig. 1A–C, E–H).

Predator-prey behaviour

We recorded a total of 64 predation attempts by *V. velutina* directed towards other insect visitors of *H. hibernica* (Table 2). Overall, the percentage of successful predation attempts was 12.5%. The Syrphidae were the most commonly targeted family, with predation attempts occurring in flight, however the success rate for such attempts was relatively low, at 3.4%. In contrast, the Vespidae and Tachinidae were attacked less frequently, but the predation success rate was much higher (50%). Successful attacks most often occurred when the prey was perching on flowers. We observed that in 10.5% (*n* = 37) of all hunting records, *V. velutina* visited a flower to consume nectar after a failed attack, indicating that the same individuals behaved as both predators

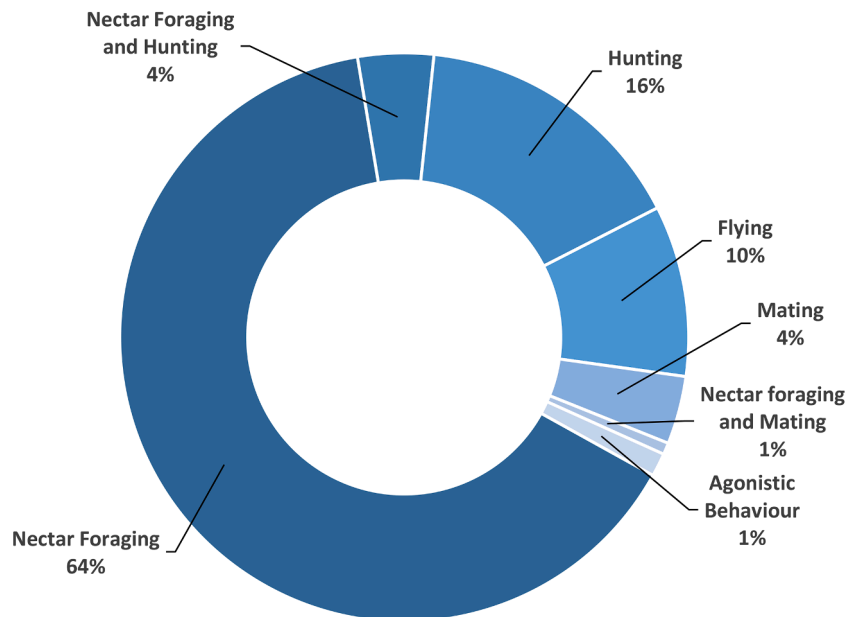


Fig. 2. Proportions of different behaviours performed by *Vespa velutina* amongst *Hedera hibernica* patches ($n = 337$). Categories containing two behaviours indicate cases where the same individual engaged in both behaviours during a single observation period.

and nectar consumers during a single foraging trip (see also Fig. 2).

The behaviour of prey after an unsuccessful attack varied (Table 2). Calliphoridae flies usually left the plant after being attacked, whilst Apidae often continued visiting the flower without any evident reaction. The high predation success of *V. velutina* on native vespids, such as *Polistes* spp. and *Vespa* spp. is notable, especially as these groups are also frequent visitors to *H. hibernica* (Tables 1 and 2; Appendix C: Table C.1).

Patch and floral visitation rate

We found no significant effect of the abundance of *V. velutina* on patch visitation rate when considering all insects together, although humidity demonstrated a significant positive influence upon this response (Appendix B: S4; Appendix D: Table D.1). In contrast, when analysing insect visits to flowers, we found a negative effect of *V. velutina* abundance on female flower visitation rate, with no significant influence of humidity (Appendix B: S5; Appendix D: Table D.1). At the order-level, *V. velutina* abundance did not significantly influence the visitation rates of either the Hymenoptera or Diptera to hermaphrodite or female flowers. Yet, when analysing responses at the family-level, several trends emerged. Both the hermaphrodite and female flower visitation rates of the Vespidae were negatively affected by the abundance of *V. velutina*, while the latter was positively influenced by temperature. Similarly, the Empididae were also negatively affected by *V. velutina* abundance, however temperature instead had a negative influence on visitation rates. Interestingly, the hermaphrodite flower visitation rate of the Colletidae was positively correlated with *V. velutina* abundance, temperature, and humidity, while the visitation rate of the Apidae (>30% *Bombus* spp.) was independent of both *V. velutina* abundance and temperature (Appendix D: Table D.1).

Floral visitation duration

The hermaphrodite flower visitation durations of the Vespidae, Syrphidae, and Colletidae were all reduced with increasing *V. velutina* abundance, and in the case of the Syrphidae, also increased with illuminance and wind speed (Fig. 1; Appendix C: S5; Appendix D: Table D.1). Conversely, the Apidae and Empididae conducted longer visits to hermaphrodite flowers with increasing *V. velutina* abundance

(Fig. 1; Appendix C: S6; Appendix D: Table D.1).

Fruit set and seeds produced per fruit

Flowers protected from insect visitors produced significantly fewer fruits in comparison to the uncovered flowers that were visited *ad libitum* by insects (GLMM, effect of treatment: $F_{1,1164} = 393.593$, $P < 0.001$, $\text{mean}_{\text{control}} = 0.011$, $\text{mean}_{\text{pollination}} = 0.547$; Fig. 3A), with site ID having a significant random effect (site random effect: $Z = 2.639$, $P = 0.008$). Similarly, the quantity of seeds per fruit was significantly lower in protected flowers (GLMM, effect of treatment: $F_{1,1177} = 28.562$, $P < 0.001$, $\text{mean}_{\text{control}} = 0.118$, $\text{mean}_{\text{pollination}} = 1.778$; Fig. 3B), however, this was independent of site ID (site random effect: $Z = 1.831$, $P = 0.067$). When considering only uncovered flowers, apical umbels were able to set more fruits (GLMM, effect of umbel type: $F_{1,1010} = 94.345$, $P < 0.001$, $\text{mean}_{\text{apical}} = 0.627$, $\text{mean}_{\text{lateral}} = 0.427$; Fig. 3A) and produce more seeds per fruit than lateral umbels (GLMM, effect of umbel type: $F_{1,1018} = 24.784$, $P < 0.001$, $\text{mean}_{\text{apical}} = 1.975$, $\text{mean}_{\text{lateral}} = 1.633$; Fig. 3B).

Notably, a higher abundance of *V. velutina* negatively affected the quantity of seeds produced per fruit (GLMM, effect of *V. velutina*: $F_{1,9} = 6.013$, $P = 0.035$; Fig. 4B), but had no significant effect on fruit set (GLMM, effect of *V. velutina*: $F_{1,14} = 1.594$, $P = 0.227$; Fig. 4A). In these cases, site ID was a significant random effect when considering fruit set (site random effect: $Z = 2.551$, $P = 0.011$), but not seeds per fruit (site random effect: $Z = 1.786$, $P = 0.074$).

Discussion

As an obligate entomophile, *H. hibernica* is unable to set fruits when deprived of insect pollination. While the flowers are visited by a diversity of native dipterans and hymenopterans, *V. velutina* is now one of the most common visitors to the plant in northwestern Spain. This is likely explained by the preference of *V. velutina* for flowers with short or open corollas, which in Europe includes *Camellia* spp., and *Hedera* spp. (Monceau et al., 2014). Additionally, the hornets' preference for *H. hibernica* may also be linked to its late flowering period, during which time young hornet queens require carbohydrates in preparation for overwintering. Notably, previous work has shown that *V. velutina* populations in parts of its invasive Asian range (Tsushima Island, Japan, and

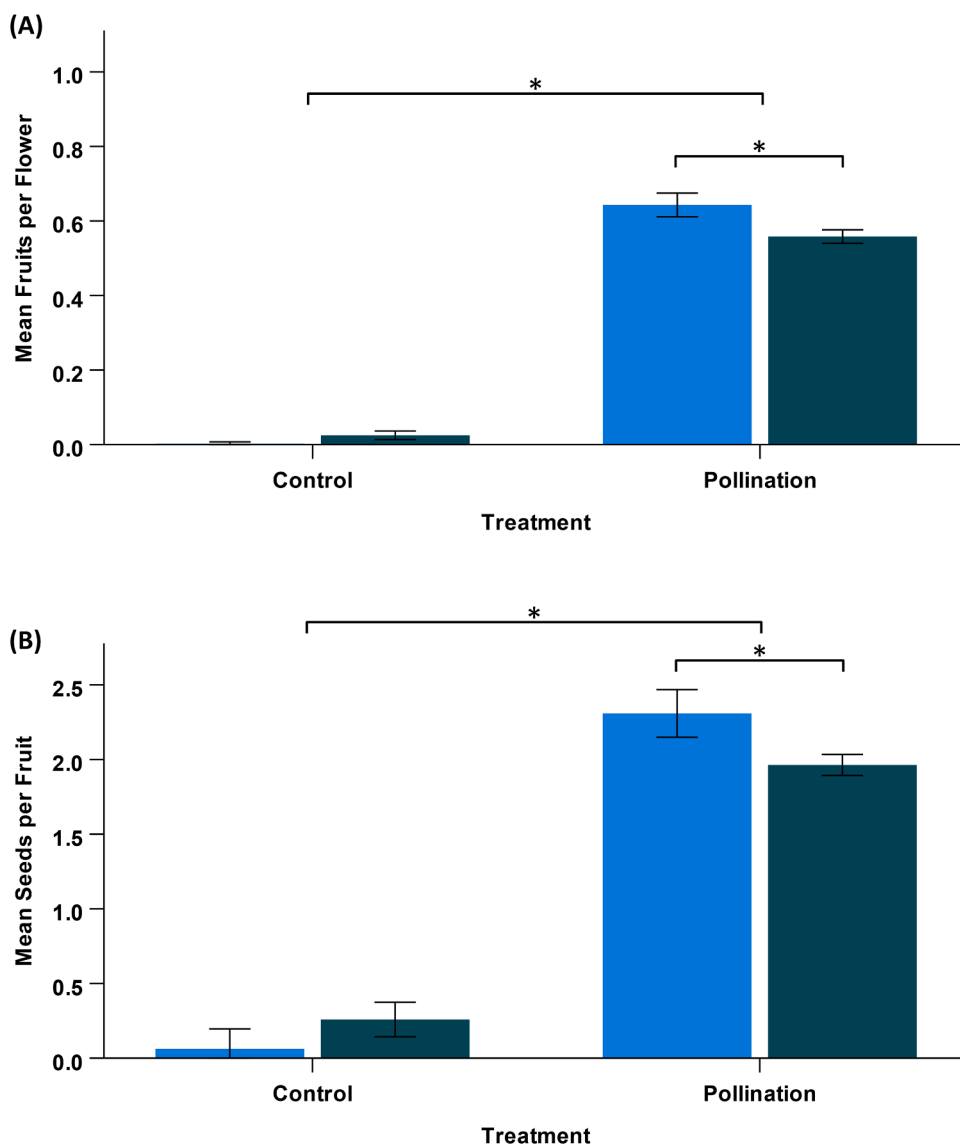


Fig. 3. (A) Number of fruits set per flower, and (B) number of seeds produced per fruit by *Hedera hibernica* under the two experimental treatments, a no-pollination control and open pollination ($n = 1182$). Bar colour indicates umbel type, with apical umbels represented by light blue, and lateral umbels by dark blue. Brackets and asterisks indicate significant differences between groups (GLMM, $P < 0.05$), while all other comparisons are not statistically significant. Black error bars represent 95% confidence intervals.

Busan, South Korea) visit at least 36 plant species, with substantial overlap between nectar foraging and predation behaviour (Ueno, 2015). Here, we demonstrate that the ecological interactions resulting from these overlaps are complex, and must be considered when evaluating subsequent invasion impacts. Our results indicate widely varying effects of *V. velutina* abundance on different insect families, and a negative correlation with the production of seeds, but not fruit set in *H. hibernica*. These findings highlight the importance of considering multiple organisational scales and effect directionalities when assessing the impacts of invasive species on plant-pollinator assemblages. Further, the occurrence of mating as observed here, suggests that late blooming plants such as *H. hibernica* may act as congregation areas for gynes and males, thus constituting an important resource in the invasion dynamics of *V. velutina*.

Impact of *Vespa velutina* as a predator

The antagonistic influence of *V. velutina* activity was evident from the negative relationship between hornet abundance, and female flower visitation rates for all insects. Whilst the exact mechanisms behind this are unclear, both direct effects via predation, and indirect effects via nectar competition are likely to have played a role. At the family-level,

the Vespidae and Tachinidae were especially vulnerable to predation. Indeed, while previous European studies have found no evidence for competition with native vespids (Carisio et al., 2022), our results suggest that the high success rate of predation attempts on these groups had a direct impact on the number of individuals foraging on flowers. It is important to note that further data would be needed to validate the generalisability of these results, however they serve to highlight potential behavioural effects that may not be clear from trapping alone. As with other hymenopterans, the Vespidae are able to incorporate risk probability when conferring resource information, thus inducing down-regulation of visits to dangerous patches (Pereira et al., 2016; Yossen et al., 2020). Indeed, the reduced visitation rates to both hermaphrodite and female flowers by the Vespidae at higher *V. velutina* abundances do suggest that a negative feedback process was present. Notably, because native vespids are the most important pollinators of ivy (Ollerton et al., 2007; Jacobs et al., 2010), the reduction in floral visits by this group may constitute one of the main factors explaining the negative relationship between *V. velutina* abundance and seed production.

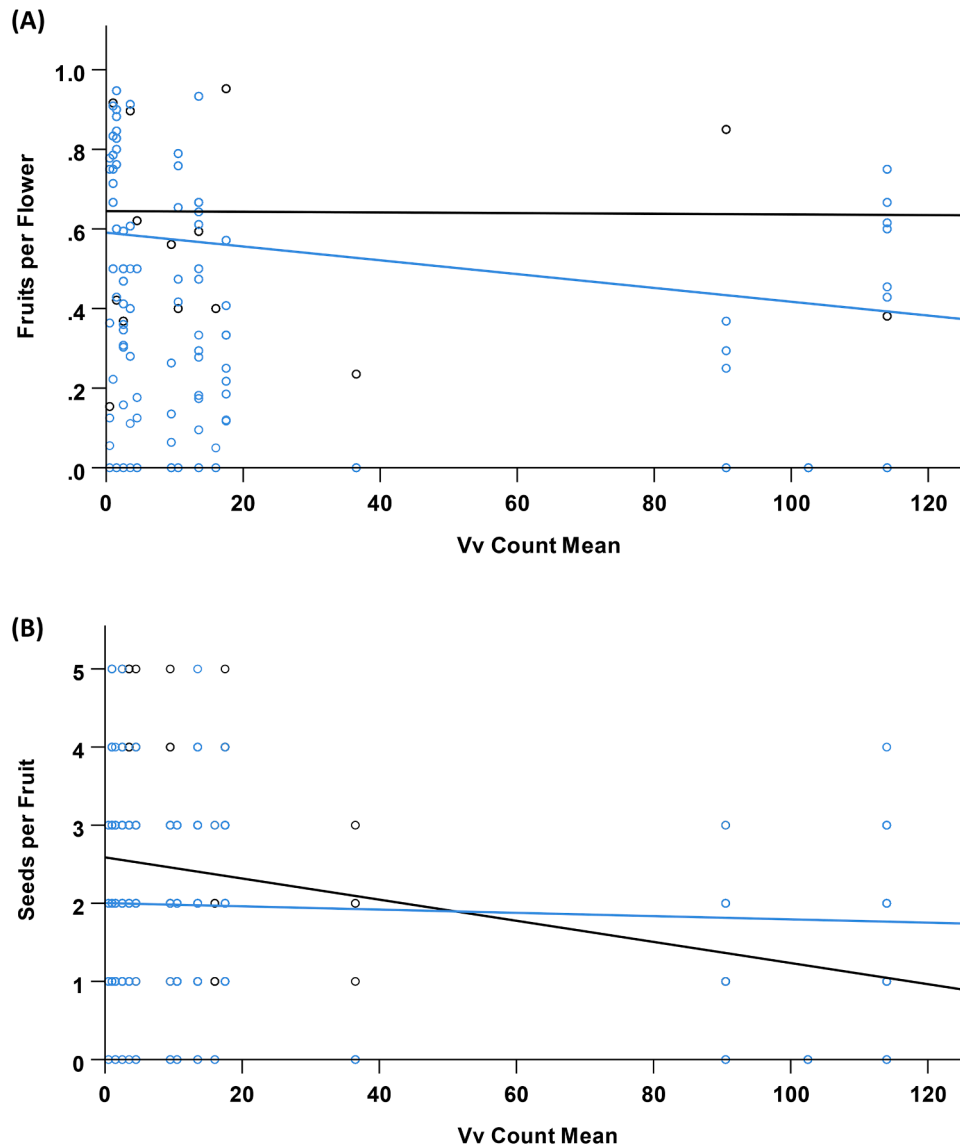


Fig. 4. (A) Number of fruits set per flower, and (B) Number of seeds produced per fruit by *Hedera hibernica* umbels across differing *Vespa velutina* abundance levels ($n = 1182$). Black points represent apical umbels, and blue points lateral umbels.

Impact of *Vespa velutina* on insect behaviour

For generalist species, the presence of a predator will often lead to changes in resource selection (Schmitz, 1998). However, the use of *H. hibernica* in our study represents a unique case, as the scarcity of other floral resources in the late summer and autumn forces both generalist and specialist species to aggregate on these plants. Consequently, we were able to observe a diversity of species in the presence of different *V. velutina* abundances, along with their concordant activity.

In the Colletidae, hermaphrodite flower visitation frequencies increased, while visitation durations decreased with increasing *V. velutina* abundance. This suggests that insects in this group switched between flowers more frequently, spending less time on each one, which is known to be a classic predator avoidance pattern (Romero et al., 2011), and may also indicate reduced nectar availability (Thomson & Page, 2020). In contrast, visitation durations to hermaphrodite flowers in the Apidae increased with higher *V. velutina* abundances, suggesting that the presence of hornets slowed the rate of movement from one flower to the next. Indeed, this is plausible, as a large number of the individuals observed belonged to the *Bombus* genus, which experienced antagonistic interactions, but never successful predation attempts.

Similarly, visitation durations increased in the Empididae with increasing *V. velutina* abundance, however unlike the Apidae, visitation frequencies decreased, suggesting a degree of negative influence. Temperature and humidity generally had a positive relationship with visitation rates and durations, although in the Empididae and Syrphidae this trend was reversed. Such varying responses between insect families highlight how prey life-histories, predation pressure, and resource competition interact to form complex outcomes, and that even within the same family, effect directionality may be different when considering various measures of activity.

Interestingly, *V. velutina* appeared to have some of the most significant effects on floral visitation not by successful predation, but by nectar consumption and repeated unsuccessful predation attempts. The latter was exemplified in the case of the Syrphidae, which were frequent predation targets, but rarely captured due to their flight speed and manoeuvrability. Notably, these unsuccessful predation attempts led to a significant reduction in the time spent by Syrphidae on flowers, as they often continued foraging despite the disruption (Table 2). In turn, this is likely to have reduced their ability to transfer pollen between plants, as differences in the duration of floral visits are often associated with changes in the quality of pollination (Romero et al., 2011; Benoit &

Kalisz, 2020). As such, by altering both the floral visitation frequency and the duration of visits, *V. velutina* may cause a reduction in the reproductive success of the plant, as indicated by a decrease in the number of seeds produced per fruit.

Such indirect effects of *V. velutina* are pertinent in the larger context of its invasion biology. Notably, several studies have shown that the greatest impact of *V. velutina* on honey bee (*Apis mellifera*) colonies is not through direct predation, but rather the induction of “foraging paralysis”, whereby workers remain in the hive as a response to perceived predation risk (Requier et al., 2019). This can eventually lead to starvation of the colony, as foragers fail to accumulate sufficient food to survive the winter (Rojas-Nossa et al., 2022). The former example, coupled with our own results, suggests that careful examinations of the behavioural interactions between *V. velutina* and native pollinators are important in order to fully understand ecosystem-level risks.

Impact of *Vespa velutina* on pollination success

Increased *V. velutina* abundance correlated with a decrease in the number of seeds per fruit in *H. hibernica*, suggesting a significantly reduced effectiveness of individual floral visits. Specifically, the number of seeds per fruit reflects the quantity and quality of pollen grains deposited on the pistil of the flower (Ne’eman et al., 2010), with our results indicating that one or both of these may be reduced at high *V. velutina* abundances. Notably, a reduced number of seeds per fruit decreases the quantity of potential progeny produced by the plant, and thus impacts overall reproductive success. In contrast, *V. velutina* abundance showed no correlation with fruit set. We thus hypothesise that pollination was only partially disrupted, allowing the ivy enough pollen for fruit production, but limiting the quantity of seeds produced per fruit.

For some plants, the number of conspecific pollen grains received per stigma must reach a sufficient threshold to allow a fruit to form, with increases above this value leading to greater seed quantities per fruit (Snow, 1982; Falque et al., 1995). Our present results are thus likely attributable to shortened floral visit durations by pollinators, leading to a reduced quantity of pollen being transferred from anthers to stigmas, and hence lowering seed set. Indeed, previous evidence of this process has been observed in the pollination of *Capsicum annuum* by *E. tenax* (Jarlan et al., 1997), and in cases where the invasive ant *Linepithema humile* shortens floral visit durations of *Diadasia* bees to the cactus *Ferocactus viridescens* (LeVan et al., 2014). Alternatively, the lower number of seeds per fruit could be due to a reduction in the quality of pollen reaching the stigma, for example by an increase in the plant’s own pollen being deposited by insects making shorter but more frequent visits. While both hypotheses are plausible, it should be noted that determination of pollen type and quantity was not possible in the present study, and thus further work would be needed to elucidate the underlying causes of reduced seed set.

It has been suggested that *V. velutina* can promote pollination within parts of its invasive range in Asia (Ueno, 2015). As such, considering that *V. velutina* is one of the most frequent visitors to *H. hibernica* in invaded areas of Europe, and that in the process of nectar foraging, hornets transport pollen between flowers (see Fig. 1D), it might likewise be expected to replace or even enhance the pollination services provided by native species. However, despite promoting pollination at some level, the decrease in seeds per fruit in *H. hibernica* associated with an increase in hornet abundance suggests that its quality as a pollinator is inferior to that of the native insects it displaces.

Conclusions

Competitive ecological interactions are often difficult to measure, however their net effects may have important consequences at the ecosystem-level. In the present study system, competitive exclusion of native pollinators at a floral resource was evident, specifically in the

reduced visitation frequencies of several insect families with increasing *V. velutina* abundance. Our results show that invasive social vespids can modify plant-pollinator interactions at several levels, and that the impacts of such modifications are complex and multidirectional. Crucially however, the net effect of *V. velutina* as a predator, or as a competitor for nectar, appears to outweigh its utility as a pollinator, ostensibly because it is less effective at transferring *H. hibernica* pollen than are the native species that it displaces.

Data availability

Relevant data are deposited in the figshare data repository (DOI:10.6084/m9.figshare.20110463).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

S.V.R.-N, S.M and J.G were supported by the Interreg Atlantic Area Program (EAPA_800/2018-Atlantic-Positive). T.A.O.-W, J.P and J.O were funded by BBSRC (Project no. BB/S015523/1). Funding for open access charge: Universidade de Vigo/CISUG. We wish to thank the Pazo da Touza and the residents of Gondomar, Nigrán, Oia, O Rosal, and Tomiño for providing us with field sites. D. Boisits, P. Kennedy, and P. Álvarez contributed to the development of the work, and A. Lagoa, R. Curtis, and L. Castro assisted with the identification of insects.

References

- Aguado, L.O., Viñuela, E., & Fereres, A. (2015). Guía de campo de los polinizadores de España. Mundi-Prensa Eds. 364pp.
- Beggs, J. R., Brockerhoff, E. G., Corley, J. C., Kenis, M., Masciocchi, M., Muller, F., et al. (2011). Ecological effects and management of invasive alien Vespidae. *BioControl*, 56, 505–526.
- Benoit, A. D., & Kalisz, S. (2020). Predator effects on plant-pollinator interactions, plant reproduction, mating systems, and evolution. *Annual Review of Ecology, Evolution, and Systematics*, 51, 319–340.
- Bischoff, I., Eckelt, E., & Kuhlmann, M. (2005). On the biology of the ivy-bee *Colletes hederæ* Schmidt & Westrich, 1993 (Hymenoptera, Apidae). *Bonner Zoologische Beiträge*, 53, 27–36.
- Bond, W. J. (1994). Keystone species. *Biodiversity and ecosystem function* (pp. 237–253). Berlin, Heidelberg: Springer.
- Carisio, L., Cerri, J., Liroy, S., et al. (2022). Impacts of the invasive hornet *Vespa velutina* on native wasp species: A first effort to understand population-level effects in an invaded area of Europe. *Journal of Insect Conservation*, 26, 663–671.
- Chinery, M. (1986). *Insects of Britain and Western Europe*. Collins eds (3d Edition, p. 320).
- Couvillon, M. J., Walter, C. M., Blows, E. M., Czaczkes, T. J., Alton, K. L., & Ratnieks, F. L. (2015). Busy bees: Variation in insect flower-visiting rates across multiple plant species. *Psyche*, 1–7.
- Falque, M., Vincent, A., Vaissiere, B. E., et al. (1995). Effect of pollination intensity on fruit and seed set in cacao (*Theobroma cacao* L.). *Sexual Plant Reproduction*, 8, 354–360.
- Friard, O., & Gamba, M. (2016). BORIS: A free, versatile open source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, 7, 1325–1330.
- Garbuzov, M., & Ratnieks, F. L. (2014). Ivy: An underappreciated key resource to flower-visiting insects in autumn. *Insect Conservation and Diversity*, 7, 91–102.
- Grivet, D., & Petit, R. J. (2002). Phylogeography of the common ivy (*Hedera* sp.) in Europe: Genetic differentiation through space and time. *Molecular Ecology*, 11, 1351–1362.
- Hanna, C., Foote, D., & Kremen, C. (2014). Competitive impacts of an invasive nectar thief on plant-pollinator mutualisms. *Ecology*, 95, 1622–1632.
- Jacobs, J. H., Clark, S. J., Denholm, I., Goulson, D., Stoate, C., & Osborne, J. L. (2009). Pollination biology of fruit-bearing hedgerow plants and the role of flower-visiting insects in fruit-set. *Annals of Botany*, 104, 1397–1404.
- Jacobs, J. H., Clark, S. J., Denholm, I., Goulson, D., Stoate, C., & Osborne, J. L. (2010). Pollinator effectiveness and fruit set in common ivy, *Hedera helix* (Araliaceae). *Arthropod-Plant Interactions*, 4, 19–28.
- Jarlan, A., De Oliveira, D., & Gingras, J. (1997). Pollination by *Eristalis tenax* (Diptera: Syrphidae) and seed set of greenhouse sweet pepper. *Journal of Economic Entomology*, 90, 1646–1649.

- Laurino, D., Lioy, S., Carisio, L., Manino, A., & Porporato, M. (2020). *Vespa velutina*: An alien driver of honey bee colony losses. *Diversity*, 12, 5.
- Leraut, P. (2007). *Insectos de España y Europa* (p. 528). Lynx Communications.
- LeVan, K. E., Hung, K. L. J., McCann, K. R., Ludka, J. T., & Holway, D. A. (2014). Floral visitation by the Argentine ant reduces pollinator visitation and seed set in the coast barrel cactus. *Ferocactus viridescens*. *Oecologia*, 174, 163–171.
- Liang, C. T., Shiels, A. B., Haines, W. P., Sandor, M. E., & Aslan, C. E. (2022). Invasive predators affect community-wide pollinator visitation. *Ecological Applications*, 32, e2522.
- McAllister, H. A., & Rutherford, A. (1990). *Hedera helix* L. and *H. hibernica* (Kirchner) bean (Araliaceae) in the British Isles, 18 pp. 7–15. Watsonia.
- Melzer, B., Steinbrecher, T., Seidel, R., Kraft, O., Schwaiger, R., & Speck, T. (2010). The attachment strategy of English ivy: A complex mechanism acting on several hierarchical levels. *Journal of the Royal Society Interface*, 7, 1383–1389.
- Metcalf, D. J. (2005). *Hedera helix* L. *Journal of Ecology*, 93, 632–648.
- Monceau, K., Arca, M., Lepêtre, L., Mougél, F., Bonnard, O., Silvain, J. F., et al. (2013). Native prey and invasive predator patterns of foraging activity: The case of the yellow-legged hornet predation at European honeybee hives. *PLoS one*, 8, e66492.
- Monceau, K., Bonnard, O., & Thiéry, D. (2014). *Vespa velutina*: A new invasive predator of honeybees in Europe. *Journal of Pest Science*, 87, 1–16.
- Ne'eman, G., Jürgens, A., Newstrom-Lloyd, L., Potts, S. G., & Dafni, A. (2010). A framework for comparing pollinator performance: Effectiveness and efficiency. *Biological Reviews*, 85, 435–451.
- Ollerton, J., Killick, A., Lamborn, E., Watts, S., & Whiston, M. (2007). Multiple meanings and modes: On the many ways to be a generalist flower. *Taxon*, 56, 717–728.
- Pereira, A. J., Pirk, G. I., & Corley, J. C. (2016). Foraging behavior interactions between two non-native social wasps, *Vespula germanica* and *V. vulgaris* (Hymenoptera: Vespidae): Implications for invasion success? *Journal of Insect Science*, 16, 78.
- Rankin, E. E. W. (2021). Emerging patterns in social wasp invasions. *Current Opinion in Insect Science*, 46, 72–77.
- Requier, F., Rome, Q., Chiron, G., Decante, D., Marion, S., Menard, M., et al. (2019). Predation of the invasive Asian hornet affects foraging activity and survival probability of honey bees in Western Europe. *Journal of Pest Science*, 92, 567–578.
- Richter, M. R. (2000). Social wasp (Hymenoptera: Vespidae) foraging behavior. *Annual Review of Entomology*, 45, 121–150.
- Rojas-Nossa, S. V., & Calviño-Cancela, M. (2020). The invasive hornet *Vespa velutina* affects pollination of a wild plant through changes in abundance and behaviour of floral visitors. *Biological Invasions*, 22, 2609–2618.
- Rojas-Nossa, S. V., Dasilva-Martins, D., Mato, S., Bartolomé, C., Maside, X., & Garrido, J. (2022). Effectiveness of electric harps in reducing *Vespa velutina* predation pressure and consequences for honey bee colony development. *Pest Management Science*, 78, 5142–5149.
- Rome, Q., Perrard, A., Muller, F., Fontaine, C., Quilès, A., Zuccon, D., et al. (2021). Not just honeybees: Predatory habits of *Vespa velutina* (Hymenoptera: Vespidae) in France. *Annales de la Société entomologique de France (NS)*, 57, 1–11.
- Romero, G. Q., Antiquera, O. A. P., & Koricheva, J. (2011). A meta-analysis of predation risk effect on pollinator behaviour. *PLoS one*, 6, e20689.
- Schmitz, O. J. (1998). Direct and indirect effects of predation and predation risk in old-field interaction webs. *American Naturalist*, 151, 327–342.
- Snow, A. A. (1982). Pollination intensity and potential seed set in *Passiflora vitifolia*. *Oecologia*, 55, 231–237.
- Thomson, D. M., & Page, M. L. (2020). The importance of competition between insect pollinators in the Anthropocene. *Current Opinion in Insect Science*, 38, 55–62.
- Traveset, A., & Richardson, D. M. (2006). Biological invasions as disruptors of plant reproductive mutualisms. *Trends in Ecology & Evolution*, 21, 208–216.
- Ueno, T. (2015). Flower-visiting by the invasive hornet *Vespa velutina nigrithorax* (Hymenoptera: Vespidae). *International Journal of Chemical, Environmental & Biological Sciences*, 3, 444–448.
- Wardle, D. A., Karl, B. J., Beggs, J. R., Yeates, G. W., Williamson, W. M., & Bonner, K. I. (2010). Determining the impact of scale insect honeydew, and invasive wasps and rodents, on the decomposer subsystem in a New Zealand beech forest. *Biological Invasions*, 12, 2619–2638.
- Willmer, P. (1985). *Bees, ants and wasps: A key to genera of the British Aculeates*, 7 p. 28). Mad River Press Inc.
- Wilson, E. E., & Holway, D. A. (2010). Multiple mechanisms underlie displacement of solitary Hawaiian Hymenoptera by an invasive social wasp. *Ecology*, 91, 3294–3302.
- Yossen, M. B., Buteler, M., & Lozada, M. (2020). Foraging experience modulates response to aversive odour cues in social wasps. *Animal Behaviour*, 164, 113–122.