

RESEARCH ARTICLE

Climatic factors, landscape composition and host plant traits co-drive fruit infestation of unmanaged walnut trees by the invasive pest fly *Rhagoletis completa* (Cresson, 1929) (Diptera: Tephritidae)

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Abstract

1. *Rhagoletis completa* (Cresson, 1929) is a North American invasive pest fly infesting walnut fruits (*Juglans* spp.). The abiotic and biotic factors driving its population dynamics and associated fruit damages remain poorly understood.
2. This study aimed, for the first time, to disentangle the relative effects of meteorological conditions, landscape characteristics, local environment and host plant traits on the abundance of this non-native pest in a European country. A total of 2433 walnut fruits were sampled and multiscale environmental variables were measured between July and December 2023 across 24 sites in northern France. Generalised linear mixed models were used to explore the relationships between the presence and abundance of the pest and the multiple environmental variables measured across various temporal and spatial scales.
3. Fruit infestation was positively associated with local factors, including large-sized fruit, walnut tree abundance and landscape characteristics such as the proximity of grasslands and the density of corridors (hedgerows, rivers). In contrast, it was negatively impacted by anthropogenic habitats such as conventional crops and orchards. Infestation rate was also affected by climatic variations, positively by the mean minimum temperature over the preceding 14 days and negatively by the heavy rainfall in the spring season.
4. Our study revealed high infestation rates of unmanaged walnut trees in northern France and showed that these trees growing spontaneously outside production areas can serve as wild reservoirs for *Rhagoletis completa*. Therefore, such unmanaged trees should be considered in Integrative Pest Management strategies to limit crop infestations.

Patrice Eslin and Olivier Chabrerie contributed equally to this work.

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KEYWORDS

biological invasion, insect pest, *Juglans regia*, multiscale environmental drivers, Tephritidae

INTRODUCTION

Insect invasions, propagated by international trade (Bertelsmeier et al., 2025) and amplified by global changes (Aluja et al., 2011; Vidal et al., 2025), constitute a major threat to biodiversity (Clarke & McGeoch, 2023; Kenis et al., 2009), agricultural productivity and food security worldwide (Deconninck et al., 2026; Sileshi et al., 2019). Among the taxa causing significant damage to fruit production, Tephritid flies occupy a central place due to their ability to rapidly colonise new territories and exploit a wide range of plant resources (Aluja & Mangan, 2008). The economic losses caused by this taxon are estimated at several billion dollars per year (Qin et al., 2021; Stonehouse et al., 1998; Verheggen et al., 2017), including direct crop losses, as well as the costs associated with pest control measures implemented to detect, contain, eradicate and prevent the spread of these pests (Aluja & Mangan, 2008). The invasion success of non-native species results primarily from the match between species invasiveness and ecosystem invasibility, regardless of the taxa (Daly et al., 2023). In Tephritidae, invasiveness has been relatively well characterised, based on a diversified set of biological traits such as phenotypic plasticity, reproductive strategies and the ability to circumvent host plant defences (Hellmann et al., 2008). However, the vulnerability of recipient agrosystems and the role of natural habitats in the surrounding landscapes, where part of the life cycle of these flies takes place, remain comparatively understudied.

The walnut husk fly, *Rhagoletis completa*, is a choice model for studying the invasion dynamics of specialist insect pests in temperate areas. Native to North America (Cresson, 1929), this oligophagous fruit fly depends on a limited number of host tree species from the genus *Juglans*. Despite its narrow trophic niche, particularly in Europe where it mainly benefits from the large agricultural production of *Juglans regia* fruit, its recent expansion across Europe and Eurasia raises questions about the mechanisms underlying its dispersal and adaptation to new recipient environments. Unlike invasive generalist and multivoltine Tephritidae flies such as *Ceratitis capitata* (Giunti et al., 2023; EPPO, 2026a) and *Bactrocera dorsalis* (Theron et al., 2017; EPPO, 2026b), which can infest hundreds of plant species, *R. completa* is characterised by a univoltine cycle, marked by a ten-month diapause during which its host plants no longer bear fruit (Boyce, 1934). Adult emergence is temperature-dependent and requires exposure of pupae to cold conditions, estimated at least 8 weeks at 5°C (Emery & Mills, 2019; Rull et al., 2019b). Emergence generally peaks in late summer (Duso & Lago, 2006), and in northern France, adults are mainly observed on walnut trees in early September (Boulembert et al., 2024). Unlike other *Rhagoletis* species, *R. completa* appears to exhibit gregarious behaviour, with multiple egg-laying in the same fruit (Lalonde & Mangel, 1994), each female producing 200–400 eggs in her lifetime (Boyce, 1934). After 3–5 weeks of development in walnut husks, third stage larvae generally leave the damaged

husk to pupate in the soil and enter into diapause (Kasana & Alinia-zee, 1994). Without crop management, the infestation rate of walnut trees can reach 100%, resulting in 80% yield losses when infestation occurs early (Verheggen et al., 2014).

The invasion history of *R. completa* on the European continent is relatively well documented. The species was first detected in 1986 in Ticino, the southernmost canton of Switzerland (EPPO, 2026c). Despite eradication attempts, *R. completa* became established in southern Switzerland by 1991 (Merz, 1991; EPPO, 1994) and was also detected in Italy (Duso, 1991). It has since spread throughout the continent: Croatia (2003; EPPO, 2009), Germany (2004; EPPO, 2004), France (2007; EPPO, 2008a), Austria (2008; EPPO, 2008b), Hungary (2011; EPPO, 2013), in 2014 in Bosnia and Herzegovina (Ostojić et al., 2014) and Spain (EPPO, 2020), Netherlands (2015; EPPO, 2016), Belgium (2016; EPPO, 2018a), Czech Republic (2017; EPPO, 2018b), in 2018 in Slovakia (EPPO, 2018c) and Corse (EPPO, 2019a), and finally in 2019 in Poland (EPPO, 2019b). It is assumed that *R. completa* has not reached its potential range yet and is currently limited by the distribution of its host plant, *Juglans regia*, which is widely distributed across Europe (Verheggen et al., 2014). The European continent does not present uncrossable geographic barriers, and its climate is suitable to the fly, which exhibits good dispersal capacity in its invasion range. Furthermore, natural physiological constraints such as low temperatures, especially at high altitudes, are diminishing with climate change (Aluja et al., 2011). Although damage has remained limited in northern France compared to the south, adult flies have recently been increasingly observed on trees, and walnuts have been more frequently attacked in recent years (Boulembert et al., 2024).

Many environmental factors may influence the success of fruit infestation by frugivorous insects such as fruit flies (Deconninck et al., 2025; Ulmer et al., 2022), including those from the *Rhagoletis* genus (Wakie et al., 2019). Three main groups of factors, local, landscape and climatic factors, are recognised to form an environmental filter sorting and selecting surviving individuals among insect populations at different spatial scales (Deconninck et al., 2025; Guinard et al., 2026). At the local scale, various biotic and abiotic factors, linked to the species' niche, shape the dynamics of fruit fly populations. In *Rhagoletis* species, these factors are mainly related to the abundance of trophic resources, that is, the quantity of fruit in a tree (Senger et al., 2009), or to their quality (Boyce, 1934; Guillén et al., 2011; Lalonde & Mangel, 1994). At the landscape scale, habitat composition is recognised as a key factor influencing the dispersal, abundance and persistence of fruit flies (Deconninck et al., 2025). Few studies have examined the impact of landscape on Tephritidae. However, their abundances are expected to be positively influenced by specific elements of landscapes including woodland patches (Rodríguez-Saona et al., 2018; Wen et al., 2023), private gardens or orchards (Krasnov et al., 2019; Wakie et al., 2019) and semi-natural features such as pastures and shrublands. Conversely, wetlands appear to have

a negative effect on Tephritidae (Wakie et al., 2019). At the global or regional scale, climatic variations are known to drive the end of pupal diapause and emergence of imago (Emery & Mills, 2019; Rull et al., 2019b), in synchronisation with fruit formations of their host plant (Toxopeus et al., 2024). Nevertheless, regional variations of temperatures, especially seasonal extremes can be buffered by local suitable microclimatic conditions, commonly found under tree canopies or within grassland vegetation (Deconninck et al., 2024b). For *R. completa*, these microhabitats, under or near the walnut trees, may shelter pupae during their winter diapause or adults during their short reproductive period in summer. Despite the importance of landscape effects on insect populations (Guinard et al., 2026; Santoiemma et al., 2018; Ulmer et al., 2024; Wen et al., 2023), no study has yet examined their influence on the presence (dispersal-limited) and abundance (resource-limited) of *R. completa*. To our knowledge, only one study examined the influence of landscape and macroclimate on two other *Rhagoletis* species infesting apple and cherry (Wakie et al., 2019).

Rhagoletis completa populations have been intensively monitored in the agricultural context of walnut cultivation (Riedl & Hoving, 2009; Sarles et al., 2018; Skuhrovec et al., 2024). However, many unmanaged walnut trees persist outside treated orchards and are scattered throughout the landscape. Seed dispersal by birds, particularly magpies and crows, promotes the establishment of isolated individuals in hedgerows and fallow fields (Lenda et al., 2011; Vander Wall, 2001). These trees thus constitute a diffuse but potentially significant network of alternative breeding sites for *R. completa* (Boulembert et al., 2024).

The present study aimed to disentangle the relative roles of climatic, landscape and local factors driving the infestations of unmanaged walnut trees by the invasive pest fly, *Rhagoletis completa*, in northern France. We hypothesised that (i) this oligophagous fly, highly specialised in the detection and evaluation of the resource suitability of its unique host, would preferentially utilise the largest walnut trees (i.e., with a large canopy) offering the highest resource availability, and would select the biggest fruits for oviposition (Guillén et al., 2011). At the landscape scale, we hypothesised that (ii) the presence of the fly would be positively associated with the proximity of natural habitats (i.e., woodland and hedgerows), which generally provide refuges, as well as dispersal corridors for many pests that depend on fleshy-fruited trees (Ulmer et al., 2024). As *R. completa* individuals overwinter as pupae, (iii) they may be affected by low temperature, particularly frost days, or precipitations. Given that this pest fly continues to expand its distribution range, it appears essential to better understand these changing environmental factors that influence its population dynamics outside agricultural systems in order to anticipate its expansion and implement appropriate management strategies.

METHODS

Study area

The study was conducted between July and December 2023 in the region of Amiens, France (49°53'40" N, 2°18'07" E). The region has

an oceanic climate, with a mean annual temperature of 10.7°C and mean annual precipitation of 691.9 mm (data from the Dury-lès-Amiens meteorological station, StatC network). The landscapes are dominated by agricultural production and form mosaics of open fields cultivated for cereals, rapeseed and sugar beet, interspersed by orchards, grasslands and woodland patches. Walnut trees are not the predominant crop and are generally cultivated in mixed orchards (with apples, pears and small red fruits), often under organic farming practices. Walnut seeds typically reach their full maturity by mid-October and are harvested until early November. Walnut trees are also commonly found in domestic gardens, urban green spaces, along roadsides and in semi-natural habitats such as hedgerows, pastures and woodland edges.

Walnut collection and fruit and tree trait measurements

Walnut fruits were collected from 24 sites selected within a landscape window of 40 × 45 km (see Tables S1 and S3). At each site, a single tree was monitored. Following the recommendation of Duso and Lago (2006) to capture the temporal dynamics of fruit infestation by *Rhagoletis completa* and to cover the walnut maturity period, eight sampling campaigns were conducted every 2 weeks between September and December 2023 (September 9–13, September 23–27, October 8–11, October 21–25, November 4–8, November 18–22, December 3–5 and December 17–19; see Figure 1 and Table S4). Two sampling campaigns preceding this temporal window were added at the end of July and August 2023 (26 July and 30 August, in 5 sites) to detect potential early infestation. Each month, at each site, twenty walnut fruits were randomly collected, ten from the canopy and ten from the ground below the canopy of a single walnut tree. After the last sampling campaign in December, no walnut fruits remained in the canopy or on the ground at any sites.

To evaluate the fruit resources available for *R. completa*, a set of quantitative and qualitative traits were measured on each walnut fruit collected (Table S2), including: (i) the whole fruit, a dehiscent pseudodrupe; (ii) the exocarp or periderm, that is, the fruit skin; (iii) the mesocarp, that is, the husk corresponding to the fleshy envelope of the fruit, used in dyeing, and the “nut” in the commercial sense, which is actually the dry stone of this drupe, consisting of (iv) the lignified endocarp named the shell of the nut and comprising two valves and (v) the edible seed, that is, the kernel formed by the two halves/cotyledons of the embryo, rich in lipids, covered by a thin yellowish-orange seed pericarp. Since fruit infestations by insect pests are known to be associated with various types of damage and changes in the chemical and physical quality of fruits, the following set of variables were targeted to characterise the fruit health and its commercial value (Duso & Lago, 2006; Solar et al., 2019). We measured the fruit length (from the flower scar to the peduncle insertion: d_1), diameters (widest: d_2 , and thinnest: d_3), mass, volume ($4/3 \times \pi \times r_1 \times r_2 \times r_3$) and skin area ($4\pi [(r_1^p \times r_2^p + r_1^p \times r_3^p + r_2^p \times r_3^p)/3]^{1/p}$, where $p = 1.6075$, according to Knud Thompsen formula), proportion of

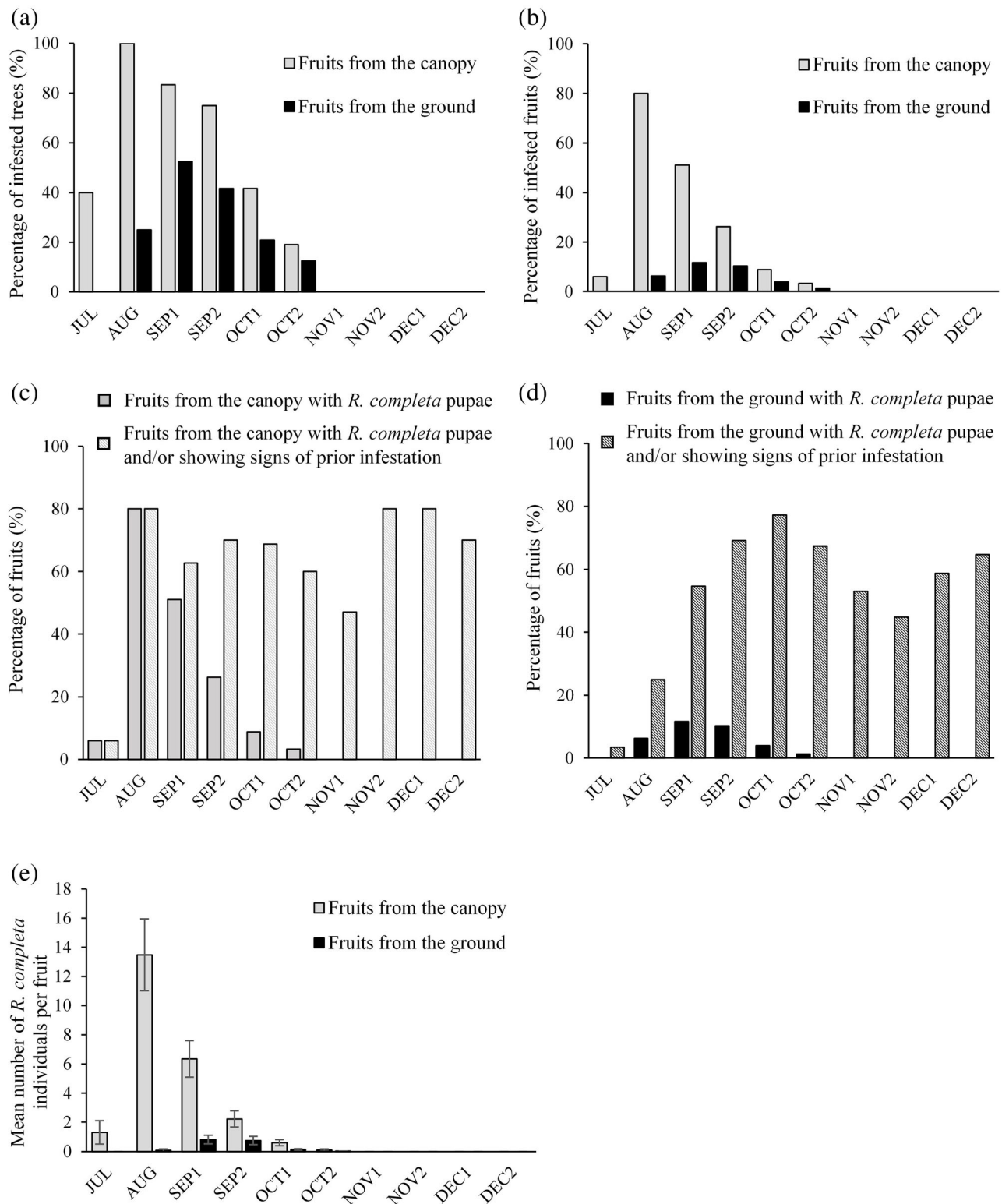


FIGURE 1 Infestation of walnut trees and fruits by *Rhagoletis completa* for each sampling campaign from July to December 2023. (a) Percentage of infested trees; (b) Percentage of infested fruits; (c) Percentage of fruits sampled from the canopy and infested, and percentage of fruits sampled from the canopy infested and/or showing signs of prior infestation; (d) Percentage of fruits sampled from the ground and infested, and percentage of fruits sampled from the ground infested and/or showing signs of prior infestation; (e) Mean ($\pm$ SE) number of *R. completa* individuals per fruit calculated between trees for each sampling campaign. Sampling period: JUL: July 26; AUG: August 30; SEP1: September 9–13; SEP2: September 23–27; OCT1: October 8–11; OCT2: October 21–25; NOV1: November 4–8; NOV2: November 18–22; DEC1: December 3–5 and DEC2: December 17–19, 2023.

healthy skin of the fruit (based on colouration), proportion of rotting surface (based on visual aspect), proportion of fruit surface with no skin (removed by physical wounds or animal foraging), proportion of visible mesocarp (due to skin removal, fissures or when husk and shell were disjoint), visible shell (due to mesocarp removal), presence of accessible seed (due to a hole in the shell or opened valves), presence of mould (i.e., *Penicillium* and *Monilinia* fungal sporophores following the identification keys of FREDEC (2002)) and the number of holes associated with galleries drilled by pests (e.g., codling moth *Cydia pomonella* or *R. completa*). The exact varieties of collected walnut trees could not be determined due to various hybridisations (Zhou et al., 2021) of these spontaneous trees. Nevertheless, we characterised the following fruit traits potentially related to their attractiveness to the pest (Tables S1 and S8). Brix values (% sugar content) and pH were measured in the healthy part of the husk. Brix values were determined using a refractometer (Bellingham+Stanley sugar 0%–50%, serial number 019568 for low volume), while pH was measured using indicator papers (Special indicator paper, REF 902 05, pH 0.5–5.5, MACHEREY-NAGEL; and pH indicator paper, pH 5.5–9.0, Supelco). The firmness of the fruit husk with the skin, were measured at two points (on the peduncle side and on the flower scar side) using a penetrometer (Penetrometer PCE-PTR 200 N, PCE INSTRUMENTS). Finally, the thickness of the fruit husk was measured using a manual calliper (Table S8).

Since tree shape and fruit load can influence attractiveness to the fly (Senger et al., 2009), the following vegetative and reproductive traits were recorded for each walnut tree under which fruits were collected, to estimate their influence on *R. completa* infestations: tree height, minimum and maximum canopy diameter, canopy area ($\pi \times \text{max canopy radius} \times \text{min canopy radius}$) and trunk circumference (at 1.50 m height). The numbers of fruits on the tree and on the ground surface under the tree's canopy in a 5 m radius around the trunk were recorded. For each tree, the mean fruit volume ($\text{mean } 4/3 \times \pi \times r_1 \times r_2 \times r_3$) and the total fruit volume of fruits per tree was calculated.

Rhagoletis completa identification and counting

Immediately after collection, walnut fruits were individually placed on wet cotton wool in cylindrical plastic transparent containers (diameter = 60 mm, height = 68 mm, volume = 769 cm³), covered with a nylon mesh and maintained in a temperature-controlled room at 20°C with a 16:8 light:dark cycle until all *R. completa* larvae pupated or imago emerged. Pupae and adults coming out of the fruits were collected daily and stored in 70% ethanol until identification. All collected fruit were maintained in the emergence room for 100 days to ensure that all *R. completa* were at the pupal stage. After this period, walnut fruits were dissected to collect any remaining *Rhagoletis* pupae from cotton wool and the fruits. *Rhagoletis completa* individuals were identified using a Leica M205C stereomicroscope (equipped with a Leica MC170 HD camera and Leica Application Suite software), following the keys provided by Carroll et al. (2004) and a collection of standard specimens available in the laboratory.

Environmental variables

Local, landscape and meteorological variables were measured at each sampling site or obtained from online databases to examine their relationships with *R. completa* infestation levels. The list of variables is provided in Table S1.

For each sampled tree, the altitude and the slope of the site were recorded. Within a 5 m-radius plot centred on the trunk, the cover and height of the tree, shrub and herbaceous layer were estimated, as well as soil litter thickness. Leaf litter and dead wood debris cover were measured, and the presence of compost was noted. The proportions of local habitats surrounding the walnut tree (i.e., wood, hedge-row, orchard, grassland, crop, garden, building, road, river and pond) were recorded within 5 m and 20 m radii. Site management practices concerning herbaceous vegetation (mown vs. grazed grasslands) and walnut trees (yearly pruned vs. rarely or not pruned; pesticide-treated vs. non-treated) were also noted.

The landscape composition around each sampled walnut tree was characterised. A geographic database was created using a Geographic Information System (GIS; ArcGIS Pro v.2.5, ESRI). The sampled walnut trees were positioned in the GIS, and buffers of 10 m to 5000 m radii around each tree were created for subsequent analyses of landscape composition (see Landscape composition section, Table S1). Landscape elements (woodland, grassland, crop, building, road and water) were extracted from the OSO database (Centre d'Expertise Scientifique OSO, THEIA, 2024) and updated using aerial photographs and field observations for buffers <100 m. The BD-Carto® database from French National Geography Institute (IGN Database, 2024) was used to refine mapping and georeferencing (Institut National de l'Information Géographique et Forestière, IGN). For each sampled tree, the cumulative area of each habitat composing the landscape was then computed within each concentric buffer.

Macroclimatic conditions were characterised for each sampling site using regional measurements. Daily meteorological data were retrieved from the three nearest weather stations to each site (Tables S5 and S6), representing large-scale climatic conditions. Daily minimum, mean and maximum temperatures, as well as rainfall and snowfall, were calculated for all sites using inverse-distance weighting (IDW) interpolation (Willmott et al., 1985) based on the data from the three nearest weather stations (detailed in Tables S5, S6 and S7). Accumulated degree-days ("Growing Degree Days", GDD) were calculated using a lower threshold of 0°C from 1 January 2023 to the sampling date (Baskerville & Emin, 1969). This threshold is a standard value commonly used in insect and plant studies (McNeil et al., 2020; White et al., 2012) and is particularly appropriate for studying temporal synchrony between flies and plant resources (Deconninck et al., 2025; Iler et al., 2013; Ulmer et al., 2022). This is particularly relevant for *R. completa*, which overwinters at the pupal stage and potentially endures extreme temperatures (Boyce, 1934; Rull et al., 2019b). From daily precipitation data, we calculated mean daily precipitation, cumulative precipitation from January to March and from April to June 2023, cumulative precipitation between 1 January

2023 and each sampling date, and within the 7- or 14-day periods preceding each sampling date.

Microclimatic temperatures were recorded at each sampling site to monitor the air temperature within the walnut tree canopies. Hobo loggers (TIDBIT data logger V2 TEMP TBI-001, ONSET Company, Bourne MA, USA) recorded temperatures every 60 min. At each sampling site, a logger was suspended 1.5 m above the ground within the tree's canopy, under the shade of a branch to avoid direct solar radiation, and oriented northward. Temperatures recorded by the loggers were extracted to compute the mean daily minimum, mean and maximum temperatures and to assess the buffering ability of the local tree's canopy relative to the air temperatures recorded by regional meteorological stations. As for macroclimate data, GDD were calculated from Hobo logger data to characterise the local microclimate under the sampled trees canopies.

Statistical analyses

To describe the dynamics of walnut fruit infestation by *R. completa*, the Fruit Infestation Rate (FIR; Deconninck et al., 2024a) was calculated for each tree at each sampling period ($\text{FIR} = \text{number of } R. completa \text{ individuals counted from a fruit sample collected from a given walnut tree} / \text{total number of fruits in this sample collected from the walnut tree}$). This index was calculated separately for fruits collected in the trees' canopy and those collected on the ground under the trees. The influence of environmental variables on fruit infestation was examined using Generalised Linear Mixed Models (GLMMs) following a two-step procedure given the high number of zero values. First, GLMMs with binomial distribution and logit link were used to test the influence of environmental variables (i.e., walnut tree characteristics, site and landscape characteristics and meteorological variables; see Table S1) on the occurrence (presence/absence) of *R. completa* in fruit samples collected from the canopy of each tree at each sampling period ($n = 116$ fruit samples, each containing a maximum of 10 fruits, from 24 trees, from July to December; Table 1). Second, among fruit samples infested by the fly ($n = 59$ fruit samples from 21 trees, from July to October), the effect of environmental

variables on FIR was analysed using GLMMs with a Gamma distribution and identity link (Table 2). "Site" was included as a random effect in all the GLMMs to account for the non-independence of walnut fruits sampled from the same tree. To reduce model complexity and to avoid overfitting, explanatory variables were preselected based on their Pearson correlation with FIR across spatial scales (buffers from 5 m to 5000 m radius around each sampling point) following Ulmer et al. (2022). Then, model selection was performed using backward selection based on the Akaike information criterion (AIC; Harrison et al., 2018). This two-step procedure involving occurrence and abundance data examined two major and successive ecological challenges that shape the population dynamics of the fruit flies over the seasons (Deconninck et al., 2025). First, their presence or absence on a host plant is determined by their ability to reach that plant, influenced by dispersal limitations related to landscape and climate. Second, once the host plant is reached, their abundance in fruits is favoured by the quantity of local resources or limited by environmental inadequacies to their specific niche requirements (Deconninck et al., 2025).

Next, to determine the spatial scales at which the different landscape habitats influence the overall infestation of walnut trees, while eliminating the effect of seasonality, the mean FIR was calculated between the fruit collection campaigns conducted from September to December for each of the 24 trees studied. Then, Pearson correlation tests were performed between $\log_{10}(x + 1)$ -transformed FIR and the proportions of habitats within radii ranging from 10 m to 5 km around each tree to identify minimum and maximum distances of influence of each habitat on tree infestations.

Finally, to estimate the damage caused by *R. completa* infestations on the quality of each walnut fruit collected in September ($n = 479$ fruits), the period of high infestation level preceding fruit harvesting in October, a set of fruit characteristics directly related to their commercial value and quality such as fruit mass, the proportion of the shell exhibiting deformation or darkening, kernel colouration and the presence of mouldy or shrivelled parts on the seed (Solar et al., 2020; see Table S1 for the exhaustive list of fruit traits) was compared between infested ($n = 185$) and uninfested ($n = 294$) walnut fruits collected in the canopy of trees using Mann-Whitney *U* tests ($\alpha = 0.05$, Figures 3 and 4). Spearman correlation analyses were performed between the

TABLE 1 Effects of environmental variables on the presence/absence of *R. completa* in walnut fruit samples collected from the canopy, analysed using a generalised linear mixed model with binomial distribution and logit link and "site" included as a random effect. $n = 116$ fruit samples of 10 fruits per tree, collected from 24 trees from July to December. MEANMIN14Js: Mean of minimum temperatures over the 14 days before sampling (weather station data), RAIN2T: Sum of daily precipitation between 01/04/2023 and 30/06/2026, WTHEIGHT: Walnut tree height, DISOSOGRASS: Nearest distance to grassland habitat.

Dependent variables	Explanatory variables	Model parameters							
		<i>F</i>	df1	df2	Estimates	SE	<i>t</i>	<i>p</i>	AIC
<i>R. completa</i> presence/absence	Model constant	6.847	4	111	20.799	10.851	1.917	0.058	595.685
	MEANMIN14Js	23.173	1	111	0.873	0.181	4.814	<0.001	
	RAIN2T	6.368	1	111	-0.579	0.229	-2.524	0.013	
	WTHEIGHT	5.005	1	111	-0.255	0.114	-2.237	0.027	
	DISOSOGRASS	4.624	1	111	-0.021	0.01	-2.15	0.034	

TABLE 2 Effects of environmental variables on Fruit Infestation Rate (FIR) analysed using a generalised linear mixed model with a Gamma distribution and identity link and “site” included as a random effect. FIR = number of *Rhagoletis completa* individuals counted from a fruit sample collected from the canopy of a given walnut tree / total number of fruits in this sample collected from the walnut tree. Only infested fruit samples were considered. $n = 59$ fruit samples of 10 fruits per tree per sampling campaign, collected from 21 trees between July and October. MEANMIN14Js: Mean of minimum temperatures over the 14 days before sampling (weather station data), WTHEIGHT: Walnut tree height, FMASSTOT1_MNSTG: Mean mass of fruit sampled from the canopy, MOLD1_MNSTG: Mean proportion of fruits with mould on the husk, DISPOLWATER: Nearest distance to river, POTA75Perc: Percentage of potato crop in a 75 m radius.

Dependent variables	Explanatory variables	Model parameters					
		F	df1	df2	Estimates	p	AIC
Fruit Infestation Rate by <i>R. completa</i>	Model constant	12.965	6	52	−5.137	<0.001	327.733
	MEANMIN14Js	23.487	1	52	0.535	<0.001	
	WTHEIGHT	6.321	1	52	−0.041	0.015	
	FMASSTOT1_MNSTG	30.304	1	52	0.146	<0.001	
	MOLD1_MNSTG	8.17	1	52	−1.49	0.006	
	DISPOLWATER	16.932	1	52	−0.001	<0.001	
	POTA75Perc	34.288	1	52	−0.094	<0.001	

number of *R. completa* individuals per walnut fruit and fruit characteristics to assess the impact of pest abundance on the degree of alteration of fruit characteristics (Table 3). Statistical analyses were performed using IBM-SPSS v.24.0 (IBM, Armonk, NY, USA).

RESULTS

A total of 2433 walnut fruits were sampled from 24 trees during 10 collection campaigns over a six-month period, including 1060 fruits (43.57%) collected in the canopy and 1373 fruits (56.43%) on the ground (Table S3). Overall, 3266 *R. completa* individuals were identified from 310 infested fruits (among the 2433 fruits sampled) corresponding to 12.74% of sampled fruits hosting at least a pupa. A total of 2944 *R. completa* individuals were recorded from 254 fruits collected in the canopy and 322 individuals from 56 fruits collected on the ground (Table S4). Consequently, 90.14% of the *R. completa* individuals were counted from fruits harvested from the canopy and 9.86% from fruits collected on the ground. The proportion of fruits with the presence of *R. completa* individuals was higher in the canopy (23.96%) than on the ground (4.08%). When including walnut fruits with cues of previous infestations (i.e., galleries or exit holes in the husk; hatched histograms in Figure 1c,d), the proportion of infested fruits increased to 63.30% in the canopy and 60.45% on the ground.

Rhagoletis completa was detected in walnut fruits over a period of 4 months, from late July to late October (Figure 1 and Table S4). The mean fruit infestation rate was (mean $\pm$ SE) 1.34 ± 0.10 individuals per fruit across the sampling period ($n = 2433$ fruits). The maximum number of *R. completa* counted in a single fruit reached 73 individuals. The infestation rate of fruits collected from the canopy (2.78 ± 0.22 individuals per fruit; $n = 1060$ fruits) was always higher than fruits sampled from the ground (0.23 ± 0.04 individuals per fruit; $n = 1373$ fruits) across the period. The peak of fruit infestation in the canopy was reached at the end of August (August 30, 2023), with 100% of

infested trees (Figure 1a), 80% of infested fruits (Figure 1b), and an average of 13.48 ± 2.47 *R. completa* individuals per fruit (Figure 1e).

The presence and abundance of *R. completa* were significantly influenced by climatic variables, landscape composition and walnut fruit and tree characteristics (GLMMs, Tables 1 and 2). Regarding climatic conditions, the mean minimum temperature during the 2 weeks preceding sampling (MEANMIN14Js, Tables 1 and 2) had a positive effect on both pest presence and abundance, whereas heavy rainfall from April to June (RAIN2T) negatively affected pest presence (Table 1). Among landscape characteristics, the increasing distance between the sampled tree and grassland habitats (DISOSOGRASS, Table 1) negatively affected the presence of *R. completa*. Pest abundance also decreased with increasing distance to rivers (DISPOLWATER, Table 2) and potato crop cover within a 75 meters radius (POTA75Perc, Table 2). At the local scale, walnut tree height (WTHEIGHT, Tables 1 and 2) had a negative effect on both the presence and abundance of the fly. Conversely, fruit mass (FMASSTOT1_MNSTG, Table 2) had a positive effect on pest presence, while the presence of mould on the husk (MOLDY1_MNSTG, Table 2) reduced pest abundance.

The ranges of spatial scales at which the different landscape habitats significantly influenced the overall infestation of walnut trees varied considerably depending on the habitat identity (Figure 2a). At the local scale, the cover of conventional potato crop (Figure 2b, POTATO%, 10–100 m) and orchard (Figure 2d, ORCHARD%, 100–300 m) decreased the abundance of the pest, whereas the number of walnut trees neighbouring the sampled trees (Figure 2c, NUMBER OF WALNUT TREES, 50–100 m) increased it. On a larger scale, the length of rivers (Figure 2e, LENGTH OF RIVERS, 1000–3000 m) and hedgerows (Figure 2g, LENGTH OF HEDGEROWS, 2750–3500 m) increased *R. completa* abundance, while the number of orchard patches (Figure 2f, NUMBER OF ORCHARD, 1750–2000 m) and the cover of rapeseed crop (Figure 2h, RAPESEED%, at 2750 m) decreased it.

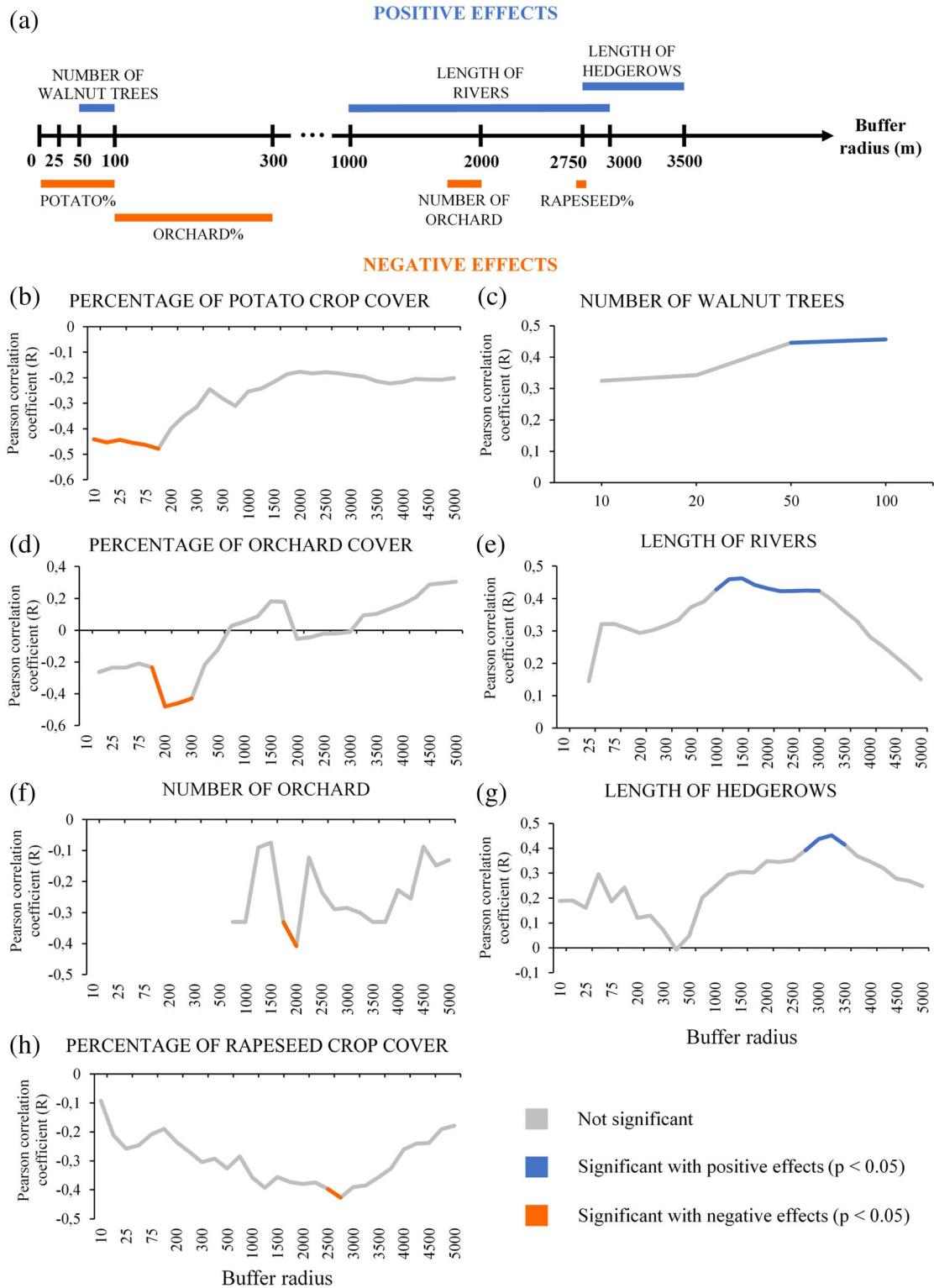


FIGURE 2 Pearson correlation coefficients between $\log_{10}(x + 1)$ -transformed mean Fruit Infestation Rate (FIR) per tree and landscape elements across spatial scales within radii ranging from 10 m to 5 km around each tree. For each of the 24 trees studied, mean FIR was calculated between the fruit collection campaigns conducted from September to December 2023. $\text{FIR} = \text{number of } Rhagoletis \text{ completa} \text{ individuals counted from a fruit sample collected from a given walnut tree} / \text{total number of fruits in this sample collected from the walnut tree}$. (a) Summary of spatial scales at which significant landscape variables influenced infestations; (b) Length of hedgerows (BD TOPO database); (c) Length of rivers (BD TOPO database); (d) Number of orchards (OSO database); (e) Number of walnut trees (field sampling); (f) Percentage of potato crop cover (OSO database); (g) Percentage of rapeseed crop cover (OSO database); (h) Percentage of orchard cover (OSO database). Grey parts of curves indicate non-significant correlations, blue parts indicate significant positive correlations and orange parts indicate significant negative correlations with FIR ($p < 0.05$, $n = 24$ trees).

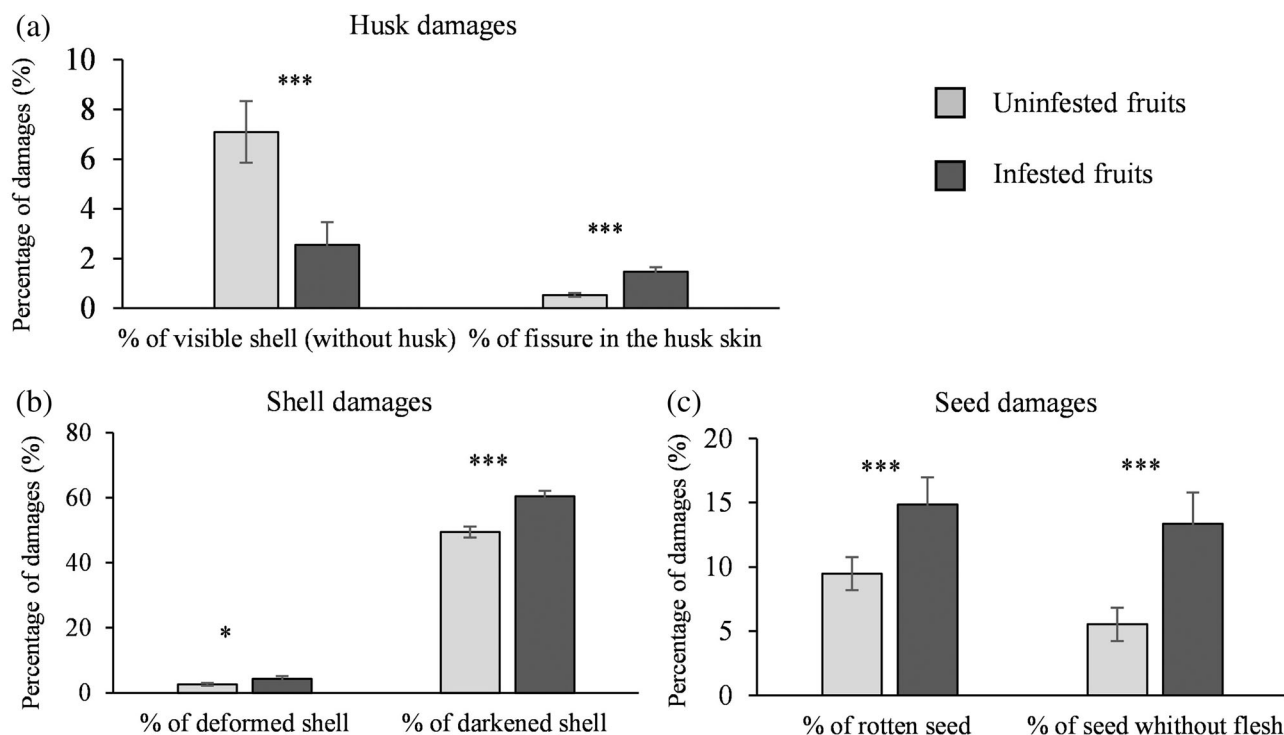


FIGURE 3 Direct damages caused by *Rhagoletis completa* infestation on walnut fruit traits measured in fruits collected in September 2023 ($n = 479$ fruits: 185 infested, 294 uninfested). (a) percentage of damaged husk; (b) percentage of damaged shell (deformed or darkened); (c) percentage of damaged seed (rotten or shrivelled). Significance levels from Mann–Whitney U test are indicated as follows: * ($p < 0.05$), ** ($p < 0.01$), *** ($p < 0.001$).

The damage caused by *R. completa* to walnut fruits and the subsequent alterations of their quality was detectable from September and varied depending on the fruit trait considered (Figures 3 and 4, and Table 3). Foremost, the husk (the tissue directly exploited by the larvae of the pest) of infested fruits showed a significantly higher proportion of black-coloured area (degraded tissue) compared with uninfested fruits (Figure 4a), and the number of *R. completa* individuals per fruit was significantly positively correlated with this proportion of darkened husk skin (variable BLACK1, Table 3). In addition, compared with uninfested fruits, the rotting husks of infested fruits remained more frequently attached and stuck to the shell (see the low percentage of visible shell, without husk, Figure 3a) preventing the release of the commercial part of the fruit (the walnut, including the shell and the kernel) and leaving dark patches on the shell surface (Figure 3b). The skin of the husk (i.e., the periderm of the fruit) of infested fruits also showed more desiccation slots, thus exposing the underlying mesoderm (i.e., the flesh of the husk) to the open air (percentage of fissure in the husk skin, Figure 3a; and variable FISSURE1%, Table 3). Conversely, the husks of uninfested fruits were naturally detached from the shell and presented fewer but deeper fissures that exposed the shell of the walnut to the open air and facilitating its release (percentage of visible shell, without husk, Figure 3a; variable NUTVISIBLE1%, Table 3). *Rhagoletis completa* was significantly more abundant in fruits with larger size (Figure 4c) and larger mass (Figure 4b). The number of *R. completa* per fruit was significantly positively correlated with fruit

volume (FVOL1, Table 3), fruit mass (FMASSTOT1, Table 3) and walnut (shell and seed) mass (WNMASS2, Table 3). The loss of fruit mass measured 3 months after sampling was significantly higher (37.38% higher) in infested than in uninfested fruits (Figure 4d). This loss of mass also increased with the number of *R. completa* individuals per fruit (variable DELTAMASS, Table 3). Moreover, infestation of fruits was associated with a significant increase in the proportion of deformed (percentage of deformed shell, Figure 3b) and blackened shell (percentage of darkened shell, Figure 3b; variable BLACKSHEEL2%, Table 3). The quality of the seeds was severely impaired after infestation by the pest. In infested fruits, the skin of the seeds was more frequently brown or black (Figure 4e) and the number of *R. completa* individuals per fruit was significantly and positively correlated with the percentage of brown seed (variable SSBROWN2%, Table 3) or black areas (variable SSBLACK2%, Table 3) covering the surface of the seed. On the contrary, the seed skin of uninfested fruits displayed a golden colour (percentage of yellow skin covering the seed, Figure 4e; and variable SSYELLOW2%, Table 3). Moreover, seeds of infested fruits showed higher proportions of mouldy surface (percentage of rotten seed, Figure 3c; variable SEEDROTTEN2%, Table 3) and shrivelled or incompletely developed seeds (percentage of shrivelled seed, without flesh, Figure 3c; variable ISNOFLESH2%, Table 3). In contrast, seeds with healthy white flesh were more frequent in uninfested fruits (percentage of seed with white flesh, Figure 4f; variable ISWHITE2%, Table 3).

TABLE 3 Spearman correlations between *R. completa* abundance and the traits of walnut fruits collected from the tree canopy in September 2023 ($n = 479$ fruits).

Variable codes	Variable description	Correlation coefficient	<i>p</i>
Measures after sampling			
FVOL1	Volume of the fruit	0.218	<0.001
FMASTOT1	Total mass of the fruit (husk and walnut)	0.323	<0.001
GREEN1	Percentage of green husk surface (healthy)	−0.058	0.206
BROWN1	Percentage of brown husk surface (damaged or rotten)	−0.031	0.503
BLACK1	Percentage of black husk surface (damaged or rotten)	0.195	<0.001
NUTVISIBLE1%	Percentage of visible walnut shell (without husk)	−0.241	<0.001
FISSURE1%	Percentage of opened husk skin (exposed flesh due to fissures)	0.215	<0.001
Measures 3 months after sampling			
FMASTOT2	Total mass of the fruit (husk and walnut)	0.122	<0.05
DELTAMASS	Difference between the mass after sampling and 3 months later	0.335	<0.001
FVOL2	Volume of the fruit	0.215	<0.001
HUSKMASS2	Mass of the husk	−0.044	0.342
WNMASS2	Mass of the walnut (without husk)	0.137	<0.005
SHELLMASS2	Mass of the shell (without husk and seed)	0.199	<0.001
SEEDMASS2	Mass of the seed (without husk and shell)	0.02	0.664
DEFSHELL2%	Percentage of deformed shell	0.077	0.091
BLACKSHEEL2%	Percentage of blackened shell	0.219	<0.001
SSYELLOW2%	Percentage of yellow seed skin surface	−0.339	<0.001
SSBROWN2%	Percentage of brown seed skin surface	0.091	<0.05
SSBLACK2%	Percentage of black seed skin surface	0.222	<0.001
SEEDROTTEN2%	Percentage of rotten seed	0.161	<0.001
SEEDDRY2%	Percentage of dry seed	0.042	0.358
ISWHITE2%	Percentage of white seed flesh	−0.129	<0.005
ISYELLOW2%	Percentage of yellow seed flesh	−0.035	0.443
ISBROWN2%	Percentage of brown seed flesh	0.061	0.186
ISBLACK2%	Percentage of black seed flesh	0.047	0.305
ISNOFLESH2%	Percentage of seed without flesh or shrivelled	0.18	<0.001

DISCUSSION

Our study demonstrates that wild unmanaged walnut trees growing spontaneously in semi-natural habitats in northern France are highly infested by the invasive pest fly *Rhagoletis completa*, altering their fruit quality. This confirms the role of these unmanaged trees as an important network of pest reservoirs and potential sources of contamination for walnut trees cultivated in agricultural stands. Here, we (i) address how climatic factors influence *R. completa* infestation across temporal and spatial scales, (ii) discuss the divergent roles of anthropised and natural habitats composing the landscape in the spread and persistence of *R. completa* populations, (iii) identify the key traits of the host plants promoting fruit infestation at a local scale and finely (iv) summarise management recommendations and highlight gaps in the knowledge of the part of the pest life cycle occurring outside walnut crop areas, in surrounding natural habitats.

State of the infestation of walnut trees by *Rhagoletis completa* in the North of France

Our study revealed a high level of infestation of walnut trees by *Rhagoletis completa* with 91.67% of the sampled trees infested. Overall, 61.69% of all collected fruits (canopy and ground fruits) were infested by *R. completa* or exhibited signs of its past presence. Among all fruit samples collected from the canopy of trees, 21.55% had 100% of their fruits infested and/or showing signs of prior infestation by the pest. These findings are consistent with a previous study that reported infestation levels ranging from 74% to 91% in fruits from untreated orchards in northern Italy (Duso & Lago, 2006). *Rhagoletis completa* is known to lay an average of 15 eggs per oviposition (Boyce, 1934). Among the 310 infested fruits examined in our study, 67 (21, 61%) contained more than 15 individuals per fruit, indicating multiple ovipositions. In early September, a maximum of 73 individuals were recorded in a single fruit

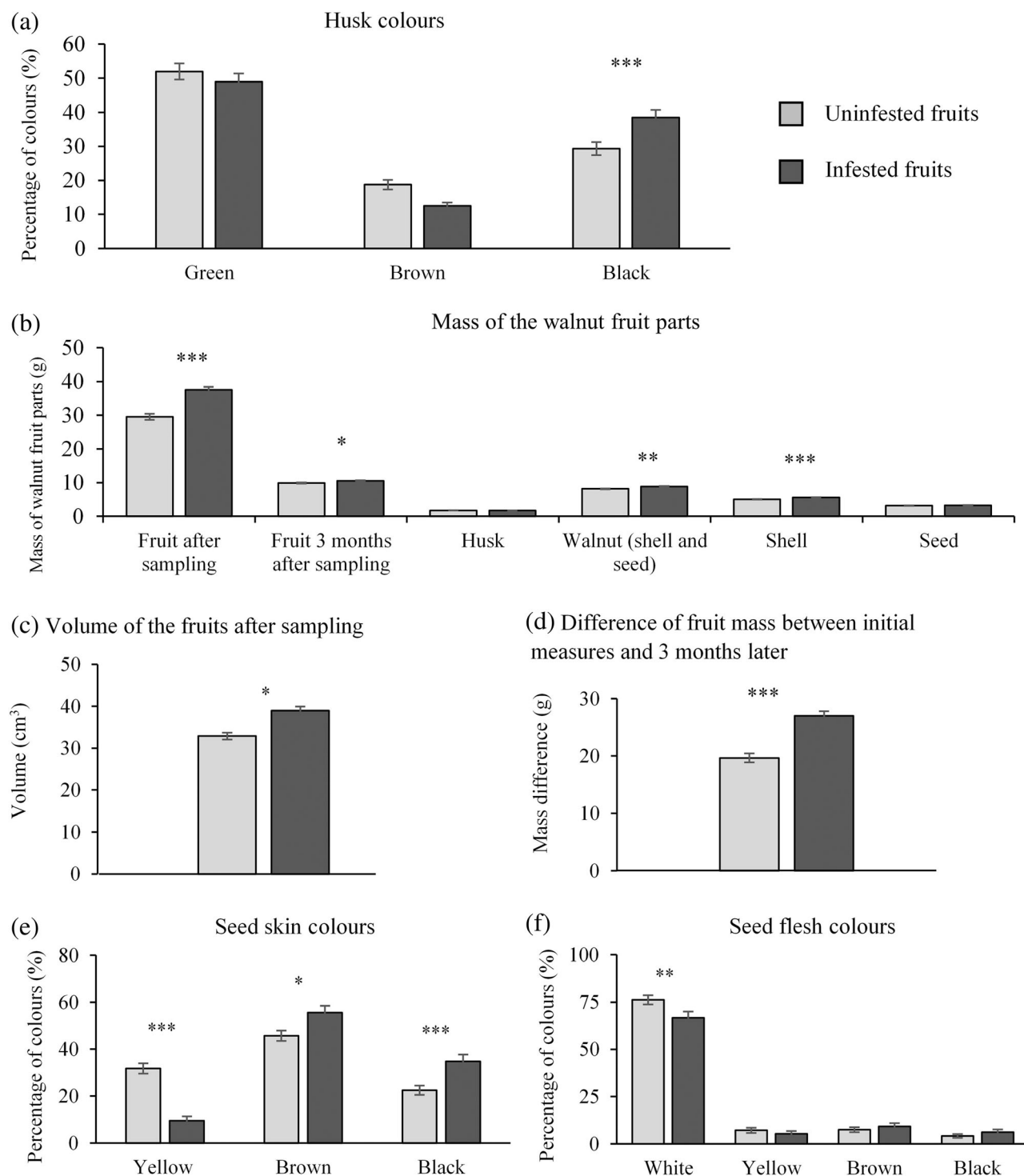


FIGURE 4 Comparison of walnut fruit traits measured in infested and uninfested fruits collected in September 2023 ($n = 479$ fruits: 185 infested, 294 uninfested). (a) percentage of colours cover of the husk surface; (b) mass of the different parts of walnut fruit measured after sampling and after 3 months; (c) fruit volume measured after sampling; (d) difference in fruit mass between the initial measurement (after sampling) and 3 months later; (e) percentage of colours cover of the seed skin (the kernel skin); (f) percentage of colours cover of the seed flesh (the kernel flesh). Significance levels from Mann–Whitney U test are indicated as follows: * ($p < 0.05$), ** ($p < 0.01$), *** ($p < 0.001$).

collected from the canopy, corresponding to the equivalent of 4.9 ovipositions. These observations illustrate the gregarious behaviour of *R. completa*, when the husk is still hard. This behaviour

decreases over time and is replaced by intraspecific avoidance when the husk is fully mature or begins to degrade (Lalonde & Mangel, 1994).

In the present study, we observed that *R. completa* affected both fruit yield and quality by impairing their edibility and visual appeal through several mechanisms. First, the husk of infested fruits remained more frequently bound to the shell, making the harvest of the walnut (shell and seed) more difficult. Second, the shells of infested fruits were frequently covered by dark patches caused by the release of husk tannins or deformed due to the degradation of tissues by the pest larvae (Grohar et al., 2025; Medic et al., 2022). Although this didn't necessarily affect seed quality, these external signs of degradation are repellent and may deter the potential consumer. This phenomenon, which reduces the commercial value of the nuts, is well-known in the walnut industry (Verheggen et al., 2014).

Furthermore, infested fruits generally suffered a greater mass loss than healthy fruits. This reduction can be attributed to damage to the vascular tissues of the husk, which disrupts nutrient transport to the kernel and thus limits its development, causing shrivelled parts with partially developed flesh. Such damage is particularly pronounced when infestation occurs early and can lead to fruit abortion (Boyce, 1934; Solar et al., 2020). The development of mould on the kernel is another symptom of the deterioration of infested fruits, confirming the significant impact of this species on walnut production, as reported in previous studies (Samietz et al., 2012; Solar et al., 2020).

Combined impacts of short-term and long-term climatic variations on infestation success

The effects of climatic variability on insect populations may act at different temporal scales (Deconninck et al., 2025; Deconninck et al., 2024b). In the short term, weather conditions in the preceding days or weeks directly influence individual activity, notably affecting flight, egg-laying or feeding (Boyce, 1934; Lehmann, 1999; Zerulla et al., 2017). In the longer term, climate history, including extreme events and conditions accumulated over several months, seasons or years, shapes population phenology and survival, particularly during critical periods such as overwintering (Harvey et al., 2020; Rull et al., 2019b). In our study, the GLMM selected climatic variables acting specifically on *R. completa* presence at these two time scales.

Concerning long-term climatic variables, although winter temperatures commonly affect pupal survival and adult emergence phenology of *R. completa* (Rull et al., 2019b), our results did not reveal any measurable negative impact of winter temperature on the pest, possibly due to the mild conditions prevailing during the year of the experiment. Previous studies suggest that winter temperatures may not represent a major limiting factor for *R. completa* in temperate regions and that thermal barriers are gradually eroding due to global climate change (Aluja et al., 2011). Only a limited number of climatic variables influenced the pest occurrence in our study, given that the macroclimate (especially temperatures) was relatively homogeneous between our study sites. Nevertheless, heavy rainfall recorded in the spring season, between April and June, was associated with a significant decrease in the presence of the pest. This relationship could be due to an increased mortality of diapausing pupae in the soil, resulting either

from asphyxiation or drowning under waterlogged conditions or from an increase of entomopathogenic infestations, particularly fungal, favoured by persistently wet conditions (McNeil et al., 2020). As a species with a prolonged nymphal stage in the soil, representing half of the annual life cycle and even extending into a two-year diapause for 8.8% to 28.7% of individuals (Boyce, 1934; Duso & Lago, 2006; Rull et al., 2022), survival is highly dependent on the physical and microbiological properties of the substrate, which govern exposure to excess moisture and pathogens present in the soil during wintering. The influence of soil moisture and relative humidity on survival and adult emergence has also been documented for *Rhagoletis pomonella* in America (Rull et al., 2019a).

Regarding short-term climatic variables, the positive correlation between the average minimum temperature during the 2 weeks preceding sampling and the pest occurrence and abundance supports the basic knowledge in *R. completa* ecophysiology. In particular, it confirms the decisive role of temperature in adult oviposition and larval development (Boyce, 1934; Kasana & Aliniaze, 1994). Based on these results, we can hypothesise that climate change in northern France, particularly rising temperatures during summer and autumn, may increase the oviposition rate of *R. completa*. This could result in a higher proportion of infested fruit and increased larval density per fruit compared with current observations.

The influence of climatic variations on insect populations also occurs at different spatial scales (Deconninck et al., 2025; Deconninck et al., 2024b; König et al., 2024). In our study, the global variations of climatic parameters were calculated using data from regional weather stations distributed across the region. We assumed that the effect of these conditions would be locally modulated by the microclimate, which was precisely measured using HOBO sensors installed beneath the canopy of each sampled walnut tree. Indeed, the discrepancy between macroclimate and microclimate is known to play a key role in insect survival during extreme events (frost, heat waves, Terlau et al., 2023) and can also delay their phenological response when individuals benefit from more buffered conditions within microhabitats (Mochizuki et al., 2024). Our results showed that only regional climatic variables from weather stations were selected by GLMMs, while small-scale temperature variations measured by sensors in the canopies were correlated but not retained in models. The greater explanatory power of regional temperature variations for the abundance of *R. completa*, compared with local variations, suggests that these flies rely more on ambient temperature (during their flights between host trees, for example) than on local microhabitat conditions to organise their activities (reproduction, egg-laying, inter-site migration). This is consistent with the biology of this highly specialised species, whose life cycle depends on a narrow time window, largely determined by climatic conditions, to emerge after winter, mate and lay eggs when the host fruit reaches optimal maturity (Lalonde & Roitberg, 1992; Takata et al., 2025). In this context, the more moderate temperatures under the canopy of walnut trees, as well as temperature variations between trees, could act as desynchronization factors, both between fly populations at the regional scale and between the insects and their host plants. It has been shown that this mismatch between the timing of

the dynamics of fly populations and that of the fruit set of their host plants, caused by contrasting climatic gradients, can significantly reduce the level of fruit infestation in other fly species (Ulmer et al., 2022).

Contrasting effects of natural and anthropised elements of the landscape on the distribution of the pest fly

Landscape composition is a major determinant of the spatial distribution and persistence of frugivorous insects (Guinard et al., 2026; Mazzi & Dorn, 2012; Ulmer et al., 2024). From the point of view of a flying insect parasitising plants, the landscape elements can be categorised into three major groups according to their roles in the life of the insect: (i) the habitats representing a danger for surviving (presence of predators, pesticides or circulating vehicles, for example) and forming a resistance to dispersal and persistence (Takata et al., 2025), (ii) the habitats representing a shelter, a corridor or hosting resources (Wakie et al., 2019) and (iii) the proximity and density of neighbouring host plants necessary for the development of offspring (Krasnov et al., 2019).

- i. Several anthropogenic habitats composing the landscape surrounding sampled trees were unfavourable to *R. completa* in our study. The fly abundance was negatively affected by conventional crops of potato and rapeseed, as well as by orchards, which were subjected to high and frequent applications of insecticide, contrasting with untreated semi-natural habitats. These treatments may negatively impact pupae, which remain in the soil for several months and were therefore directly exposed to phytosanitary substances drifting from neighbouring crops and accumulating in the soil (Chagnon et al., 2015; Ortega et al., 2023). In addition, these treatments may also negatively affect adults, both on their natal tree, particularly when it is located at field margins, or when imagoes cross crop fields during the dispersal phase. These phytosanitary substances thus constitute barriers between adult flies and their host plants as shown in several insect species (Uhl & Brühl, 2019; Wan et al., 2025).
- ii. In the present study, the abundance of *R. completa* was positively influenced by the proximity of semi-natural habitats such as grasslands and riparian vegetation, validating our second hypothesis. These environments, which are generally less anthropised, are likely to offer more favourable conditions for pest survival, particularly due to a lower level of disturbance than in conventional agricultural stands. The positive effect of the length of rivers (often associated with riparian forests in the region) and hedgerows on pest abundance suggests a role of ecological corridors of these linear landscape features. They may facilitate fly dispersal to favourable habitats, increasing landscape connectivity and resource continuity in space. *Rhagoletis completa* is recognised to have a high dispersal capacity even if contrasted results exist in the literature about its migration distance and endurance. In fact, while release-recapture experiments indicated limited dispersal within walnut orchards, laboratory endurance tests

revealed that males and females could fly an average distance of 2.5 km and 1.6 km, respectively, within a few hours (Opp et al., 2003). One extreme case reported that a female covered 11.5 km in 7.2 h, suggesting that under adverse conditions, adults may well be capable of travelling several kilometres in search of a new host tree (Opp et al., 2003). This dispersal trait of the fly likely contributed significantly to the invasiveness of the species, which, coupled with the invasibility of the landscape, ensured the successful invasion of the pest.

- iii. A major challenge for *R. completa* is to find host plants during its short adult life. We showed that the infestation of fruits by the pest increased with the abundance of other walnut trees within a radius of 50 to 100 m. In this distance range, the location of host trees by the fly is probably facilitated by the detection of volatile organic compounds (VOCs) emitted by the walnut husk. These chemical signals, recognised by adult flies, act as attractants and may enhance the efficiency of dispersal in a connected landscape (Sarles et al., 2017). The dense network of hosts within flight range could act as contamination sources and help this oligophagous and univoltine fly to subsist in the long term, as the fruit resource of a tree can fluctuate from year to year (see the phenomenon of alternate bearing of fruit; Haim et al., 2021; Jangid et al., 2023). In addition, the high occurrence of spontaneous and unmanaged walnut trees in hedgerows, field margins and fallow lands emphasises the important contribution of semi-natural habitats to the persistence of wild populations of walnut trees. These wild trees, likely originating from seeds dispersed by birds (Lenda et al., 2011; Vander Wall, 2001) from cultivated or garden walnut trees, bears witness to the crucial role of animal-mediated dispersal in the establishment of unplanted trees within agricultural and peri-urban landscapes (Lenda et al., 2018). These trees may act as stepping stones in the landscape and facilitate the spread of pests in unfavourable cultivated areas (Alharbi & Petrovskii, 2019) and thus influence the structure and persistence of local fly populations.

Attractiveness of host plant traits and fruit quality to the fly

The spatial configuration of host trees, their architecture and fruit availability are likely to influence residence or dispersal decisions of the univoltine Tephritidae. For these species, the choice between remaining on the natal tree or dispersing in search of alternative host trees depends on both the local quality of the resource and the structural characteristics of the environment (Miklavc et al., 2009).

In our study, the height of walnut trees was paradoxically negatively correlated with the abundance of *R. completa*, invalidating our first resource-based hypothesis. This result may be explained by a dilution effect (Deconninck et al., 2024a) caused by the high quantity of fruits produced by the largest trees, diluting the infestation rate of each of its individual fruits. A second hypothesis is that taller trees, which are typically characterised by a single large but bare trunk, create an open micro-environment under the tree, exposed to the wind

and unfavourable for adult flies. Conversely, smaller trees often had a multi-stemmed architecture and a bushier structure, which could create a more stable microclimate (reduced wind, higher humidity, moderate temperature) and provided more shelters (see the case of *Mahonia* in Deconninck et al., 2025), attractive to adult flies.

We observed a positive correlation between the presence of flies and fruit size, validating the predominance of the fruit size effect of our first hypothesis. Large fruit may provide a more abundant and stable resource for larval development, rendering them particularly attractive to gravid females. These results are consistent with the observations of Guillén et al. (2011), who showed an increased attraction of the pest to varieties producing large fruits, associated with higher egg-laying rates and greater pupal mass.

We also found that the pest was more frequently detected in fruits harvested from the canopy than in those collected from the ground, suggesting that mature larvae quickly exit the fruit to burrow into the soil and undergo pupation, as described by Berlocher (1984). Thus, the relative absence of larvae in fruit sampled on the ground does not necessarily reflect a low initial infestation rate, since traces of the pest presence such as galleries remain visible at rates comparable to those from tree canopies, but rather indicates a more advanced stage of the development cycle.

Finally, the abundance of *R. completa* decreased significantly in the presence of mould on the husk, suggesting a preference for intact fruit, consistent with the pioneer species status of this pest. Tephritidae females are also known to exhibit a fine host-selection ability, to detect subtle physical and chemical cues that indicate the suitability of the substrate for larval development (Lalonde & Roitberg, 1992). Decaying or microbiologically degraded fruits may have reduced nutritional value, increased levels of defence compounds produced by the fruit (Grohar et al., 2025) and host antagonistic microorganisms that could affect larval survival. Selecting healthy fruits may thus optimise reproductive performance and offspring survival. The dispersal of individuals to a new host is therefore expected to occur while the husk remains healthy or at the early stage of degradation, thereby enabling successful colonisation and establishment of flies at the new site.

Overall, these results show the joint importance of the structural characteristics of the host plant and the fruit quality in local infestation dynamics. They suggest that, beyond the mere presence of *Juglans regia*, the morphological traits of the trees and fruit attributes modulate habitat quality for *R. completa*, influencing both oviposition decisions and local population persistence.

Perspective on pest management and gaps in the knowledge of insect pest ecology

From the perspective of invasion ecology, *Rhagoletis completa* perfectly illustrates the profile of a successful oligophagous invader, with a rapid and large population expansion determined by the spatial distribution of its host plant and a high infestation rate once established. Our study highlights the importance of unmanaged walnut trees near orchards, which constitute a strategic ecological reservoir capable of

sustaining fly population dynamics and fuelling local infestations. Thereby, unmanaged walnut trees within 100 m of orchards should warrant special attention from growers. Incorporating these factors into the spatial planning of orchards and surveillance areas could improve the effectiveness of integrated pest management strategies, particularly by identifying potential pest population reservoirs, with the ultimate aim of establishing pest-free areas (PFAs).

Moreover, the removal of infested husks at harvest time (November) appears insufficient given the rapid exit of larvae from the fruit since September. Preventive measures against early pupation of larvae in the soil should be considered, such as the deployment of soil nets (Özbek Çatal & Ulusoy, 2018) or alternative ground-covering strategies (Renkema et al., 2011; Yee, 2013). In parallel, additional bio-control approaches could be implemented to reduce pupal survival in the soil. These may involve the enhancement of natural predators (Renkema et al., 2012; Urbaneja et al., 2006), as well as the application of entomopathogenic organisms, such as fungi or nematodes (Takata et al., 2025).

Furthermore, while most studies have focused on the agro-economic impact of *R. completa* (fruit quality, phenology of adult emergence), the ecological consequences of its invasion remain largely unexplored. The introduction of non-native insects is associated with a potential risk of disrupting native insect communities (Fortuna et al., 2022). A few studies have explored interactions between invasive and native Tephritidae species, reporting larval competition and aggressive behaviour of non-native males defending oviposition sites (Biasazin et al., 2021; Deus et al., 2016; Ekesi et al., 2009). However, no study has yet investigated interactions between a non-native Tephritidae and the native fruit fly community in Europe, notably Drosophilidae species, which play a key role in the decomposition of decaying fruit (Deconninck et al., 2024b). These gaps highlight the need to integrate invasion ecology and landscape structure into pest management, to prevent not only agricultural losses but also impacts on biodiversity and ecosystem functioning.

AUTHOR CONTRIBUTIONS

MB: Writing & editing, methodology, sampling, data curation, formal analysis; WD: Writing—review & editing, sampling; AC: Writing—review & editing, supervision, methodology; EGM: Writing—review & editing, data curation, formal analysis; PE: Writing & editing, validation, supervision, methodology, sampling, conceptualisation; OC: Writing & editing, validation, supervision, methodology, data curation, formal analysis, conceptualisation, funding acquisition. All authors read and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

None of the authors have a conflict of interest to disclose.

DATA AVAILABILITY STATEMENT

The dataset of this study (Boulembert et al., 2026) has been deposited in the Dryad Digital Repository and is publicly accessible at <https://doi.org/10.5061/dryad.63xsj3vhp>.

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SUPPORTING INFORMATION

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

Table S1. List of the variables assessed in the study. P/A: Presence/Absence.

Figure S2. Diagram of a walnut fruit.

Table S3. Site information and number of walnut fruits sampled per site (one site = one walnut tree).

Table S4. Number of *R. completa* individuals emerged from walnut fruit samples collected on each walnut tree (J1, J2, ...) between July and December 2023. Sampling campaigns: JUL: July 26; AUG: August 30; SEP1: September 9–13; SEP2: September 23–27; OCT1: October 8–11; OCT2: October 21–25; NOV1: November 4–8; NOV2: November 18–22; DEC1: December 3–5 and DEC2: December 17–19, 2023. Tree: total number of *R. completa* individuals emerged from fruits collected in the canopy of trees; Ground: total number of *R. completa* individuals emerged from fruits collected from the ground.

Table S5. Weather station information. Department: name of the administrative department of the weather station; weather station city: municipality name (postcode) of the location of the weather station; weather station city coordinates: geographic coordinates of the location of the city where the weather station is located; the location of these regional weather stations of Météo-France can also be found

using Historique Météo web site (<https://www.historique-meteo.net/>). Coordinate system: WGS 84.

Table S6. The three nearest weather stations (city names) and their distance from the sampling sites (kilometres). HOBO logger: serial number of the logger.

Table S7. The three nearest HOBO logger and their distance from the sampling sites (kilometres), for sites with damaged loggers.

Table S8. Mean ($\pm$ SE) of walnut fruit characteristics measured from 15 fruits sampled from the tree canopy for the 24 sites. Site codes: site/walnut tree abbreviation; Fruit height: length of the fruit (walnut and husk) from the flower scar to the fruit peduncle; Fruit length: fruit largest width (mm); Fruit width: fruit finest width (mm); Fruit mass: total mass of the fruit (husk and walnut, g); Husk sugar concentration: husk sugar content (brix degree); Husk pH: husk pH; Husk hardness near peduncle, near the scar and mean: husk

hardness near the peduncle, near the flower scar and the mean of the two measures, respectively (N); Husk thickness: thickness of the husk (mm).

Figure S9. Photograph of an adult of *R. completa* that emerged from a walnut sample of the study sites (Leica M205C stereomicroscope).

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