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# Macroecological patterns of fruit infestation rates by the invasive fly *Drosophila suzukii* in the wild reservoir host plant *Sambucus nigra*

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## Abstract

1. The invasive pest *Drosophila suzukii* is a fruit fly native to Asia that infests a wide variety of fruits. Wild plant species are major reservoirs for *D. suzukii* populations but their infestation rates vary greatly among geographical areas.
2. We aimed at disentangling the relative roles of macroclimatic, landscape and local factors in the rate of *D. suzukii* infestation of elderberry fruits (*Sambucus nigra*), a major wild host plant in Europe.
3. We collected elderberry fruits across 215 sites distributed in 13 regions from North to South of France. We counted the number of emerging *D. suzukii* adults and

tested for the effect of macroclimatic, landscape, local biotic and abiotic variables, as well as plant traits using linear mixed models.

4. Site latitude and mean daily maximum temperature since the beginning of the year had respectively the strongest positive and negative effects on mean infestation rates across regions. Infestation rates also increased with forest cover in a 100 m radius around sampling sites.
5. This study shows the importance of taking into account multiple scales and factors, from the fruit characteristics (i.e. maturity) to landscape composition and macroclimatic variables, when studying the interaction between *D. suzukii* and its host plants.

**KEYWORDS**

climatic cline, insect invasion, landscape composition, non-crop host plant, plant traits, polyphagous insect, spotted-wing drosophila, temperature

## INTRODUCTION

The recent anthropogenic acceleration of intercontinental movements of species combined with climate change has caused an increase in the number of invasive alien species worldwide, including insect pests (Seebens et al., 2017; Skendžić et al., 2021). One of the most widespread and economically impacting invasive alien species nowadays is the fruit fly *Drosophila suzukii* (Matsumura, 1931), an insect pest native to Asia. Since 2008, it has spread rapidly across Europe (Cini et al., 2014) and North America (Walsh et al., 2011), causing important damage to agricultural production with considerable economic impact (Asplen et al., 2015; Yeh et al., 2020). Indeed, this polyphagous pest infests a wide variety of cultivated (Lee et al., 2011), ornamental and wild fruits (Kenis et al., 2016; Poyet et al., 2015). Research on sustainable methods of biocontrol is still in progress (Ulmer et al., 2020, 2021; Wang, 2020). Given the rapidity of its expansion, disentangling the respective roles of local (fruit resource quantity and quality), landscape (land uses) and global (macroclimatic factors) conditions in determining the ecological niche of *D. suzukii* and driving its population dynamics is crucial to improve management strategies and better predict its future spread.

The interactions between *D. suzukii* and crop plants are well documented due to its important damages on fruit production. Although non-crop fleshy-fruited plant species represent major reservoirs for populations of *D. suzukii* (Delbac et al., 2020b; Kenis et al., 2016; Poyet et al., 2015), their role in the invasion and spread of the fly has been much less studied. Deciphering the role of non-crop plants is also crucial for understanding population dynamics across seasons. Wild plants are often categorized as either host or non-host (Bolton et al., 2021; Yan et al., 2017), but this dichotomy overlooks the potential variability in infestation rates among wild plants in the field, both among species and among population within the same species (e.g., due to variation in climatic conditions among geographic locations or due to variations in local factors, Kenis et al., 2016). Yet, very few studies have looked at the impact of environmental factors on the infestation rates of wild and cultivated fruits by this fly (Delbac et al., 2020b; Tonina et al., 2016). More importantly, most studies exploring environmental drivers of *D. suzukii* abundance were conducted using traps in the field and were not based on direct measures of fruit infestation rates (dos Santos et al., 2017; Santoiemma et al., 2019; Stockton et al., 2019b). Therefore, these studies do not provide accurate estimates of the contribution of a particular host reservoir to fly population dynamics.

Many factors may influence the success of fruit infestation by *D. suzukii*. At macroecological scales, latitudinal and longitudinal gradients have been reported to affect the distribution of Drosophila species (dos Santos et al., 2017). Latitudinal gradients could affect *D. suzukii* either directly through abiotic factors (e.g., temperature or humidity) or indirectly through biotic interactions (e.g., through the indirect effects of temperature or humidity on the host plants of *D. suzukii*). Latitudinal gradients are often correlated with macroclimatic variables, including temperature and rainfall, which are important drivers of the ecological niche of *D. suzukii* based on species distribution modelling (SDM) at large geographical scales (dos Santos et al., 2017; Langille et al., 2017; Ørsted & Ørsted, 2019). Macroecological studies show larger populations of *D. suzukii* in places with mild winters and humid environments (Ørsted & Ørsted, 2019). *Drosophila suzukii* abundance generally increases with latitude (to a certain degree) in the northern hemisphere, as observed in North America (Langille et al., 2017) and Europe (Ørsted & Ørsted, 2019). Experimental studies are concordant with these macroecological observations, which suggests that latitudinal effects are partly due to direct effects of abiotic variables. Indeed, experimental studies show an optimal growth of *D. suzukii* populations around 22°C with a relative tolerance to cold but frost susceptibility (Jakobs et al., 2015; Stephens et al., 2015; Tochen et al., 2014) and a preference for high relative humidity (Tochen et al., 2016). Furthermore, because of the effect of temperature, increasing altitude may locally have the same effect as increasing latitude, and it has been shown that *D. suzukii* can move to higher altitude particularly during summer (Mitsui et al., 2010; Santoiemma et al., 2019; Tait et al., 2018). Latitudinal gradients can also impact the interactions between phytophagous insects and their host plants (Woods et al., 2012). For example, rates of herbivory decrease with latitude in other plant-insect systems (Lehndal & Ågren, 2015; Więski & Pennings, 2014). For *D. suzukii*, macroclimatic factors could indirectly affect infestation rates through their impact on the number and quality of fruits produced by host plants (including content in toxic compounds, number of fruits or fruit size; Senica et al., 2017; Menzel, 2021).

At a finer scale, the landscape composition, i.e. the cover of natural and anthropic habitats and the length of corridors (hedgerows, rivers and roads) surrounding a site, is a key driver of the diversity and abundance of insects (Bianchi et al., 2006; Burel et al., 1998) including pests (Villa et al., 2020). Landscape is an important scale of analysis for the understanding of population dynamics and the management of pest populations. Studies that examine the relationships between *D. suzukii* populations and landscape features remain scarce (Delbac et al., 2020a; Santoiemma et al., 2019; Schmidt et al., 2019). *D. suzukii* uses a wide range of non-crop hosts scattered across the invaded landscapes (Arnó et al., 2016; Delbac et al., 2020b; Diepenbrock et al., 2016; Kenis et al., 2016; Poyet et al., 2015) and its populations alternatively move between fruit crop stands and natural habitats (Tonina et al., 2018). Some non-crop hosts could even be responsible for maintaining *D. suzukii* populations in landscapes and therefore for the infestation of crop plants (Diepenbrock et al., 2016). There is increasing evidence that forest habitats serve as refuges, resource reservoirs and, finally, potential sources of *D. suzukii* to adjacent cultivated areas (Delbac et al., 2020b; Haro-Barchin et al., 2018; Poyet et al., 2014; Urbaneja-Bernat et al., 2020). Earlier infestation risks could occur in farms in high woodland landscapes (Pelton et al., 2016). Linear elements in landscape also appear to enhance the development and spread of *D. suzukii* populations. Maceda-Veiga et al. (2021) found a positive association between *D. suzukii* captures and spatial proximity to streams. Moreover, hedgerow networks are also suspected to foster populations of *D. suzukii* (Santoiemma et al., 2019; Siffert et al., 2021). Finally, similarly to other Drosophila species, the dispersal of *D. suzukii* follows commercial fruit routes (Cini et al., 2014; Lavrinienko et al., 2017) ending in urban areas. Thus, *D. suzukii* abundance is likely to be influenced by road and building density.

At the local scale, various biotic and abiotic environmental factors shape the dynamics of *D. suzukii* populations. The population size of polyphagous pests, that infest plants from different families, increases with the diversity of habitats in the very close vicinity of a sampling plot, even if this diversity also fosters the presence of natural enemies (Chaplin-Kramer & Kremen, 2012; Schmidt et al., 2019). For *D. suzukii*, this positive effect of the diversity of neighbouring habitats is likely linked to a local diversity of fleshy-fruited plants which increases the resource in potential hosts (Kenis et al., 2016; Poyet et al., 2015). Moreover, the abundance of *D. suzukii* populations is likely to increase with both the quantity and quality of infested fruits, which are influenced by local environmental factors such as the slope level and aspect, which determine exposure to solar radiation (Kaul et al., 2001). Indeed, local factors can influence the maturation process of the fruits, which is linked to other fruit characteristics such as the colour or the sugar content, both being important cues in *D. suzukii* oviposition choice (Biolchini et al., 2017; Rice et al., 2016).

This study aims at disentangling the relative roles of macroclimatic, landscape and local factors that could affect infestation rates of a wild host plant by *D. suzukii*. We focused on the elderberry (*Sambucus nigra* L.) because this plant is a major host present across the invaded area of *D. suzukii* in Western Europe (Kenis et al., 2016) and North America (Lee et al., 2015). This approach allows us to decipher the relative importance of each environmental factor on infestation rates across a wide geographical range by fixing host plant identity. The elderberry *Sambucus nigra* shows high rates of infestation in the wild (Kenis et al., 2016) as well as in laboratory conditions (Poyet et al., 2015). This deciduous shrub grows in various climatic conditions, from Mediterranean to oceanic, continental and mountain areas, although hot and dry climates are less favourable for its development (Rameau et al., 2008). This species is often present in disturbed and nitrogen-rich soils. It is found in woodland margins, floodplains, hedgerows, wastelands and other habitats characterized by eutrophic soils (Atkinson & Atkinson, 2002). The infructescence corresponds to a corymbiform cyme (hereafter named corymb) that can bear large amounts of drupe-type fruits (up to more than 500 per cyme). As they ripen, the colour of the fruits changes from green to reddish and then to black. Fruits within corymbs can be heterogeneous in their maturity, with black fruits contiguous to green fruits (Künsch & Temperli, 1978).

Given the ecology of this host plant, we hypothesized that, at a global scale, the latitudinal and climatic gradients shape the level of fruit production of *S. nigra* and thus the reproduction opportunities for *D. suzukii* on this host. More specifically, we hypothesized that *D. suzukii* might show an increasing infestation gradient of *S. nigra* with latitude. The climatic niche of this host plant is optimal under northern temperate climates compared to the Mediterranean climates which is too dry and characterized by heat waves (Rameau et al., 2008), thus showing a larger quantity of available corymbs in the North of France. At a finer scale, we expect infestation rates to be modulated by landscape and local environmental factors that condition the presence of *D. suzukii* populations and/or their accessibility to elderberry fruits. Particularly, as forest habitats are commonly reported as natural refugia for *D. suzukii*, we expected a strong increase of fruit infestations across sampling sites with an increase in neighbouring forest cover. Using elderberry fruits collected from 215 sites along a latitudinal gradient in France, we estimated the variation in *D. suzukii* infestation rates and tested for an effect of macroclimatic (temperature, rain, latitude), landscape (land cover, hedgerow and watercourse length around sites) and local abiotic and biotic variables (slope, aspect, altitude, habitat, fleshy-fruited plant species presence), as well as plant traits (number of fruits, maturity, diameter, tree height, leaf and corymb sizes). We assessed the variation in resource quality among sites using fruit maturity (colour and associated sugar content) and the variation in resource quantity by counting the number of fruits per corymb and corymbs per shrub. Complementary laboratory experiments were thereafter carried out to document the effect of fruit maturity on *D. suzukii* oviposition preference and development success. Indeed, sugar content in host fruits is a major attractant of *D. suzukii* (Travaillard, 2020) and a primary compound of its diet (Biolchini et al., 2017).

# METHODS

## Collection and measures of *Sambucus nigra* fruits and plant traits

Elderberry corymbs were sampled between July 17th and September 1st 2020 in 13 different regions in France (from North to South, see Figure 1 and Table 1). Depending on their availability in the field (the shrubs were scattered and rare in some regions due to the dominance of open crop fields in the agricultural landscape) and after a maximum of one week of search effort to locate elderberry trees bearing fruits, between 15 and 30 shrubs were randomly sampled per region, resulting in a total of 215 sampled shrubs (Table 1). The shrubs were at least 500 m apart from each other. One corymb, bearing between 26 and 535 fruits, was collected per shrub to avoid spatial dependency between samples. The following reproductive and vegetative traits were measured for each shrub: the size of the sampled corymb, the number of fruits of each stage of maturity (green, red, reddish-black, black, overripe or dry), the fruit diameter (measured from five black fruits randomly chosen within each corymb), the number of corymbs on the shrub, the height of the shrub, the size and number of leaflets of the largest leaf. For each elder shrub, we also estimated the mean volume of a fruit (mean radius$^3 \times \pi \times 4/3$), the volume of fruits on the collected corymb and the total volume of fruits on the shrub.

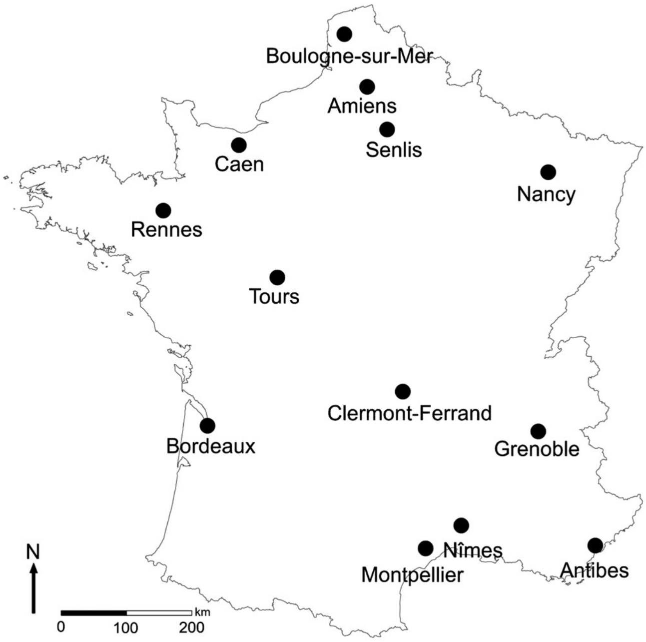

**FIGURE 1** Location of the 13 French cities which determined the studied regions

## Environmental variables

To examine the effects of regional and local environmental conditions on the number of fruits and infestation rates, local, landscape and global environmental variables (Table S1) were measured at each site or gathered from online databases. For each variable, average values were computed across sampling sites for each region.

The list of variables, their units and their codes are shown in Table S1. Climatic conditions were characterized for each sampling site. The daily meteorological data between 01/01/2020 and the day of sampling of elderberry fruits were retrieved from the nearest meteorological station of each site (https://www.historique-meteo.net/

**TABLE 1** Main features of the studied regions

| Region (main city) | Latitude (north) | Longitude (east) | No. shrubs | No. fruits | Mean daily T°C | Rainfall (mm) | Sampling date (year 2020) |
|---|---|---|---|---|---|---|---|
| Amiens | 49.99132599 | 2.049682805 | 20 | 4111 | 11.99 | 466.00 | 26/08–27/08 |
| Antibes | 43.681302 | 7.014837333 | 15 | 3139 | 16.21 | 436.73 | 02/08–13/08 |
| Bordeaux | 44.78864067 | −0.574883333 | 15 | 1939 | 14.64 | 458.42 | 17/07–26/07 |
| Boulogne-Sur-Mer | 50.68915 | 1.79804 | 15 | 2484 | 11.6 | 663.20 | 01/09 |
| Caen | 49.2187354 | −0.253846533 | 15 | 2722 | 12.06 | 666.12 | 21/08 |
| Clermont-Ferrand | 45.72989216 | 3.036544607 | 30 | 5205 | 11.81 | 727.92 | 12/08–27/08 |
| Grenoble | 45.13711667 | 5.773169333 | 15 | 1855 | 11.91 | 1180.20 | 24/08–27/08 |
| Montpellier | 43.66069372 | 3.860189919 | 10 | 1738 | 16.91 | 389.30 | 27/08 |
| Nancy | 48.63302603 | 6.172230627 | 15 | 2104 | 12.09 | 728.57 | 18/08–20/08 |
| Nîmes | 43.83743718 | 4.663794356 | 18 | 2913 | 16.14 | 285.41 | 28/07–06/08 |
| Rennes | 48.15523387 | −1.5560282 | 15 | 1766 | 12.6 | 575.23 | 24/08–27/08 |
| Senlis | 49.32474962 | 2.599874817 | 20 | 4126 | 12.45 | 676.19 | 18/08–30/08 |
| Tours | 47.38374259 | 0.887736111 | 12 | 2165 | 13.53 | 618.27 | 24/08–25/08 |

*Note*: Values represent variable means computed over all sampled sites in each region. Geographic coordinates of the sampling sites follow Lambert93 projection system. No. shrubs: Number of *S. nigra* shrubs sampled per region; no. fruits: Total number of *S. nigra* fruits collected per region; mean daily T°C and rainfall (mm): Mean daily temperatures and cumulative rainfall calculated with daily values measured between 01/01/2020 and the day of sampling.

france/). Daily minimum, mean and maximum temperatures were extracted for each day from January 1st to the day of sampling, allowing us to calculate the mean daily difference in temperature (daily maximum - daily minimum) as well as the number of frost days since the beginning of the year. Degree-days were calculated using a lower threshold of 0°C between 01/01/2020 and the day of sampling (Baskerville & Emin, 1969). The baseline value of 0°C is a standard threshold commonly used in insect and plant studies (McNeil et al., 2020; White et al., 2012). This threshold is particularly adapted to study the temporal synchrony between flies and plant resources (Iler et al., 2013). This threshold was also chosen as we observed and captured *D. suzukii* individuals in activity at very low temperature (<5°C) during winter days (January–February in Amiens, R. Ulmer and O. Chabrerie; and also in Bordeaux, L. Delbac). Mean and cumulative rainfall between 01/01/2020 and the day of sampling were also calculated.

We characterized the landscape composition around each sampled shrub. A geographic database was created using a Geographic Information System (GIS; ArcGIS Pro v.2.5, ESRI). The sampled shrubs were positioned in the GIS and buffers of 100, 500 and 1000 m radii around each shrub were created for subsequent analyses of landscape composition. Landscape polygonal elements (forest, grassland, heathland, crop, garden, building, water) were extracted from the OSO database (Centre d'Expertise Scientifique OSO, 2018) and linear elements (hedgerow, road, river) from BD TOPO (French National Geography Institute, 2019) and updated by aerial photographs and field observations. The BD-Carto® database from French National Geography Institute was used to refine mapping and georeferencing. For each sampled shrub, the cumulated area of polygonal elements or length of linear elements composing landscape were then computed in each concentric buffer.

For each sampled shrub, we recorded the altitude, the slope and the shrub orientation. We subsequently computed a South orientation index (Chabrerie et al., 2013) using the formula: OSOUTH = 180°-Absolute Value (measured orientation-180°). This index ranges from 0 (North-facing plots) to 180 (South-facing plots). In addition to these local abiotic variables, we noted the presence of other plant species with fleshy fruits in a 10 m radius around sampled shrubs and the types of habitats surrounding the shrub (woodland, grassland, crop, building, garden, fallow, road, river and pond).

### Emergences of drosophila species

After collection, the elderberry corymbs were individually placed on paper towels in mesh-covered plastic containers. They were kept at room temperature and humidified to keep the paper towels wet. Adult flies were picked up, as they emerged from the corymbs, and placed in ethanol. Flies were then identified to the species level and the *D. suzukii* individuals were sexed using a Leica M205C stereomicroscope equipped with a Leica MC170 HD camera and the software Leica Application Suite.

## Laboratory study of the effect of fruit maturity on *D. suzukii* oviposition preference and egg-to-adult viability

### Fruit collection and *D. suzukii* rearing conditions

To better understand the role of the maturity of the fruits in *D. suzukii* preferences and infestation success, we carried out experimental assays in controlled conditions at the site of Amiens. Indeed, results from our observational field data (see GLM results, hereafter) strongly suggested that the number of *D. suzukii* flies emerging from *S. nigra* fruits may depend on their ripening level. Colour changes in *S. nigra* fruits are well pronounced during maturation (Künsch & Temperli, 1978). Therefore, laboratory experiments were developed to assess the attractiveness and suitability of three ripening stages of *S. nigra* fruits, according to their colour (Künsch & Temperli, 1978; Mitsui et al., 2006; Poyet et al., 2014): entirely green (unripe), entirely red (ripening) and entirely black (ripe). Fruits were collected on 20 elder shrubs (2000 fruits per individual) scattered in the region of Amiens (North of France). The elderberries used in these experiments were collected in the morning before each experiment between September 3rd and September 10th 2020. The laboratory strain of *D. suzukii* used has been described by Poyet et al. (2014). *D. suzukii* individuals were reared on a banana-based substrate (50 ml Water, 200 g fresh banana, 15 g yeast, 15 ml 96% ethanol, 10 g sucrose, 10 g agar, 2 g Nipagin™). Mated females aged between 6 and 10 days were used for the experiment.

### Fruit infestation rates and *D. suzukii* survival in fruits at different ripening levels

In order to determine the variation in infestation rates among elderberry fruits in the field as well as the variation in survival rates of *D. suzukii* offspring among fruits with increasing ripening levels, we randomly selected 100 fruits of each colour (green, red and black, i.e. 300 fruits per shrub). Fifty fruits randomly selected from the 100 were observed under the stereomicroscope to count the eggs laid by wild *D. suzukii*. All the fruits were then placed on cotton in mesh-covered plastic containers, humidified regularly and kept at 20°C. Adult flies emerging from the fruits were placed in ethanol and counted. *Drosophila suzukii* was the only species emerging from the fruits in this experiment.

### Oviposition preference of *D. suzukii* survival between fruits of different ripening levels

To assess the preference of female *D. suzukii* in terms of fruit maturity for a suitable oviposition site, we conducted an experimental choice test in controlled laboratory conditions. One female was placed in a rectangular plastic box (L: 110 mm × W: 95 mm × H: 50 mm) covered with nylon mesh, along with, spaced 10 cm apart, two elderberry fruits of different colours, collected from the same corymb and free of field *D. suzukii* eggs (visual inspection). After 24 h at 20°C, the fly was removed and the eggs on each fruit were counted. Thirty replicates of each paired combination of fruit maturity (green vs. red, green vs. black, red vs. black) were done. The only boxes used in the subsequent analyses were those where the female laid at least one egg on one of the fruits.

## Sugar content of *S. nigra* fruits at different ripening levels

To investigate how changes in the sugar content of elderberries during maturation affect their attractiveness to *D. suzukii*, we measured the level of three types of sugar (glucose, fructose and sucrose) in the remaining 50 fruits of *S. nigra* of the different colour categories (green, red and black). The fruits were quickly frozen at −80°C for 24 h, then kept at −20°C. Before the measurement, they were placed at 4°C for 10 min in order to defrost. Slightly thawed fruits were mashed in a blender. Aliquots of 100 mg of mashed fruit were then used for sugar extractions, using a succession of three cold hydroalcoholic extractions: a first extraction for 4 h at 4°C in 80% ethanol under constant agitation (120 rpm) in an orbital shaker, a second extraction in 60% ethanol, and a third extraction in purified water. After each extraction, the solution was centrifuged at 12,000 g for 5 min, and the three supernatants obtained were mixed to obtain the hydroalcoholic extract. The extracts were then evaporated using a CentriVap Concentrator (Labconco, Kansas City, USA) and then resuspended in distilled water to obtain a concentrated extract. The sugar contents were measured using a Glucose/Fructose/Sucrose kit from Boehringer Mannheim (R-Biopharm, Darmstadt, Germany) by reading the absorbance at 340 nm with UV-spectrophotometer (EON, BioTek Instruments Inc., USA). We used three replicates of concentrated extract per sample and three sugar measurement replicates per concentrated extract. To express the sugar content as a percentage of dry matter, 100 mg of fruit were freeze-dried and the ratio of fresh matter to dry matter determined.

## Statistical analyses

We examined the relationships between explanatory environmental variables and each of three fruit infestation variables that where either site-specific (SUZUt: the number of *D. suzukii* flies emerging per corymb, or the fruit infestation rate, INFEST = 100 × SUZUt/number of fruits in the corymb) or region-specific (frequency of infested corymbs in each region, Finfest = number of infested corymbs in a region/number of sampled corymbs in the same region; available only at the region scale). For each of the three fruit infestation variables (SUZUt, INFEST and Finfest), we tested for the influence of environmental variables (number of fruits produced by *S. nigra*, local abiotic conditions, diversity of fleshy-fruited plants, landscape compositional and configurational diversity and climate) using either mixed models (GLMMs) at the site scale ($n = 215$ sites) or general linear models (GLMs) at the region scale ($n = 13$ regions). Region was also introduced as a random effect in site-scale GLMMs to account for the non-independence among sampling sites within the same region. For each of the three fruit infestation variables, a preselection of explanatory variables in the models was made by using the variable that correlated (Spearman correlation) the most with each of the three fruit infestation variables among the three spatial scales assessed (buffers of 100, 500 and 1000 m radius around each sampling point). A backward selection of explanatory variables and the second-order Akaike information criterion (AICc; Hurvich & Tsai, 1989) were used to select the most parsimonious model, i.e. the model with lowest AICc. Homoscedasticity was checked using biplots of residuals and model predictions. GLMs, GLMMs and correlation analyses were performed with SPSS version 24.0 (IBM Corporation).

To test whether the numbers of eggs laid by *D. suzukii* in the sets of 50 fruits sampled in the field and whether the numbers of emerging adults varied across ripening levels, we used Kruskal–Wallis tests (the data did not follow a normal distribution, as residuals deviated from homoscedasticity). Post-hoc pairwise comparisons between ripening levels were performed using Mann–Whitney U tests and corrected using the Bonferroni-Holm method ($\alpha = 0.05$). To test whether the numbers of eggs laid in the laboratory choice tests differed between pairs of fruits of different colours (green vs. red, green vs. black, red vs. black), we used Wilcoxon Signed Rank tests. In addition, to test for the effect of fruit colour/maturity on fruit sugar content, we used Kruskal–Wallis tests followed by post-hoc Mann–Whitney U tests. All statistical comparisons between fruit colour categories were performed using R version 4.0.5 (R Core Team, 2021).

# RESULTS

## Field collection

The sampled *S. nigra* shrubs were on average 4.18 m (± SE 1.58) high and bore between 8 and 800 corymbs (mean 149.5 ± 147.3). The mean size (i.e. area) of the corymb was 132.9 $\text{cm}^2$ and ranged from 10.22 $\text{cm}^2$ to 380.52 $\text{cm}^2$. The number of fruits on them ranged from 26 to 532, with a mean of 168.7 (± 96.8) fruits per corymb. Fruit ripeness showed a great heterogeneity, with the proportion of green fruits ranging from 0% to 53.5% (mean 8.9% ± 12.26) and the proportion of black fruits ranging from 0% to 100% (mean 53.5% ± 25.74). The diameter of fruits ranged from 4.1 mm to 7.2 mm (mean 5.2 mm ± 0.72), and the estimated fruit volume on the shrub ranged from 63 $\text{cm}^3$ to 18,294 $\text{cm}^3$ with a mean of 3071 $\text{cm}^3$ ± 3735.

A total of 3891 *D. suzukii* individuals emerged out of a total of 36,267 *S. nigra* fruits collected. This corresponded to a mean infestation rate of 0.11 individuals per fruit with a range varying from 0 to 0.817 individuals per fruit across sites. The sex ratio of males/females was 0.89 for the total individuals of the study. The frequency of infested corymbs (Finfest) ranged from 0.33 to 1 across the 13 regions. Very few other species emerged from the sampled fruits

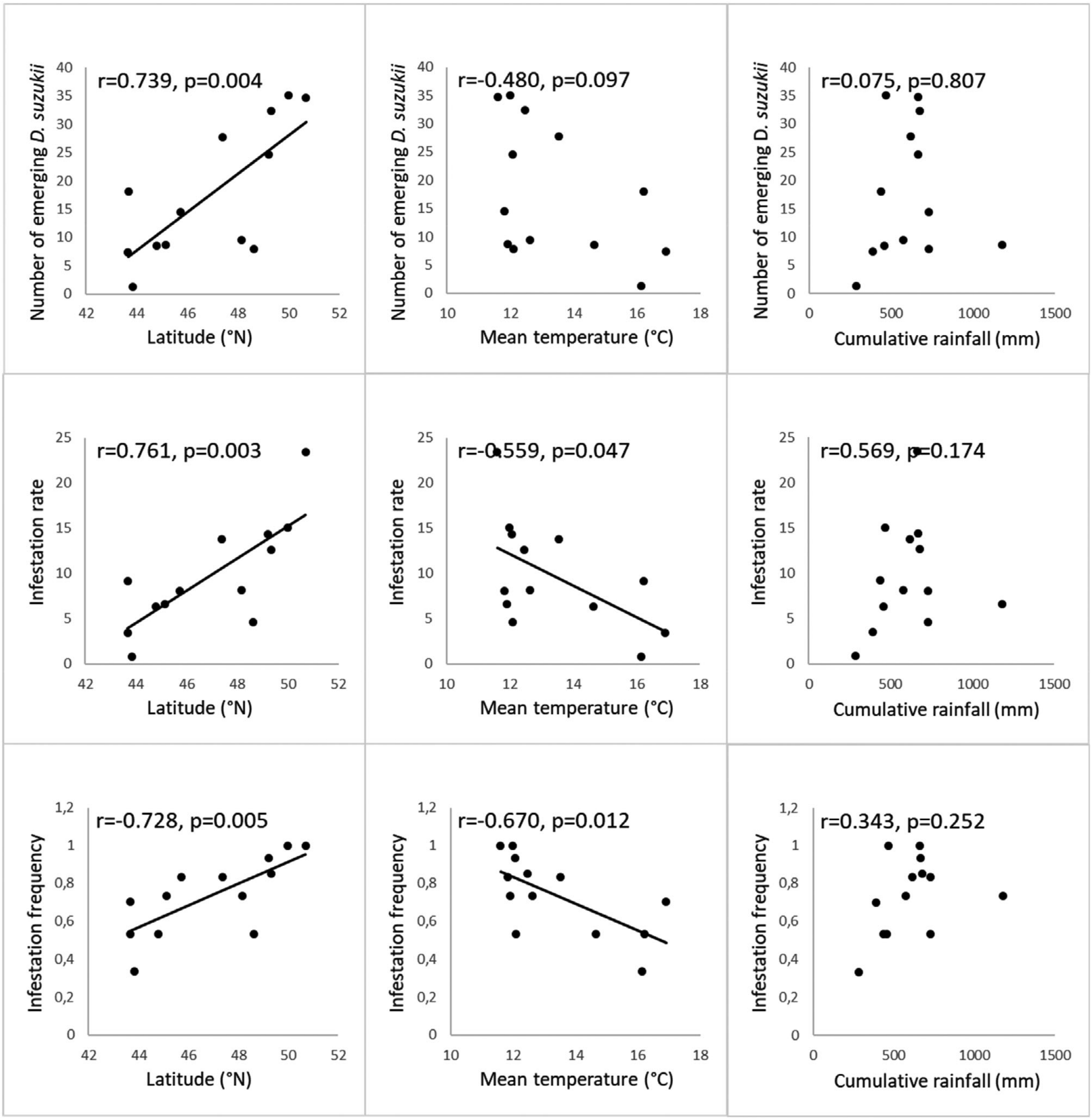

**FIGURE 2** Association across the 13 regions between (a) number of *D. suzukii* emerging per corymb (SUZUt), (b) fruit infestation rate (INFEST = 100 × SUZUt/number of fruits in a corymb) and (c) proportion of infested corymbs per region (Finfest = number of infested corymbs in a region/number of sampled corymbs in the same region) and latitude, mean temperature or cumulative rainfall

(eight *Drosophila melanogaster*, two *Drosophila simulans*, one *Drosophila hydei* and one *Phortica semivirgo*). Daily mean temperature and cumulative rainfall were respectively negatively and positively correlated with latitude (r = −0.652, $p < 0.001$ and r = 0.355, $p < 0.001$, respectively). The effect of these macroclimatic variables on the infestation variables (SUZUt: number of flies emerging per corymb; INFEST: rate of fruit infestation per corymb; and Finfest: frequency of corymb infestation within regions) is shown in Figure 2. Overall, the infestation of *S. nigra* fruits by *D. suzukii* was strongly positively correlated with latitude, and negatively with daily mean temperature between the first day of the year and the day of the sampling. Infestation rates were not correlated with cumulative rainfall at the region scale (Figure 2). The effect of the same macroclimatic variables only significantly impacted the number of corymbs and total volume of fruit produced per shrub, which were negatively correlated with mean of the daily minimum temperature (r = −0.310, $p < 0.001$ and r = −0.199, $p$ = 0.005, respectively) and cumulative temperature (r = −0.354, $p < 0.001$ and r = −0.273, $p < 0.001$) and positively correlated with cumulative rainfall (r = 0.302, $p < 0.001$ and r = 0.169, $p$ = 0.018). The same total volume of fruit per shrub was positively

**TABLE 2** Effect of environmental variables and elderberry traits on (a) the number of emerging *Drosophila suzukii* per corymb (SUZUt), (b) the fruit infestation rate per corymb (INFEST = 100 × SUZUt/number of fruits in a corymb) and (c) the frequency of corymb infestation per region (Finfest = number of infested corymbs in a region/number of sampled corymbs in the same region) at the scale of the sampling site (*n* = 215) and/or the region (*n* = 13).

(a)

| Scale/response variable | | Model parameters | | | | | |
|---|---|---|---|---|---|---|---|
| **Site (GLMM)** | **Explanatory variables** | **F** | **Estimate** | **SE** | **d.f.** | **t** | ***p*** |
| SUZUt | Model constant | 17.235 | −155.900326 | 37.553146 | 194.000 | −4.151 | <0.001 |
| | LATITUDE | 15.920 | 3.186290 | 0.798564 | 194 | 3.990 | <0.001 |
| | NFRUIT | 58.461 | 0.146184 | 0.019119 | 194 | 7.646 | <0.001 |
| **Region (GLM)** | | **Wald χ2** | **B** | **Standard residuals** | **d.f.** | | ***p*** |
| SUZUt | Model constant | 49.287 | −140.035 | 19.9466 | 1 | | <0.001 |
| | LATITUDE | 36.990 | 2.603 | 0.4279 | 1 | | <0.001 |
| | NFRUIT | 30.517 | 0.187 | 0.0338 | 1 | | <0.001 |
| | FORE500 | 8.372 | 2.789E-05 | 9.6383E-06 | 1 | | 0.004 |

(b)

| Scale/response variable | | Model parameters | | | | | |
|---|---|---|---|---|---|---|---|
| **Site (GLMM)** | **Explanatory variables** | **F** | **Estimate** | **SE** | **d.f.** | **t** | ***p*** |
| INFEST | Model constant | 15.933 | 38.711 | 9.698192 | 14.805 | 3.992 | 0.001 |
| | Black fruit | 10.066 | 0.038 | 0.011895 | 189.476 | 3.173 | 0.002 |
| | Tmax | 13.190 | −2.003 | 0.551621 | 13.880 | −3.632 | 0.003 |
| | FORE100 | 6.098 | 0.000 | 0.000103 | 123.841 | 2.469 | 0.015 |
| **Region (GLM)** | | **Wald $\chi^2$** | **B** | **Standard residuals** | **d.f.** | | ***p*** |
| INFEST | Model constant | 10.671 | 26.900 | 8.2346 | 1 | | 0.001 |
| | Tmax | 21.624 | −1.938 | 0.4168 | 1 | | <0.001 |
| | NFRUIT | 16.930 | 0.083 | 0.0202 | 1 | | <0.001 |
| | Wood | 9.710 | 9.090 | 2.9172 | 1 | | 0.002 |

(c)

| Scale/response variable | | Model parameters | | | | |
|---|---|---|---|---|---|---|
| **Region (GLM)** | **Explanatory variables** | **Wald $\chi^2$** | **B** | **Standard residuals** | **d.f.** | ***p*** |
| Finfest | Model constant | 67.834 | 0.713 | 0.0866 | 1 | <0.001 |
| | NFRUIT | 27.163 | 0.002 | 0.0004 | 1 | <0.001 |
| | PLANTC | 121.699 | −0.554 | 0.0503 | 1 | <0.001 |
| | ROAD1000 | 62.096 | −1.131E-05 | 1.4352E-06 | 1 | <0.001 |

*Note*: Region was used as a random factor in the mixed models. Variable codes: LATITUDE: North latitude coordinate of the sampling sites (Lambert93 projection system); NFRUIT: Number of fruits on the corymb; FORE500: Area covered by forest ($m^2$) in a 500 m radius around the sampling site; Black fruit: Number of black (ripe) fruits on the corymb; Tmax: Mean of maximum daily temperatures (°C) between 01/01/2020 and the day of sampling; FORE100: Area covered by forest ($m^2$) in a 100 m radius around the sampling site; PLANTC: Number of cultivated plant species with fleshy fruits; wood: Frequency of wooded habitat present in the close vicinity (<10 m) of the sampled elder shrub in a within a region.

correlated with the number of emerging *D. suzukii* (SUZUt; $r = 0.190$, $p = 0.007$). Only few other elderberry traits were correlated to latitude (leaf length: $r = -0.137$, $p = 0.044$; corymb maximum diameter: $R = -0.204$, $p = 0.003$; and corymb area: $r = -0.196$, $p = 0.004$) and none of them were related to infestation rates. No significant correlation was observed between latitude and total fruit number per corymb ($p = 0.085$) or fruit diameter ($p = 0.077$).

The number of *D. suzukii* emerging per corymb (SUZUt) strongly increased with latitude and the number of fruits per corymb at the local scale (Table 2a). Within each region, the number of *D. suzukii* emerging per corymb increased with forest cover in a 500 m radius around the sampling site (Table 2a). The rate of fruit infestation (INFEST) decreased with the mean daily maximum temperature, both across and within regions (Table 2b). The rate of fruit infestation

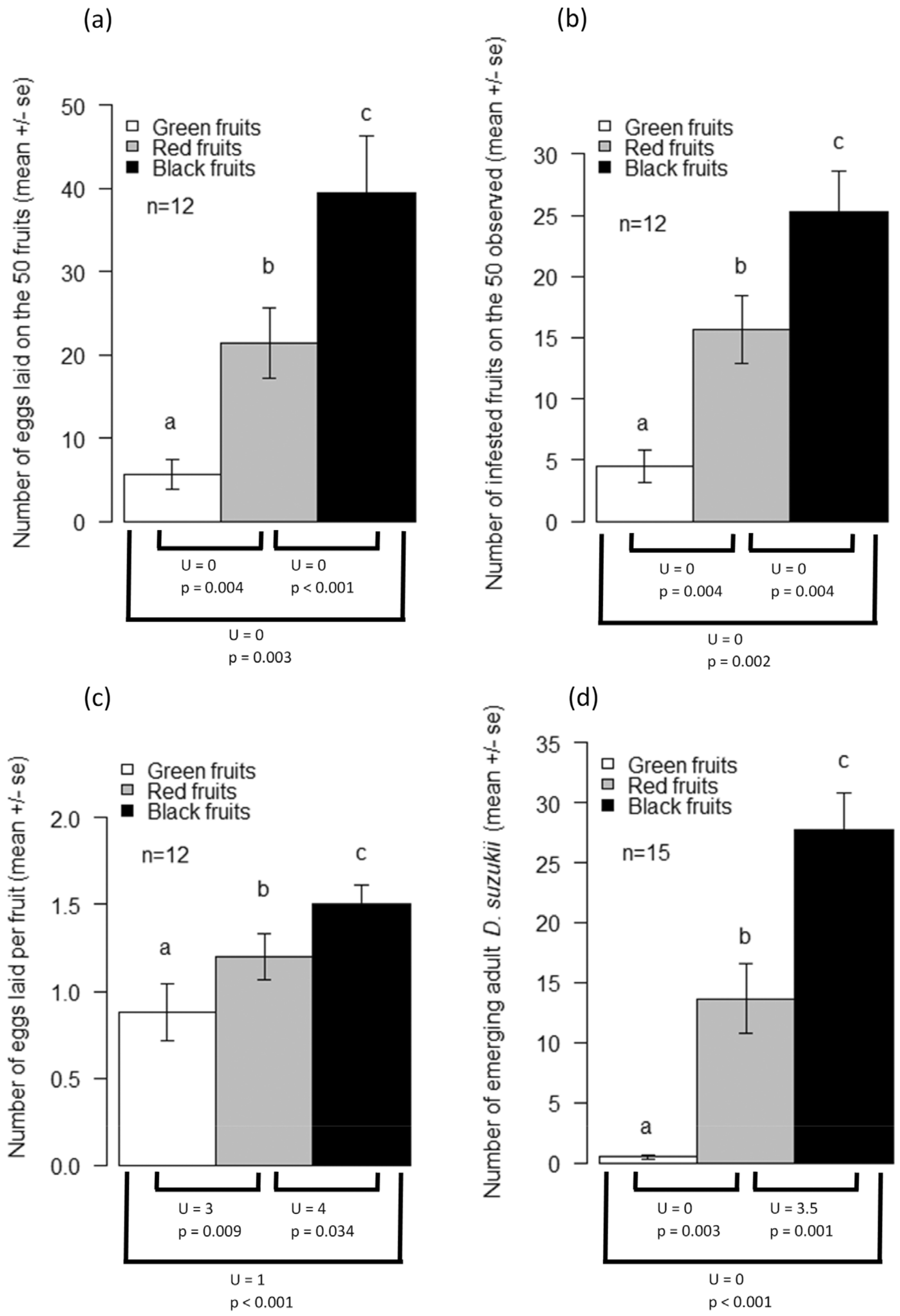

**FIGURE 3** Comparison of (a) mean number of eggs, (b) proportion of infested fruits, (c) mean number of eggs per fruits and (d) egg-to-adult viability between the three different stages of fruit maturity (i.e. green, red and black). For each fruit colour category, 12 sets of 50 fruits from different shrubs were observed under a stereomicroscope and the eggs were counted. (a) Mean number of eggs found on the 50 observed fruits (Kruskal-Wallis test: $\chi^2 = 18.99$, $p < 0.001$). (b) Mean number of infested fruits (i.e. fruits with at least 1 egg laid on them) on the 50 observed fruits ($\chi^2 = 19.35$, $p < 0.001$). (c) Mean number of eggs laid per infested fruit ($\chi^2 = 9.46$, $p = 0.009$). (d) Number of emerging *D. suzukii* adults on sets of 50 unmanipulated fruits. $N = 15$ sets of 50 fruits for each colour category from different elderberry shrubs ($\chi^2 = 28.32$, $p < 0.001$). Significant differences are displayed by different letters (post-hoc Mann–Whitney tests between colour categories)

increased with the presence of forest in a 100 m radius around the sampling site and with the number of fruits per corymb (only black ones within each region, total number of fruits across regions, Table 2b). Forest cover was also negatively correlated with the cover of buildings ($r = -0.402$, $p < 0.001$), but the latter variable was not retained in models. The infestation frequency of corymbs (Finfest, region scale, Table 2c) was increased with the number of fruits, but decreased with the presence of cultivated fruits around the sampling site and the road cover in a 1000 m radius. Infestation variables were not correlated with the proportion of dry/overripe fruits. Within each region, Spearman correlations between environmental variables and both the rate of fruit infestation per corymb (INFEST) and the number

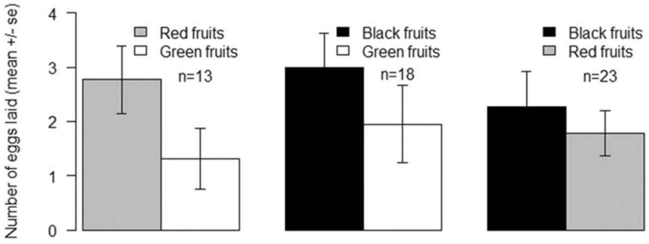

**FIGURE 4** Comparison of the oviposition preference of single *D. suzukii* females between pairs of fruits with different maturity ($n = 30$ replicates for each pair of fruits) in experimental choice tests in controlled laboratory conditions. Only tests where the female laid at least one egg were included in the analyses. None of the comparisons showed significant differences (Wilcoxon signed rank tests)

of fruits on the corymb (variable NFRUIT) are shown in Tables S2 and S3, respectively. These correlations showed that infestation rates and fruit production were locally associated with a wide set of environmental variables that were specific to each region. For example, altitude positively influenced fruit infestation rates per corymb in the mountain region of Clermont-Ferrand, naturally characterized by topographical contrasts (the summary of all associations between infestation rate and local environmental variables is given in Table S2).

## Laboratory experiments

We found a significant effect of colour/maturity of fruits collected in the field near Amiens on the total number of eggs laid ($\chi^2 = 18.99$, $p < 0.001$; Figure 3a), the number of infested fruits ($\chi^2 = 19.35$, $p < 0.001$; Figure 3b) and the number of eggs laid per infested fruit ($\chi^2 = 9.45$, $p = 0.009$; Figure 3c). The preference increasing order was always green, red and black. The preferences of *D. suzukii* for a fruit maturity/colour were however not significant in the laboratory choice tests, although a trend was observed toward more eggs being laid on black fruits than on red fruits, black than on green and red than on green (Figure 4).

We also found a significant effect of fruit colour/maturity on the number of *D. suzukii* adults emerging from fruits collected in the field, with the same order as for colour preference measured previously (i.e. green < red < black; $\chi^2 = 28.32$, $p < 0.001$; Figure 3d). Since there was a significant difference (Wilcoxon, $W = 547.5$, $p = 0.011$) between the mean number of adults emerging from the 50 fruits on which we counted the eggs (4.92 ± 1.18) and the 50 fruits that were left unhandled (13.95 ± 2.17), we assumed that the manipulation of fruits impacted greatly the egg-to-adult survival rate. Knowing both the mean infestation rate found in the wild (Figure 3a) and the mean number of flies that emerged (Figure 3d), an estimated egg-to-adult survival rate could be calculated for each maturity stage. The egg-to-adult development success (number of adults × 100/number of eggs) was estimated at 8.24%, 63.78% and 70.2% in green, red and black fruits, respectively.

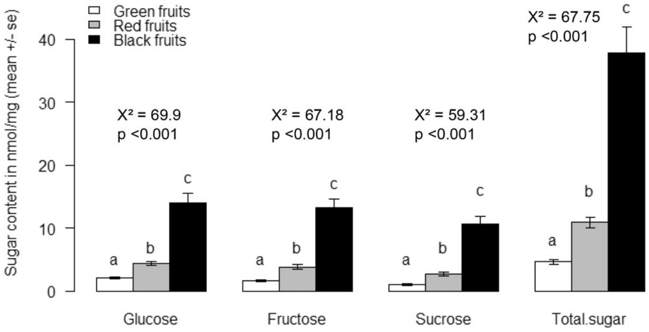

**FIGURE 5** Comparison of sugar content across fruits with different maturity stages (assessed based on fruit colour). Contents (nmol/mg) in three sugar molecules were expressed in dry matter. Total sugar represents the sum of the three different types of sugar. $N = 30$ measurements for each maturity stage. Significant differences are displayed by different letters (Mann–Whitney tests)

Chemical analyses of sugar in *S. nigra* fruit revealed that for each type of sugar tested (glucose, fructose and sucrose), differences between the maturity stages were significant and sugar contents followed the order green<red<black (Figure 5). This indicated that sugar content increased during fruit maturation, with a total concentration 8.10 and 3.47 folds higher in black fruits than in green and red fruits, respectively.

## DISCUSSION

Our study showed that three main categories of environmental factors systematically influenced fruit infestation: (i) latitude and associated climatic factors, (ii) landscape composition and (iii) local environmental factors. We also demonstrated that a plant generally considered as a "good host" for *D. suzukii* such as *S. nigra* shows a high variability of fruit infestation rates both across and within regions. Fruit infestation rates varied greatly among geographic regions (min = Nîmes 0.83%, max = Boulogne-Sur-Mer 23.5%), which translated into a significant inter-regional effect of environmental factors (climatic gradient). Fruit infestation rates also varied among sampling sites within each region (e.g., from 0.37% to 46.44% in the region of Amiens) due to an intra-regional heterogeneity of the environment (e.g., contrasting landscapes).

### Latitude and associated climatic factors

We found that latitude, which is negatively and positively related to temperature and cumulative rainfall respectively, was a major variable that positively correlated with infestation rates. This geographical/climatic gradient affects the host plant, the pest insect and their interaction strength.

Like many other plant species characterized by a wide ecological niche and distributed along a large latitudinal gradient, *S. nigra* was expected to show phenotypic variations in both vegetative and reproductive traits along climatic clines (Dong et al., 2020; Zhang et al., 2019). Indeed, we found that leaf length, corymb diameter and area varied with latitude but none of these variables were related to infestation rates over the whole study including 215 sites. We did not find any correlation between latitude and total fruit number per corymb or fruit diameter. Other local factors such as competition for light with neighbouring shrubs, soil characteristics, shrub management history and age, local genetic diversity or the abundance of local pollinators are likely to modulate plant performances (e.g., growth, nutritional quality, etc.), thereby explaining the observed phenotypic variations (Llorens et al., 2018; Patten & Wang, 1994).

The total number of corymbs and total volume of fruits produced per shrub were also negatively correlated with temperature and positively with rainfall showing that the temperate climate conditions of northern France may be more favourable to *S. nigra* reproduction output. The number of *D. suzukii* emerging per corymb increased with this overall volume of fruits hanging on the whole shrub. These results confirm our hypothesis that the northern temperate climate, more suitable to *S. nigra*, promotes the overall production of fruits, which has a positive cascading effect on infestation rates. Nevertheless, this hypothesis is only partially validated as most of the other elderberry traits did not respond to latitude. Olfactory or visual cues such as the size of the fruit resource are known to be used by other pests such as Tephritidae fruits flies to forage for food (Prokopy et al., 1973; Prokopy & Roitberg, 1984). We thus can hypothesize that shrubs bearing larger amounts of fruits in temperate regions could be more easily detected by the flies when moving across the landscape, and consequently more attractive.

The rate of infestation of *S. nigra* was strongly correlated with latitude (SUZUt and INFEST variables). Studies on other model species, particularly agricultural pests (Yadav et al., 2018), have shown positive relationships between insect abundance and latitude. This could be the case here as the rate of infestation is likely to increase with *D. suzukii* abundance. Moreover, the proportion of dipteran species among flower-visiting insects was shown to increase with the latitude, at least in Europe (Elberling & Olesen, 1999). However, the impact of latitude on insect distribution is complex and cannot be reduced to a pure geographical (i.e. spatial) effect. Many other factors such as macroclimatic ones are probably involved in this latitude-insect infestation success relationship. For example, in northern Europe during cold years, abundance of birch feeding leafminers significantly decreased with latitude, while during warm years their abundance increased with latitude (Kozlov et al., 2013). In the meantime, other data suggest that insects living at lower latitude (i.e. tropics) are less tolerant to climate warming than insects living at higher latitude (Deutsch et al., 2008), although this relationship may be modulated by microclimatic patterns in herbivores (Pincebourde & Casas, 2019). *D. suzukii*, living mostly in a temperate climate, has developed specific adaptations to survive cold winters (Enriquez & Colinet, 2017). *Drosophila suzukii* is supposed to overwinter as dormant adults, mainly females. This 'winter phenotype' is characterized by darker coloration, increased cold tolerance and a reversible arrest of reproduction (i.e. reproductive dormancy) (Enriquez & Colinet, 2019a; Enriquez & Colinet, 2019b; Panel et al., 2018; Shearer et al., 2016). Thanks to these cold adaptations, *D. suzukii* could be more adapted to climatic conditions in the north of France (wet and mild winter and summer) compared to those found in the south of France (dry winter, very hot summer). The hot summers of Mediterranean climate could explain lower infestation rates of *S. nigra* at low latitude during summer, as *D. suzukii* is known to be sensitive to heat. Temperatures above 30°C, often reached during Mediterranean summers, are very detrimental to its development and survival (Kimura, 2004; Kinjo et al., 2014; Tochen et al., 2014). The dry environment may also negatively affect *D. suzukii* populations, as this species shows a better development and reproduction at high humidity levels (Guédot et al., 2018; Hamby et al., 2016; Tochen et al., 2016). In agreement with this, a low relative humidity seems to reduce its resistance to heat (Enriquez & Colinet, 2017). Moreover, in the dry climatic conditions of southern France, it is possible that water-deprived parasitic wasps kill more pupae of *D. suzukii* as shown in a recent study (Bezerra Da Silva et al., 2019) and thus accentuate the negative relationship between *D. suzukii* population abundances and latitude.

In view of these characteristics of the biology of *S. nigra* and *D. suzukii*, the decrease of fruit infestation at lower latitudes may be the result of a mismatch between the phenologies of the fly and elderberry fruiting in the South of France. *D. suzukii* displays two main peaks of activity in southern regions, one in spring and one in the end of summer and fall (Haviland et al., 2016 in California, USA; Weydert et al., 2016, in southern France). By contrast, the elderberry fruiting occurs at early to mid-summer in the South of France and therefore in between the two peaks of activity of the fly at low latitude. On the other hand, in northern regions of France, *D. suzukii* shows a single peak of activity from the end of summer to fall when elderberry, and other fleshy-fruited plants, produces fruits (Poyet et al., 2015). This delayed phenology and late-season build-up of *D. suzukii* populations also found in colder locations were already shown by Gutierrez et al. (2016) in their analysis of trapping records by Dalton et al. (2011) in the United States.

The chemical composition of plants plays an important role in modulating herbivory. For example, phosphorus is a nutrient present in plants that play an important role in the reproduction of female Drosophila (Markow & O'Grady, 2008) and its content seems to be an important cue in *D. suzukii* oviposition preferences (Olazcuaga et al., 2019). This primary compound is present in leaves, fruits and seeds of *Sambucus* species (Pandia et al., 2018; Short & Epps, 1976). Interestingly, the concentration of phosphorus in plants is positively correlated with latitude (Garibaldi et al., 2011; Han et al., 2005; Moreira et al., 2018). Higher phosphorus content in elderberry fruits at high latitudes could hence play a role in the infestation rates observed in our study. Further chemical analyses should be carried out to understand better the role of phosphorus, and other components, in this host plant-insect relationship.

## Landscape composition

At the landscape scale, infestation rates increased with the presence of forest habitats in the vicinity of the sampling site, confirming our hypothesis that land covers such as forests are a major source of *D. suzukii* for adjacent areas. This result is concordant with previous studies showing that the abundance of *D. suzukii* in crops increases with the cover of forest in the surrounding landscape (Champagne-Cauchon et al., 2020; Haro-Barchin et al., 2018; Santoiemma et al., 2018; Tait et al., 2020). Moreover, *D. suzukii* abundance is known to increase from the forest edge toward the forest interior (Poyet et al., 2014), indicating the close association between this fly species and wooded habitats. The affinity of *D. suzukii* for forest habitats is also reported in its native range (Mitsui & Kimura, 2010). Forest patches act as refuge areas for *D. suzukii* for two reasons. First, forest ecosystems provide a multitude of shelters including branches, leaves and litter (Briem et al., 2018) and is characterized by a buffered microclimate protecting the pest from extreme temperatures (Wallingford et al., 2018). Second, forest environments offer varied food resources for both the adults and the larvae such as fleshy-fruited species and mushrooms (Kenis et al., 2016; Poyet et al., 2015; Stockton et al., 2019a). In our study, this positive effect of wood cover was mainly observed in a radius inferior or equal to 500 m (i.e. in a 500 m or a 100 m radius and in the immediate vicinity). A previous study showed that *D. suzukii* has a relatively low dispersal capacity, with a daily flight distance below 100 m (Vacas et al., 2019), which could explain this positive forest effect only at small distance ranges.

### Local trophic resources

*D. suzukii* infestation rates were positively associated with the number of fruits per corymb in the field (Table 2). This could be caused by bigger populations where *S. nigra* bear higher numbers of fruits. *D. suzukii* could also be able to estimate the local resource quantity on the shrub and target the optimal infructescence to oviposit. In agreement with this, *D. suzukii* is more attracted by large shapes (Poyet et al., 2015; Rice et al., 2016) and large groups of fruits probably emit high quantities of volatile chemicals attractive to the fly (Urbaneja-Bernat et al., 2021). The quantity and quality of local resources however depend on other fleshy-fruited species present around the sampling site. *D. suzukii* is a highly polyphagous species (Kenis et al., 2016; Poyet et al., 2015) and, as such, can use many other plant species as food. The negative effect of the presence of cultivated fruits in the surroundings of the sampling site on *S. nigra* infestation suggests a competition between *S. nigra* and other attractive food sources in *D. suzukii* oviposition choices. With more resources available, the proportion of eggs laid by female *D. suzukii* in the elderberry might be hence lower. Insecticides used in cultivated areas could also have a negative impact on *D. suzukii* living nearby.

Our laboratory experiments suggest that ripe (black) fruits are subjected to higher infestations in the wild and allow a higher egg-to-adult survival rate than unripe fruits on cut corymbs in laboratory conditions. Even if the oviposition preference was not clearly demonstrated in controlled conditions, likely due to a small number of repetitions, observation on wild fruits showed a consistent trend of infestation following the maturity of the fruit in the order green<red<black. Red and black are the two most visually attractive colours for *D. suzukii* (Rice et al., 2016), which could explain the higher number of eggs found on fruits of these colours. As shown in our chemical analyses, these fruits also have higher sugar contents, which are essential cues in the fly's oviposition preferences (Biolchini et al., 2017; Travaillard, 2020). Thus, both skin colour and sugar content could act in synergy in fruit attractiveness to the fly. Other chemical compounds that were not measured in this study could also interfere in fruit attractiveness. For instance, *S. nigra* fruits are known to be rich in anthocyanins (Veberic et al., 2009), pigments that are usually red but can appear purple, blue or even black depending on various chemical factors (Lev-Yadun & Gould, 2009). In many species, anthocyanin content is positively correlated with latitude (Åkerström et al., 2010; Jaakola & Hohtola, 2010; Lätti et al., 2008). Altitude, which has an effect similar to latitude, seems to be positively correlated to the anthocyanin content in *S. nigra* fruits (Senica et al., 2017). Anthocyanins being a source of antioxidants, their consumption has been proven beneficial for *Drosophila melanogaster* (Valenza et al., 2018; Wang et al., 2016). A higher number of reddish-black fruits as well as higher contents of anthocyanins could therefore mean resources of better quality for *D. suzukii* and explain the higher infestation of elderberry at high latitudes. Although it is likely that other factors than the sole fruit maturity play a role in *D. suzukii*'s preferences, black fruits were more infested than red ones in the wild even if *D. suzukii* is generally considered to prefer ripening fruits to fully ripe ones (Poyet et al., 2014). However, this could be explained, at least partly, by a delay between the egg-laying and the sampling, leaving time for the fruit to mature from red to black.

## CONCLUSION AND PERSPECTIVES

Our study shows the importance of taking multiple scales and multiple factors into consideration when studying the interaction between *D. suzukii* and its host plants. One host plant species can display highly contrasted mean rates of infestation depending on its geographical location. This means that studying a host plant infestation at the local scale involves considering the fact that observed infestation rates do not only reflect inner preferences of the fly, but are the result of complex interactions between the pest, the host plant, and multifactorial environmental variables acting at different scales. A better understanding about how these variables shape the suitability of a wild host plant species as a reservoir for *D. suzukii* is crucial in predicting the movements of the pest populations and crop infestation risks and could have application in population management. For instance, if host plants show different importance as reservoir hosts depending on the geographical location, a plant of little concern in the South might become crucial to take into consideration in management strategies in the north. Moreover, in a context of global climate change, knowing the impact of environmental, and particularly macroclimatic, variables on the plant-insect relationships is a key information to parameterize pest distribution models (Skendžić et al., 2021) and to predict changes in the pest invasion process. The present study predicts that global warming, by increasing the phenological mismatch between the fly and its host plant, should reduce its infestation, especially in southern Europe, but the risks of *S. nigra* infestation should be displaced toward northern Europe, generating a new ecosystem dis-service to agriculture in higher latitudes.

## ACKNOWLEDGMENTS

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## CONFLICT OF INTEREST

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

**Table S1.** Supporting Information.

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