



# Phenology, population trends and natural enemy complex of *Illinoia liriodendri* in Spain

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**Abstract** *Illinoia liriodendri* (Monell) (Hemiptera: Aphididae) is an Eastern North American native aphid species that infests ornamental tulip trees, *Liriodendron tulipifera* L. (Magnoliales: Magnoliaceae), in many localities of Spain and southern Europe. This is a comprehensive three-year study on the biology and ecology of the aphid, where its life cycle, phenology, population dynamic trends, comfort damages, natural enemy complex and its potential to control

aphid populations have been investigated for the first time in Europe. The monoecic-holocyclic annual cycle of *I. liriodendri* has been demonstrated. The highest infestation levels were recorded in May and June, but infestation severity varied among localities. No clear trend regarding the effect of planting site (pit vs. ground) on aphid abundance was observed. A strong positive relationship between the aphid infestation severity and the honeydew dripping was recorded. There was a wide complex of natural enemies associated with the aphid. Coccinellidae were the most abundant predators (<95%) and showed a positive numerical response to the aphid infestation. Several parasitoid species (mainly Hymenoptera: Aphidiinae and Hymenoptera: Aphelinidae) were found parasitizing *I. liriodendri* in Spain. The role of natural enemies as agents for controlling the aphid populations is discussed.

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## Introduction

More than half of the global population currently reside in urban areas, a proportion that is expected to increase over the following years (UN-Habitat, 2022). In these areas, green spaces (e.g., parks, gardens, roadside trees) are essential components help to

maintain the urban quality of life (Kabisch & Haase, 2013) by providing ecological, economic, social, recreational and health benefits (Barrico et al., 2018; van den Berg et al., 2015). However, urban green areas are also considered as footholds for the expansion of alien pest species (Kawakami et al., 2016). Ornamental plants are usually selected mainly on the basis of aesthetics, uses, climatic adaptability, space availability, growth characteristics and maintenance, (Conway & Vander Vecht, 2015; Ghafari et al., 2020), but little importance is given to the plant species origin and their associated pests in their native range (Conway & Vander Vecht, 2015). In addition, environmentally stressed plants in these anthropic ecosystems (e.g., pollution, water supply irregularities, disturbed soil nutrient cycles), are prone to severe pest infestations (Bell et al., 1993; Sloggett, 2017) which may easily spread due to the common use of a single plant species in large green areas (Gilbert et al., 2003; Stemmel et al., 2020).

The tulip tree, *Liriodendron tulipifera* L. (Magnoliales: Magnoliaceae), is an ornamental species native to Eastern North America. It is adapted to deep, rich, well drained soils with plenty of moisture during its seasonal growth, whereas drought and air pollution stress trees in poorly drained soils covered with pavement (Dreistadt & Dahlsten, 1986). This tree species has been used in many urban green areas all over the world due to its attractive aesthetics and benefits as a shade tree. *Liriodendron tulipifera* is commonly attacked by *Illinoia liriodendri* (Monell) (Hemiptera: Aphididae). The aphid is also native to North America, where it is monoecious holocyclic on its host tree (Blackman, 2023). *Illinoia liriodendri* rapidly invaded California and numerous other western states of the U.S.A. (Dreistadt & Dahlsten, 1986; Van Driesche et al., 1996), and usually occurs wherever tulip trees are grown (Dreistadt & Dahlsten, 1988). *Illinoia liriodendri* has recently been recorded in Asia (Kim et al., 2011) and several European countries, i.e., France, Germany, Luxembourg, Italy, Greece, United Kingdom, Serbia, Slovakia, Hungary, Croatia, Poland, Italy, Portugal and Spain (Bella, 2014; Blackman, 2023; Bozsik, 2012; Pons et al., 2018).

In recent years, *L. tulipifera* was introduced into urban areas in several regions of Spain, especially in Catalonia (Northeast of Spain). Following the introduction of *L. tulipifera*, *I. liriodendri* was recorded for the first time in Spain in 2010, when it was found

on tulip trees in the city of Lleida. Later, this alien species was recorded in many other localities of Spain. The aphid occurrence was also documented in Bragança (Portugal) in summer 2023 by F. Madeira (Fig. 1).

Trees attacked by *I. liriodendri* may show mildly distorted buds, leaf discoloration and premature defoliation (Jucker et al., 2008; Kollár & Barta, 2016). However, the main problem associated with this invasive species is the profuse honeydew excretion, which becomes a nuisance to citizens due to dripping on pavements and parked cars (Bozsik, 2012; Dreistadt & Dahlsten, 1988). In severe infestations, black sooty mold associated with honeydew can also compromise trees' health by limiting their photosynthetic capability (Bozsik, 2012).

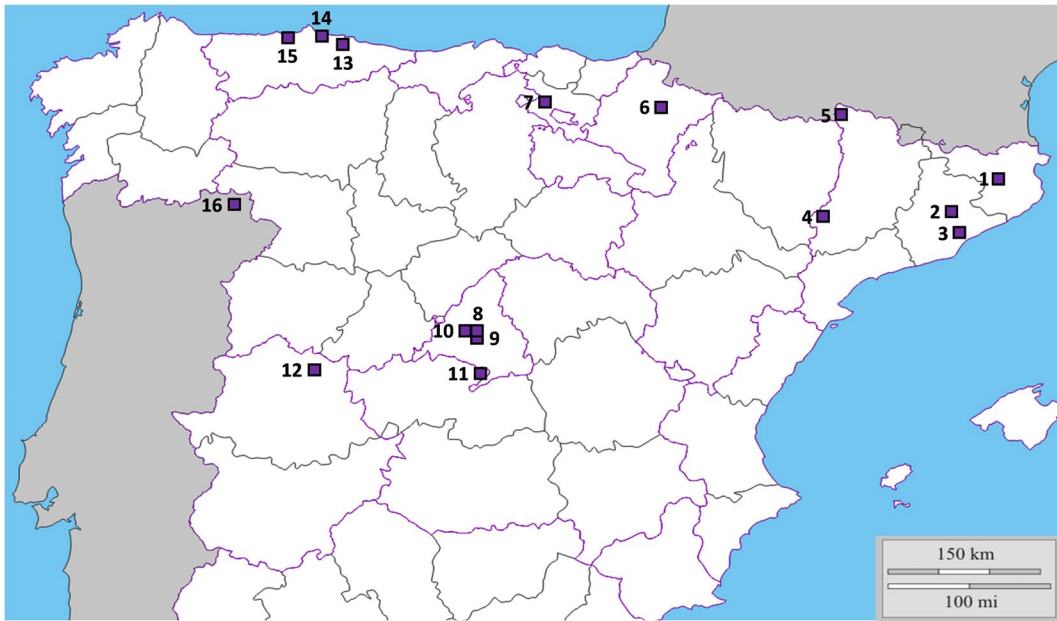
Although *I. liriodendri* has been established in Europe for several years, the European scientific literature on this alien species is very scarce, and the few existing reports focus mainly on the aphid morphology. To contribute to a comprehensive knowledge of *I. liriodendri*'s biology, ecology, damage and propose potential control strategies in Europe, we developed a three-year study in three different localities of Catalonia, where tulip trees are the most affected by this pest. The aims of the present study were:

- i) To determine the phenology and the population development trends of *I. liriodendri* in Spain.
- ii) To compare the infestation severity between ground and pit planting sites. In Spain, tulip trees are planted on street alignments by using both planting sites. Here, we assume that pit planting stresses the growing conditions and enhance the aphid infestation.
- iii) To quantify and correlate the honeydew dripping with the aphid abundance.
- iv) To define the *I. liriodendri* natural enemy complex and evaluate their biocontrol capacity.

## Materials and methods

### Location

This study was conducted in the urban area of three different localities of Catalonia (Spain): Vic (41°55'49"N 2°15'16"E), Barcelona (41°22'57"N 2°10'37"E) and Lleida (41°37'00"N 0°38'00"E). Vic



**Fig. 1** Localities where *Illinoia liriodendri* has been recorded in the Iberian Peninsula. (1) Girona, (2) Vic, (3) Barcelona, (4) Lleida, (5) Viella, (6) Pamplona, (7) Vitoria, (8) El Pardo, (9)

Madrid, (10) Majadahonda, 11. Aranjuez, 12. Yuste, 13. Vilaviciosa, 14. Gijón, 15. Muros de Nalón, 16. Bragança (Portugal)

is an inland locality of central Catalonia of about 50,000 inhabitants sited in a plain mainly surrounded by arable crops. Mean temperature and rainfall from May to July are around 19 °C and 100 mm, respectively (<https://es.weatherspark.com>). Barcelona is a large city of > 1.5 million inhabitants in the east of Catalonia, surrounded by other urban areas and bordered by the Mediterranean Sea. The average temperature and rainfall from May to July are around 21 °C and 85 mm, respectively (<https://es.weatherspark.com>). Lleida is also an inland city of about 150,000 inhabitants in the west of Catalonia, surrounded by small industrial areas and agricultural lands. The average temperature and rainfall from May to July are approximately 22 °C and 65 mm, respectively (<https://es.weatherspark.com>).

Determination of the phenology and population dynamics of *I. liriodendri* and effect of the planting site

In Vic, two different locations were sampled: four streets adjacent to a public outdoors car park and bordered with a total of 70 tulip trees planted in pits, and a boulevard bordered with 80 tulip trees planted

directly on the ground. Trees were between 6 and 8 m height. Forty-two trees in each location were randomly selected and visually inspected for 30 s at two different canopy heights. The low part was observed from the ground level whereas for the medium part, a ladder was used, with the observer at 2.5 m above the ground level. Observers for lower and medium canopy heights changed regularly to avoid recording bias. Due to the height of the trees, the upper canopy was unreachable and therefore excluded from sampling (Hajek & Dahlsten, 1988). The aphid density at each of the canopy heights was estimated using a categorical scale going from 0 (absence of aphids) to 5 (very high aphid density) (Table 1). The scale was a modification of those reported for other aphid species in urban green areas (Lumbierres et al., 2004; Madeira et al., 2022; Pons & Lumbierres, 2009). In Barcelona, observations were conducted at three different locations: a small interior park surrounded by buildings where 15 tulip trees were directly planted on the ground (all were observed) and two streets bordered with a total of 70 and 30 tulip trees planted in pits, where 40 and 15 trees were respectively observed. Trees in Barcelona ranged from 3 to 5 m height. In Lleida, observations were performed in a garden with 40 tulip trees (20 planted on pits and 20

**Table 1** Scale of aphid infestation severity on tulip trees

| Class | Infestation | Characteristics  |
|-------|-------------|--|
| 0     | Null        | Absence of aphids  |
| 1     | Presence    | Isolated individuals or small colonies on some leaves of the sampling unit                               |
| 2     | Low         | Small colonies on few leaves (<25%)  |
| 3     | Medium      | Small or medium colonies on some leaves of the sampling unit (25–50%) and presence of honeydew           |
| 4     | High        | Medium or big colonies on some or many leaves of the sampling unit (50–75%) and abundant honeydew        |
| 5     | Very high   | Big colonies occupying nearly all leaves of the sampling unit (>75%) and very high abundance of honeydew |

directly on the ground) of about 4–6 m height. Fifteen trees on each planting site were observed. The sampling effort in Barcelona and Lleida was lower when compared to that in Vic. Due to the lower height of the trees, a single observation per tree was taken, and no distinctions between the lower and the upper parts were done. The rest of the sampling methodology was the same as the one used in Vic. Globally, regular sampling was conducted every 7 or 15 days, depending on the weather conditions, between April and September, during the time frame 2019–2021. In each locality, preliminary visual inspections were conducted early in the season to determine the appearance of the first individuals and, thus, the beginning of regular sampling. Sampling ended when very few or no aphids were observed.

In October, November and December, sampling was conducted with the sole objective of finding sexual morphs to gather more information about the annual reproductive cycle of *I. liriodendri*. If small aphid colonies or isolated individuals were found they were carefully collected and brought to the laboratory for inspection under the stereoscope. Males were easily distinguished from alate parthenogenetic females by the external genitalia. Oviparae were distinguished from parthenogenetic apterae females by the presence of the numerous sensoria on the hind tibiae (Davis, 1909). To ensure correct identification, specimens were also dissected to see whether they contained eggs or nymphs inside.

#### Quantification of honeydew dripping

Honeydew dripping sampling was performed in 2021, in one of the Vic's locations, concretely in the four streets adjacent to the outdoors car park. There, four tulip trees per street were randomly selected and two yellow water-sensitive spray cards (26×76 mm; Syngenta, Spain) per tree were placed under the tree canopy, close to the

tree pit margins. The surface of the yellow cards turns blue when they come into contact with aphid honeydew droplets. Cards were left for two hours and then carefully collected and stored individually in small paper envelopes. The envelopes were then brought to the laboratory, where the number of blue contacts in each card was recorded. Card sampling started once the aphid populations were fully developed and honeydew presence was evident (end of May) and continued until they started to collapse (mid-July). Four different samplings were carried out throughout this period.

#### Natural enemy complex of *I. Liriodendri*

Predators feeding on *I. liriodendri* were recorded and identified simultaneously with the aphid density samplings. However, some specimens of the different predator species were collected and brought to the laboratory for a more precise identification using specific keys. We used Eizaguirre (2015), Cardoso Raimundo and Gomes Alves (1986), and Nedved (2015) for ladybeetles (Coleoptera: Coccinellidae); Pericart (1972) and Wagner and Weber (1964) for heteropterans (Hemiptera: Anthocoridae and Miridae); Stubbs and Falk (2002) for hoverflies (Diptera: Syrphidae); and Monserrat (2016) for lacewings (Neuroptera: Chrysopidae). In the case of coccinellids, when newly hatched larvae or doubtful pupae were found, they were brought to the laboratory and reared until their identification at species level was possible.

For determining parasitoid species associated to *I. liriodendri*, aphid mummies observed during the sampling period were collected, transported to the laboratory, and reared individually in vials at 24–26 °C, RH 30–40%, until parasitoid emergence. In 2021, to estimate the parasitism rate, leaves infested with *I. liriodendri* were collected throughout the sampling period. They were brought to the laboratory and placed in

500 ml polyethylene cages (minimum 100 aphids per cage) covered by a mesh to facilitate aeration. They were reared under the afore-mentioned laboratory conditions. Fresh *L. tulipifera* leaves were provided every 2 days and parasitoid emergence was recorded over the following month. Emerged parasitoids were conserved in vials with ethanol 70%. Species identification was conducted by N.G. Kavallieratos. To evaluate the control capacity of natural enemies, numerical responses between the most abundant natural enemies and the aphid abundance were determined.

### Statistical analysis

A General Linear Mixed Model (GLMM) was fitted for the response variable (aphid infestation severity). The explanatory variables were the sample height (low vs. medium part of the tree), locality (Vic vs. Barcelona vs. Lleida), planting site (pit vs. ground) and month (May vs. June). The year was used as a random factor. Because the response variable was estimated as levels of infestation and this variable was categorical and ordinal, it was converted to a factor using the `as.factor()` function. The function `glmmTMB` (family = binomial) from the “glmmTMB” package (Mollie et al., 2017) was used to fit the models. Overall differences were checked using the likelihood-ratio Chi-square test with the `anova()` function from the “car” package (Fox & Weisberg, 2018). When significant differences were found, a Tukey test for the post-hoc analysis were performed using the `emmeans()` function from the “emmeans” package (Lenth et al., 2023). Firstly, a comparison was performed between the infestation severity records from the medium and lower parts of the tree canopies with data collected in Vic. The comparison of the infestation severity between localities and tree planting site (pits or ground) was performed considering only the highest aphid abundance months (May and June).

The relationship between the aphid infestation severity and the number of honeydew droplets recorded on yellow water sensitive cards was analyzed by a simple regression. The average number of impacts in the yellow water sensitive cards and the proportion of infestation severity classes equal or higher than 3 were used as variables. We used this threshold because no or very few honeydew was observed on the pavement under the trees with infestation severity classes below 3.

The numerical relationships between the most abundant natural enemy group and the aphid abundance, estimated as the absolute frequency of observations with aphid infestation severity class > 1, was determined by a correlation analysis (`cor()` function). The `Shapiro.test()` function was used to check for normality before and after transforming the data as  $\log(x + 1)$ . The data did not follow a normal distribution; therefore, the Spearman correlation test was used. This analysis was performed with data from Vic.

Statistical analyses were performed with R version 4.0.3 (R Core Team, 2018).

## Results

### Population trends and aphid phenology

The presence of *I. liriodendri* was recorded from March to December. After the initial infestation, the population increased quickly and peaked by the end of May or June, depending on the locality and year. Then, the degree of infestation decreased rapidly.

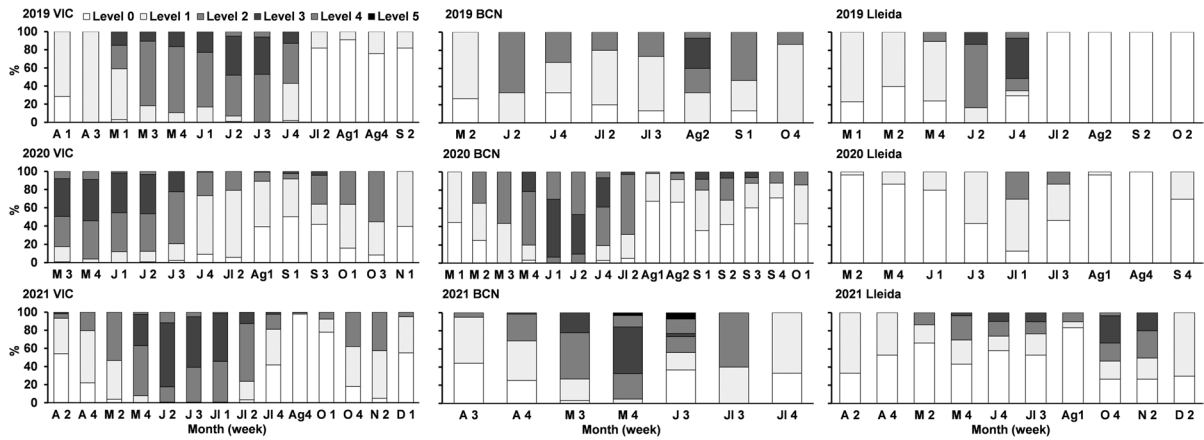
By the end of July some colonies remained on the leaves, but the degree of infestation was very low (Fig. 2). The population during the described period was compound by several generations of alate and apterae parthenogenetic females (exules).

In October, sexual morphs occurred (Fig. 3). Therefore, the generation of sexuparae should have been produced earlier, but we could not distinguish them from the alate exules. Males and oviparae females remained present until December, while overwintering eggs occurred since November.

### Vertical distribution of the aphids on trees and effect of locality and planting site

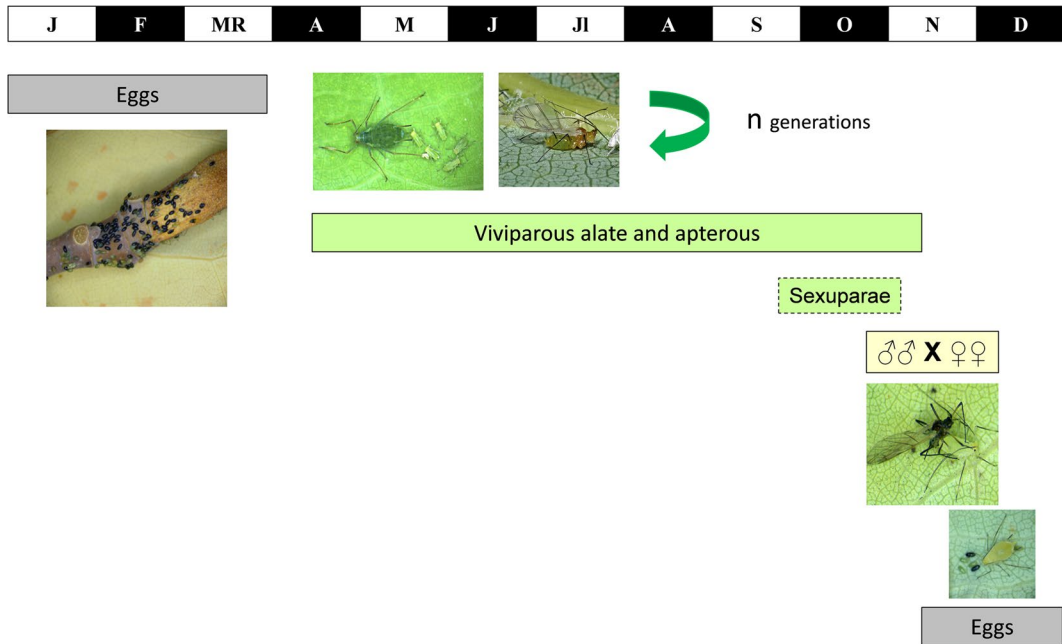
There were not significant differences between the infestation severity levels recorded at the two different canopy heights (lower and medium) ( $\chi^2=0.23$ ,  $df=1$ ,  $P=0.63$ ). Aphid infestation levels were then compared between localities (Vic, Barcelona, and Lleida) and tree planting site (pit vs. ground).

There were significant differences in the infestation severity of *I. liriodendri* among localities ( $\chi^2=332.32$ ,  $df=2$ ,  $P<0.001$ ) (Fig. 4). The highest infestation was recorded in Vic and the lower in



**Fig. 2** Relative frequency of each infestation severity class of *I. liriodendri* on tulip trees of Vic, Barcelona, and Lleida in the study period, 2019–2021. A, M, J, Jl, Ag, S, O, N, D indi-

cates the initials of the months from April to December and the number indicates the week

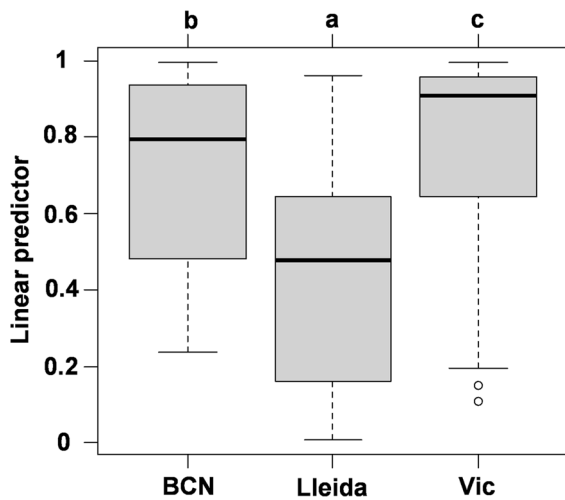


**Fig. 3** Phenology of *I. liriodendri* in Spain

Lleida, being Barcelona in an intermediate level. In Lleida, no aphid colonies were found after the end of June 2019 and only small colonies were found at the beginning of August of 2020. In the other two localities, aphid colonies were always recorded along the summer sampling period.

Although the planting site was globally non-significant ( $\chi^2=0.63$ ,  $df=1$ ,  $P=0.43$ ), this variable

interacted with the sampling month ( $\chi^2=4.89$ ,  $df=1$ ,  $P=0.03$ ) and the locality ( $\chi^2=48.90$ ,  $df=2$ ,  $P<0.001$ ). Moreover, there was a significant interaction between the sampling month and the locality ( $\chi^2=10.63$ ,  $df=2$ ,  $P=0.005$ , see Online Resource 1). Therefore, an analysis of the effect of the planting site and locality on the aphid infestation severity was performed by month.



**Fig. 4** Estimated marginal means of *I. liriodendri* infestation severity in the three studied localities: Barcelona, Lleida and Vic based on the Tukey post hoc test results

In May, there were significant differences among localities ( $\chi^2=150.13$ ,  $df=2$ ,  $P<0.001$ ) with the highest infestation levels being observed in Vic and the lowest in Lleida. The interaction locality\*planting site was also significant ( $\chi^2=45.00$ ,  $df=2$ ,  $P<0.001$ ), and trees planted in pits suffered highest infestation levels in Vic and Barcelona but not in Lleida (see Online Resource 1). In June, the tulip trees of the three different localities also bore significantly different levels of aphid infestation ( $\chi^2=182.96$ ,  $df=2$ ,  $P<0.001$ ), being Lleida the location with lower infestation levels. During this month, trees

planted in pits significantly differed from those planted on the ground ( $\chi^2=4.39$ ,  $df=1$ ,  $P=0.04$ ). However, the interaction locality\*planting site was also significant ( $\chi^2=12.99$ ,  $df=2$ ,  $P=0.002$ ). While trees planted in pits experienced heavier aphid infestations in Vic the opposite was observed in Barcelona and Lleida.

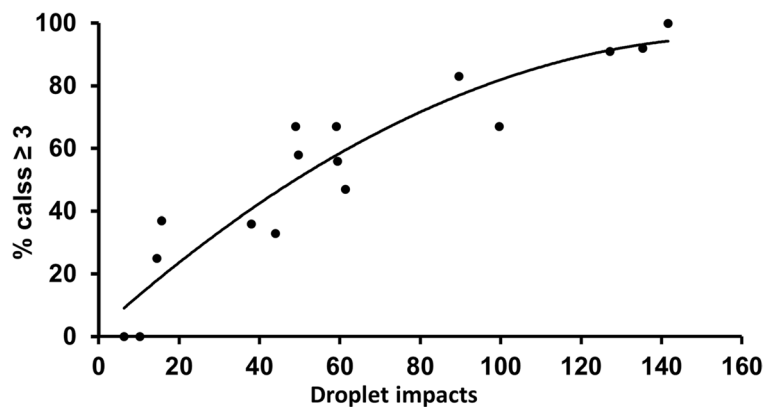
#### Honeydew dripping

There was a positive significant correlation ( $R^2=0.88$ ;  $F=47.40$ ;  $P<0.001$ ) between the proportion of aphid infestation severity classes equal or higher than 3 and the quantity of honeydew dripping (Fig. 5).

#### Natural enemy complex

A wide range of natural enemy species were associated with *I. liriodendri* (Table 2). Pirate bugs (Hemiptera: Anthocoridae), true bugs (Hemiptera: Miridae), hoverflies (Diptera: Syrphidae), lacewings (Neuroptera: Chrysopidae), lady beetles (Coleoptera: Coccinellidae) and spiders were the predatory groups. Species of Aphidiinae and Aphelinidae were also found parasitizing the tulip tree aphid.

Lady beetles were the most common group of predators, with 7013 individuals recorded, accounting for more than 90% of the total predator specimens. Eight species were recorded in Vic, 6 in Barcelona and only 4 in Lleida. *Coccinella septempunctata* L., was only recorded in Vic, occurring punctually in



**Fig. 5** Relationship ( $y = -0.0036x^2 + 1.1547x + 1.9581$ ) between the average number of droplets recorded in yellow water-sensitive cards for 2 hours, and the severity infestation classes equal or above class 3 of *I. liriodendri* on tulip tree

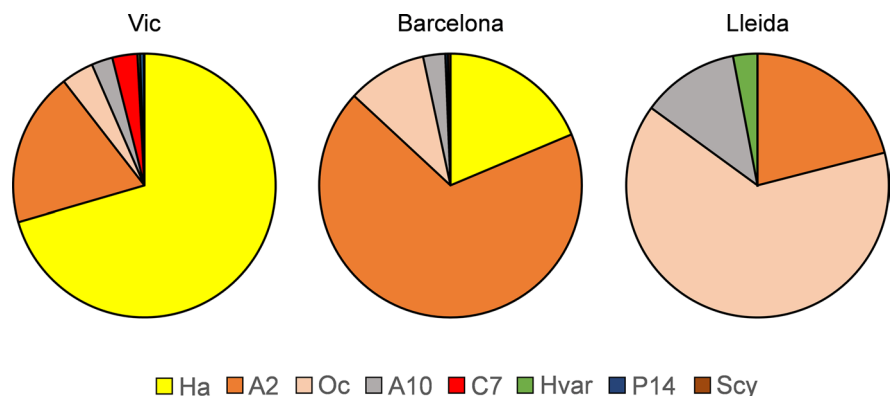
**Table 2** Predator and parasitoid species associated to *I. liriodendri*

| Predators |            |               |  |  |                         |   |
|-----------|------------|---------------|--|--|-------------------------|---|
| Class     | Order      | Family        | Species / Genus                                |  |                         |   |
| Insecta   | Hemiptera  | Anthocoridae  | <i>Anthocoris nemoralis</i> (F.)               |  |                         |   |
|           |            | Miridae       | <i>Daraeocoris</i> sp.<br>Unidentified species |  |                         |   |
|           |            | Diptera       | Syrphidae                                      | <i>Episyrphus balteatus</i> (De Geer)<br><i>Sphaerophoria</i> sp.  |                         |   |
|           | Neuroptera | Chrysopidae   | <i>Chrysoperla carnea</i> (group) (Stephens)   |  |                         |   |
|           | Coleoptera | Coccinellidae |  | <i>Adalia bipunctata</i> (L.)<br><i>Adalia decempunctata</i> (L.)<br><i>Coccinella septempunctata</i> L.<br><i>Harmonia axyridis</i> (Pallas)<br><i>Oenopia conglobata</i> (L.)<br><i>Propylea quatuordecimpunctata</i> (L.)<br><i>Scymnus</i> sp. |                         |   |
|           |            |               | Arachnida                                      | Araneae  | Unidentified            |   |
|           |            |               | Parasitoids                                    |  |                         |   |
|           |            |               | Insecta  | Hymenoptera  | Braconidae (Aphidiinae) | <i>Aphidius ervi</i> (Haliday)<br><i>Aphidius transcaspicus</i> Telenga<br><i>Diaretiella rapae</i> (M'Intosh)<br><i>Lysiphlebus testaceipes</i> (Cresson)<br><i>Ephedrus</i> sp.<br><i>Praon</i> sp.<br><i>Praon volucre</i> (Haliday) |
|           |            |               |  |  |                         | Aphelinidae   |

the second fortnight of June. The relative abundances of lady beetles varied with the locality. In Vic and Barcelona, *Harmonia axyridis* (Pallas) and *Adalia bipunctata* (L.) were, respectively, the prevalent species, accounting for the 71% and 68% of the total observed individuals (Fig. 6). In Lleida, the prevalent species was *Oenopia conglobata* (L.), whose relative abundance was, globally, nearly 65% of the total recorded individuals during the three-year study.

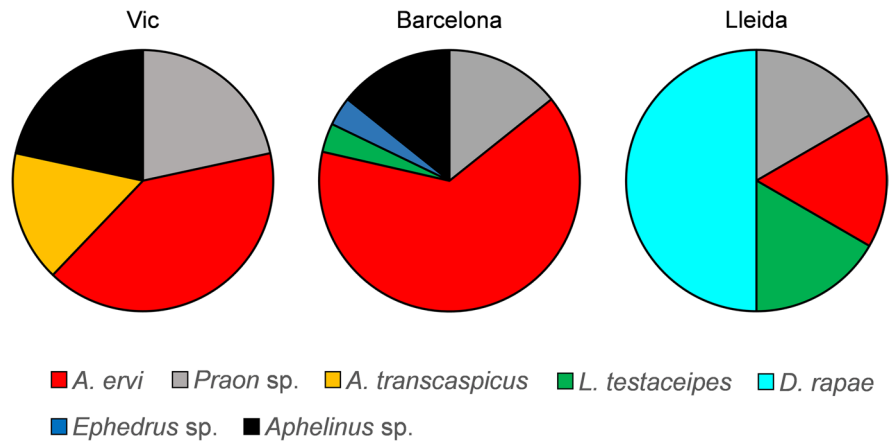
The occurrence of parasitized aphids was much lower than that of predators. Most of the parasitized aphids were recorded early in the season. From mummies collected and reared in the laboratory, 71 adults emerged. In Vic and Barcelona, the prevalent species was *Aphidius ervi* (Haliday), followed by the genus *Praon*, mainly *Praon volucre* (Haliday), and by some specimens of the genus *Aphelinus* (Fig. 7). In Lleida, few individuals emerged and half of them were *D.*

**Fig. 6** Relative abundance of lady beetles associated to *I. liriodendri* on tulip trees in Vic, Barcelona and Lleida. Ha – *Harmonia axyridis*, A2 – *Adalia bipunctata*, Oc – *Oenopia conglobata*, A10 – *Adalia decempunctata*, C7 – *Coccinella septempunctata*, Hvar – *Hippodamia variegata*, P14 – *Propylea quatuordecimpunctata*, Scy – *Scymnus* sp





**Fig. 7** Parasitoid complex of *I. liriodendri* and proportion of parasitized aphids by the different parasitoid species/genus

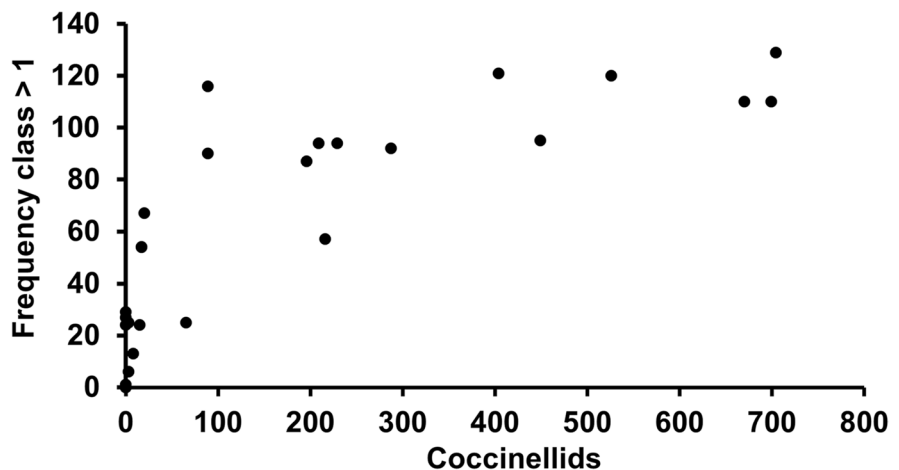


*rapae*. The overall parasitism rate was extremely low. From nearly 4000 aphids collected along the season, only 26 (0.65%) resulted in mummies, from which only 12 parasitoids emerged (0.30%). The rate of parasitism ranged from 0 to 3%, depending on the sampling date.

#### Effect of natural enemies on the *I. liriodendri* abundance

There was a strong correlation ( $\rho=0.89$ ;  $t=9.31$ ;  $P<0.0001$ ) between the abundance of ladybeetles, the most common group of natural enemies recorded, and the abundance of *I. liriodendri*, estimated as the absolute frequency of observations with an infestation severity class higher than 1 (Fig. 8).

**Fig. 8** Correlation between the number of coccinellids and the absolute frequency of observations with an aphid infestation severity class higher than 1 in samplings performed in Vic



## Discussion

### Phenology and life cycle

First records of *I. liriodendri* in Europe date from 1998 in France (Blackman, 2023). Since then, new records have been reported (Bozsik, 2012; Franjević et al., 2015; Kanturski et al., 2017; Kollár & Barta, 2016; Petrović-Obradović et al., 2018). However, studies on the ecology, damage estimation, and beneficial insects associated to this aphid, do not exist in Europe. Our work contributes to all these issues and proposes easy tools for sampling and estimating the abundance and damage of this invasive pest.

The occurrence of *I. liriodendri* in the studied region shows that it may form colonies on the underside of tulip tree leaves starting from April. Then, population peaks in May or June and decreases

during the hottest summer weeks. During this period, aphid populations are composed by apterous and alate virginoparous parthenogenetic females. This phenology is quite alike the one reported in California (Dreistadt & Dahlsten, 1988). In Serbia and Slovakia, the occurrence period of the aphid goes from June to September (Kollár & Barta, 2016; Petrović-Obradović et al., 2018), however no further details are reported. In October, sexual morphs (males and oviparae females) and eggs laid in the bark crevices or buds were recorded regularly in our samplings. This fact confirms that *I. liriodendri* is holocyclic in Spain, completing the typical life cycle on a single tree species, as in North America (Blackman, 2023), Korea, and Japan (Kim et al., 2011). However, Petrović-Obradović et al. (2018) reported that the aphid is anholocyclic in Serbia because no sexual morphs were found. Sexual morphs are mainly induced by short day length and low temperatures (Blackman, 1987; Dixon, 1988). Thus, taking into account the northern latitude and colder weather of Serbia when compared to the northeastern Spain, we believe that sexual morphs may also occur in Serbia, and *I. liriodendri* should be considered holocyclic in Southeastern Europe. Further sampling efforts are needed to confirm this hypothesis.

#### Vertical distribution, locality, and planting site

The distribution patterns of aphids in the tree canopy may vary not only with the aphid species, but also with the host plant and locality. Even within the same tree species, the aphid distribution may change with the leaf age and the season of the year (Dixon, 2005; Platková et al., 2020; Straw et al., 2006). Higher abundances of *Eucallipterus tiliae* (L.) and *Myzocallis walshii* (Monell) (Hemiptera: Aphididae) in the low than in the high canopy of lindens (Dahlsten et al., 1999) and red oaks (Pons & Lumbierres, 2010), respectively, have been reported. However, we did not find any significant differences in the *I. liriodendri* infestation severity between the lower and the middle part of the sampled tulip trees, and we assume that vertical stratification of this aphid does not depend on the canopy height during the spring and summer infestation. These results agree with other studies performed with several tree aphids leaving on maples, ashes, oaks, elms, lindens or birches (Hajek

& Dahlsten, 1988; Platková et al., 2020) or with adelgids on pines (Chilima & Leather, 2001).

There was a significant variation in the infestation levels between localities, probably due to different environmental conditions (e.g., temperature, relative humidity, tree nutrient availability, urban-rural gradient). In Lleida, there were extremely high temperatures at the end of June 2019 (maximum temperatures above 40 °C for one week ([www.meteocat.cat](http://www.meteocat.cat)), which caused the disappearance of the aphids. The milder temperatures of Vic and Barcelona during the same period probably led to an increase of the aphid populations life span in those areas. Raupp et al. (2010) claimed that free living aphids increase their abundance along an urbanization gradient. We could not confirm this issue in our study because the highest aphid abundance was recorded in Vic, with the lowest gradient of urbanization, followed by Barcelona, with the highest one. In Lleida, with an intermediate gradient of urbanization, the aphid abundance was the lowest. Dobrosavljević et al. (2023) reported no influence of rural gradient on gallicolous aphids in poplars and they attribute this to their capacity to manipulate the micro-environment of the leaf inside the galls.

Although no data about soil characteristics of the different localities were recorded, we expected trees planted in pits to live in more stressing conditions than those planted directly on the ground, thus, being more prone to suffer from aphid infestations. This partially occurred and varied with the month and locality. Therefore, the planting site may affect the aphid abundance but there is not a clear pattern, and it may vary among localities. As far as we know this is the first study addressing the influence of the tree planting site on aphid abundance.

#### Relationship between honeydew dripping and aphid abundance

The relationship between aphid abundance and honeydew dripping has been previously demonstrated by counting aphids and using water sensitive yellow cards in California (USA) (Dreistadt & Dahlsten, 1988). In the present study, instead of counting aphids, we characterized the aphid abundance with a categorical scale composed by several infestation classes. The good relationship between the number of aphids and its attributed infestation class was clearly demonstrated in Pons et al. (2006). In addition, using

this categorical sampling method, honeydew dripping was well correlated with aphid abundance (Pons et al., 2006; Pons & Lumbierres, 2009). However, the authors used the mean of the classes recorded to perform the analysis. In the present study we found a good correlation using only the absolute frequency of abundance classes which suppose honeydew dripping ( $\geq 3$ ). Averaging abundance classes, when they are represented as levels or categories without a consistent numerical relationship between them, may underestimate the number of cases where honeydew dripping was present, so we believe that using the abovementioned approach is more accurate to correlate data. In any case, the results confirm the utility of using this method in combination with the yellow water-sensitive cards to easily estimate the potential damage caused by *I. liriodendri* and to establish damage thresholds.

#### Natural enemy complex

Our results are the first extensive study on the occurrence of predator and parasitoids associated to the tulip tree aphid in Europe.

Regarding predators, 12 insect taxa and some unidentified spiders were recorded. The predator complex resembles to that associated with aphids in urban green areas of Catalonia and Spain (Lumbierres et al., 2005; Pons & Lumbierres, 2013). By far, coccinellids were the prevalent group. *Harmonia axyridis* was recorded attacking *I. liriodendri* colonies in central Europe (Bozsik, 2012) but no other ladybeetles were reported feeding on this aphid species. In Vic and Barcelona, areas where this exotic and invasive ladybird has expanded (Meseguer et al., 2022), it was also recorded feeding on *I. liriodendri*, along with other ladybird species. In Vic, *H. axyridis* was clearly the dominant ladybird throughout the study period and it may be displacing the local species (Meseguer et al., 2022). In Barcelona, the prevalent species was *A. bipunctata*. Regular releases of this species in Barcelona as a biological control method against aphids in green public spaces, may explain its dominance. In Lleida, located in an area still not invaded by *H. axyridis* and where regular releases of *A. bipunctata* for biocontrol purposes are quite recent, *O. conglobata* predominates (Lumbierres et al., 2005, 2021; Meseguer et al., 2022). In USA, *C. carnea* seems to be an efficient predator (Dreistadt & Dahlsten, 1988), but

its occurrence in Catalonia has been very low and we do not think it had any incidence on the aphid population dynamics.

Here, parasitoids associated with *I. liriodendri* belong to the complex usually found in urban areas of Spain (Pons et al., 2018). Although most of the genera recorded in this study were also reported from the USA (Zuparko & Dahlsten, 1993) there are differences at species level. The most common species in Catalonia was the cosmopolitan *A. ervi*, mainly parasitizing aphids of arable crops (Lumbierres et al., 2007; Pons et al., 2011; Pons & Starý, 2003) and urban areas (Pons et al., 2018). *Praon volucre*, the second most abundant aphidiine, exhibits Eastern/ Western Palaearctic, Oriental, and Neotropical distribution, parasitizing numerous aphid species on a wide spectrum of crop and non-crop plants (Kavallieratos et al., 2004, 2013, 2016; Rakhshani et al., 2019). The association of *L. testaceipes* with *I. liriodendri* is interesting. This parasitoid was originally introduced in Europe from Cuba during seventies for the control of citrus aphids (Starý et al., 1988). *Lysiphlebus testaceipes* has expanded along the Mediterranean coast and the Iberian Peninsula inland (Starý et al., 2004), becoming one of the most common species in crops and urban green areas (Lumbierres et al., 2005; Pons et al., 2018). It prefers to parasitize aphids of the Aphidina tribe rather than those of Macrosphina tribe (Pons et al., 2018; Rakhshani et al., 2019; Tomanović et al., 2018), such as *I. liriodendri*. It should be noted that *L. testaceipes* association with Macrosphina has been previously confirmed in Catalonia (Pons et al., 2018). The occurrence of *Areopraon silvestre* (Starý) was not recorded in our study even though it was found parasitizing *I. liriodendri* in Croatia (Franjević et al., 2015), indicating that different geographical areas of Europe favor different *I. liriodendri* parasitoids.

#### Effect of natural enemies

The positive correlation between coccinellids and the aphid infestation level, points out a type of numerical response that has been already found in some other studies dealing with aphids and coccinellids in crops of the same study region (Meseguer et al., 2021) and urban green areas (Rocha et al., 2018). However, this does not explain the decrease of the aphid population in summer. Although lady beetles can arrive soon to

the infested trees and may start exploiting aphid colonies early in the season, the aphid population rate of increase is much higher than that of the ladybeetles; thus, their capacity for decreasing aphid populations is not sufficient. Since coccinellids were, by far, the most abundant predators associated with the tulip tree aphid, it seems very improbable that the other predators play a significant role in modulating the aphid populations. Despite the occurrence of several parasitoid species, the parasitism rate was very low, suggesting an irrelevant role in controlling *I. liriodendri*. Similar results with parasitoids were reported by Zuparko and Dahlsten (1993) in USA. However, according to the enemy release hypothesis (Keane & Crawley, 2002; Roy et al., 2011), parasitism rates may increase in the future when the local parasitoid species become more adapted to this alien aphid. In this frame, if *A. ervi* remains the dominant aphidiine parasitizing *I. liriodendri* and given that it is commercially available (Muller et al., 2014), it could be considered as the principal species on a parasitoid based biocontrol program in the future. By the moment, natural enemies are insufficient to control by themselves the aphid, which remains a major pest so far. It seems that the decrease/collapse of the aphid populations, is rather due to the hot weather conditions, especially to the sustained maximum temperatures above 35 °C for several days.

## Conclusions

For the first time in Europe, the biology and ecology of the tulip tree aphid, *I. liriodendri*, has been studied in a comprehensive way. It has been demonstrated that the aphid is a monoecic and holocyclic species. High infestations occurred in May and June, with profuse honeydew dripping. The infestation severity was not dependent on the tree planting site (pits vs. ground). In this study, the sampling methods used to estimate the aphid abundance and honeydew dripping, allowed to well relate both variables; thus, this approach may be used as a tool for future determination of damage thresholds. Furthermore, a wide range of natural enemies associated with *I. liriodendri* occurred. Whereas predators were very common (specially Coccinellidae), parasitoids were scarce. Although a numerical response of coccinellids to the aphid abundance was recorded, it does not seem that

natural enemies are able, by the moment, to control aphid populations.

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**Data availability** The datasets analyzed during the current study are available from the corresponding author on reasonable request.

## Declarations

**Competing interests** The authors declare no competing interests.

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