Contents lists available at ScienceDirect

Biological Control

journal homepage: www.elsevier.com/locate/ybcon

Impact of woody semi-natural habitats on the abundance and diversity of green lacewings in olive orchards

Rafael Alcalá Herrera [a,b,*], Francisca Ruano [c]

[a] *Plant Protection Group, Department of Environmental Protection, Estación Experimental del Zaidín (EEZ-CSIC), C/ Profesor Albareda 1, 18008 Granada, Spain*
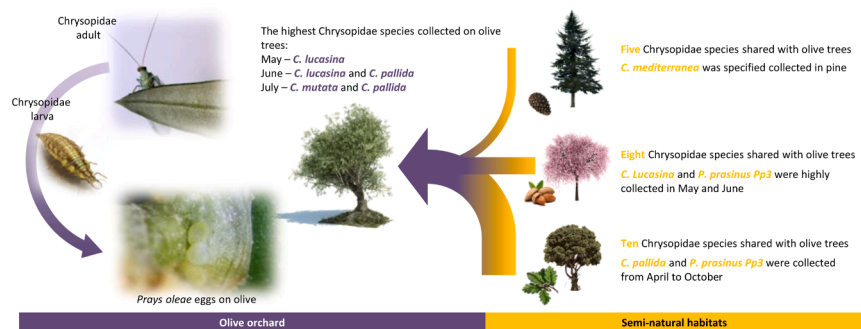[b] *Plant-Soil Relationships Group, Department of Environmental Protection, Estación Experimental del Zaidín (EEZ-CSIC), C/ Profesor Albareda 1, 18008 Granada, Spain*
[c] *Department of Zoology, University of Granada, Campus de Fuentenueva s/n, 18071 Granada, Spain*

HIGHLIGHTS

- Tree species, specifically oak and almond trees, in SNHs has a positive effect on Chrysopidae adults and larvae population in organic olive orchards.
- Oak trees had the highest species richness and diversity in Chrysopidae adults as compared to the other tree species studied.
- The dominant species *C. mutata, C. pallida, P. (prasinus) pp3, A. benedictae* and *P. (prasinus) pp2* were responsible for temporal changes among tree species with respect to the Chrysopidae community.
- The larger number of adult Chrysopidae from tree species in SNHs translated into a larger number of larvae in olive trees. This coincided in time with the anthophagous and carpophagous generations of the olive moth, *Prays oleae,* thus highlighting the potential role of tree species in SNHs in improving *P. oleae* control.
- The number of larvae in olive trees showed a positive correlation with the percentage of predated eggs in the anthophagous and carpophagous generations *of Prays oleae.*

GRAPHICAL ABSTRACT

ARTICLE INFO

ABSTRACT

Habitat management is a conservation biological control technique which helps to reduce the use of inputs in olive orchards and also to improve sustainability. Recent studies of olive orchards have pointed out that vegetation cover, which provides food resources, as well as reproduction and refuge sites, increases Chrysopidae populations and diversity. However, little is known about the effect of woody semi-natural habitats (SNHs) in

---

* Corresponding author.
  E-mail addresses: rafa.alcala@eez.csic.es (R. Alcalá Herrera), fruano@ugr.es (F. Ruano).

Prunus dulcis
Quercus rotundifolia

olive orchards. In this context, our study aims to determine the attraction of adult Chrysopidae to different tree species in SNHs adjacent to olive orchards in order to promote the conservation biological control of this key predator. We vacuumed 75 almond, oak, olive and pine trees fortnightly between April and October of 2016. The trees were chosen at random and evenly distributed among five organic olive orchards selected according to their availability. Oak trees recorded the highest abundance, species richness and diversity levels of adult Chrysopidae, while olive trees had the highest abundance of Chrysopidae larvae. A total of 20 green lacewing species, belonging to seven different genera, were collected, of which *Chrysoperla mutata* (McLachlan, 1898), *Chrysoperla pallida* Henry et al., 2002 and *Pseudomallada (prasinus) pp3* (Duelli and Henry, 2020) were the most abundant during the period of the study and had a preference for olive trees (*C. mutata* and *C. pallida*) and oak trees *P. (prasinus) pp3*. Furthermore, the number of Chrysopidae larvae collected showed a positive correlation with the percentage of predated eggs in the anthophagous and carpophagous generations of *Prays oleae*.

1. Introduction

The greatest challenge facing agriculture today is the need to reduce the use of inputs in order to enhance the sustainability of agroecosystems. From an ecological perspective, this would involve efficient input usage and organic pest management, while, at the same time, ensuring profitable crop yields without harming the environment (Reddy, 2017).

Conservation biological control is a sustainable approach to controlling pests, which could help to cut back the use of pesticides as part of an integrated pest management strategy (Begg et al., 2017), especially with respect to perennial crops (Rieux et al., 1999). Conservation biological control mainly aims to conserve natural enemy populations (Barbosa, 1998) in which semi-natural habitats (SNHs), defined as any habitat within or outside a cultivated crop area containing non-crop plant species (Holland et al., 2017), are an important tool. These habitats provide natural enemies with essential resources, such as pollen, nectar, honeydew, alternative hosts and prey, as well as with refuge and reproduction sites (Bianchi et al., 2013; Duelli and Obrist, 2003; Landis et al., 2000). As SNHs tend to diminish with the expansion and intensification of agricultural practices in olive orchards (Gúzman-Alvarez et al., 2009), it is important to determine their impact on natural enemies in order to conserve and promote their populations in olive orchards for biological control propose.

The European agricultural landscape has a wide variety of SNHs, whose functions and characteristics (vegetative composition, structure, shape and area) determine their ability to maintain natural enemies and to contribute to biological control (Holland et al., 2016). Thus, the incorporation of SNHs can clearly increase the populations and diversity of natural enemies (Albertini et al., 2017; Hatt et al., 2017; Holland and Fahrig, 2000; Pfister et al., 2017; Sorribas et al., 2016). Nevertheless, the relative potential of SNHs to control pests can vary drastically according to crop type, pest, predator, habitat management and landscape structure. All these factors need to be taken into account when designing measures to improve biological control services through habitat restoration and management (Tscharntke et al., 2016). It is therefore crucial to increase our knowledge of the diverse range of SNHs in order to maximise their effectiveness in integrated pest management programs (Holland et al., 2017, 2016; Tscharntke et al., 2012).

Green lacewings, which can be found in virtually all agricultural ecosystems, are efficient biological control agents among the natural enemy populations of agroecosystems (Duelli, 2001; McEwen and Senior, 1998; Monserrat, 2016; New, 1975; Nicoli Aldini, 2002). Their larval stage feeds on a wide variety of small, soft-bodied insects and mites, as well as lepidopteran eggs and small larvae (Ridgway and Murphy, 1984). The adult stage of most species, which depends on the vegetation to feed on nectar, pollen and honeydew, has a palynoglycophagous diet (Devetak and Klokocovnik, 2016; Villenave et al., 2006). Previous studies have reported that some plant species are specifically associated with Chrysopidae species, some of which have a preference for trees species while others prefer herbaceous species (Aspöck et al., 1980; Duelli et al., 2002; Monserrat and Marín, 2001, 1994; Nielsen, 1977; Sziraki, 1996; Villenave-Chasset and Denis, 2013).

In Mediterranean olive orchards, the predominant genera are *Chrysoperla* Steinmann, 1964 and *Pseudomallada* Tsukaguchi, 1995 (Szentkirályi, 2001a). *Chrysoperla carnea sensu lato* (Stephens, 1836), in particular, which is present in olive orchards all year round, plays a key role in the predation of the eggs and larvae of the olive moth, *Prays oleae* (Bernard, 1788), one of the principal olive pests (Campos, 1989; Ramos et al., 1984a; Szentkirályi, 2001a). Furthermore, due to its agricultural importance, *C. carnea s.l.* was declared insect of the year in 1999 (Dathe, 1999). While the precise characterization of certain sibling *C. carnea s.l.* species with respect to morphological characteristics, habitat, courtship songs and molecular techniques has provided a better understanding of their biology and ethology in the context of the conservation biological control (Cordero-Rivera and Galicia-Mendoza, 2017), their taxonomy has not been fully elucidated (Monserrat, 2016). Furthermore, recent studies have identified three new Chrysopidae species in the *Pseudomallada* complex (Duelli and Henry, 2020; Duelli and Obrist, 2019), which has been taxonomically affected by the rediagnosed genus *Apertochrysa* Tjeder, 1966 (Breitkreuz et al., 2021).

Previous studies of SNHs have revealed how Chrysopidae use vegetation cover for reproduction and feeding (Alcalá Herrera et al., 2019b; Franin et al., 2016; McEwen and Ruiz, 1994; Villenave et al., 2005, 2006) which also has a positive impact on Chrysopidae abundance and diversity in olive orchards (Porcel et al., 2017). Earlier studies found that tree species in adjacent SNHs sometimes boost Chrysopidae abundance in citrus orchards and, at other times, diminish their abundance in carrot crops (Mignon et al., 2003; Sorribas et al., 2016). González et al. (2008) found that Chrysopidae abundance and diversity in an olive orchard adjacent to *Pinus halepensis* Mill. (pine) trees were lower than in one bordered by *Quercus rotundifolia* Lam. (oak) trees.

In this context, our study aimed to evaluate the attraction of green lacewing adults to different tree species in SNHs adjacent to Mediterranean olive orchards to promote their populations in olive orchard. On the one hand, to identify the potential of each tree species to improve Chrysopidae species which could help to increase a *P. oleae* pest control. In the SNHs of the olive orchards studied, the predominant tree species were *Q. rotundifolia*, *Prunus dulcis* (Mill.) D. A. Webb (almond) and *P. halepensis*, which bordered the olive orchards in vegetation patches and individually. We therefore hypothesized that green lacewing abundance and diversity in each tree species differ, while the presence of *P. oleae* in the agro-ecosystems may influence the Chrysopidae community.

2. Material and methods

2.1. Area of study

The study was carried out in the province of Granada in the south of Spain, where 49,927 hectares (ha) are devoted to olive orchards (Junta de Andalucía, 2014a). Interspersed in a landscape dominated by olive orchards are vegetation patches bordering and/or inside the cultivated crop areas composed of *P. halepensis*, *Q. rotundifolia*, *P. dulcis* and *Quercus coccifera* L. (Fagales: *Fagaceae*) trees and/or native shrubs such as *Juniperus oxycedrus* L. (Pinales: *Cupressaceae*), *Cistus albidus* L.

(Malvales: *Cistaceae*), *Cistus clusii* Dunal (Malvales: *Cistaceae*), *Genista cinerea* (Vill.) DC. (Fabales: *Fabaceae*), *Lavandula latifolia* Medik. (Lamiales: *Lamiaceae*), *Pistacia terebinthus* L. (Sapindales: *Anacardiaceae*) and *Rosmarinus officinalis* L. (Lamiales: *Lamiaceae*). These types of vegetation are the remains of pre-crop vegetal formations, reforestation and, in some cases, plants sown by farmers.

Weather conditions are characterized by an oceanic-pluviseasonal Mediterranean bioclimate, an upper *meso*-Mediterranean thermotype and a low subhumid ombrotype, with an annual average temperature and precipitation of 14 °C and 672.3 mm, respectively (Valle Tendero et al., 2005).

We selected five organic olive orchards (*Olea europaea* L.) of a Picual variety (Table 1) located at similar altitudes of between 800 and 1100 m above sea level, covering an area of between 0.9 and 215 ha. All five olive orchards have spontaneous vegetation cover, which is removed by mowing, tillage or grazing between April and May. In addition, during the post-harvest period, the soil was fertilized with organic material, and crushed pruning waste was placed in the rows between orchards to create inert cover. The incidence of the pest *P. oleae* and the disease *Fusicladium oleagineum,* was remedied by timely and targeted treatments (one for the pest in local patches and two for the disease) with *Bacillus thuringiensis* var. *kurstaki* (strain PB54) and copper oxychloride (50–70 % w/v), which are listed in Annex II of Commission Regulation (EC) no. 889/2008 concerning organic management (European Union, 2008).

2.2. Collection of Chrysopidae from tree species

Chrysopidae adults and larvae were collected from a total of 75 trees per species – olive, oak, almond and pine – per sampling date from five sites, whose distribution in each site depended on their availability in each olive orchard (Table 1). The trees were randomly selected, with a minimum distance of 15 m between trees to ensure spatial independence. Almond, oak and pine trees were located in the SNHs edge and in the vegetation patch in SNHs, and olive trees were part of the orchard. Canopy suction samples were obtained using a field aspirator (Insecta-Zooka BioQuip®, Rancho Dominguez, CA, USA), which was pre-tested for capturing small arthropods, especially Chrysopidae (Doxon et al., 2011; Hossain et al., 1999; Macleod et al., 1994; Samu and Sarospataki, 1995; Sanders and Entling, 2011; Sorribas et al., 2016; Wilson et al., 1993). For each sample, the aspirator was moved up to a height of three meters for two minutes to cover the whole sampled tree. This precise suction sampling technique enables arthropod fauna to be collected, specifically from individual trees and/or vegetation cover of interest, differs from other methods, such as water traps and McPhail traps, and can also collect larger quantities of arthropods than pitfall traps or branch beating sampling (Brook et al., 2008). A total of 13 samplings were carried out fortnightly between April and October 2016. The sampling period was chosen to avoid winter inactivity of the olive orchard insect community (Ruano et al., 2004; Santos et al., 2007). The suction samples were cold-stored in the field and stored in a freezer at −20 °C until identification. The adult Chrysopidae collected were counted and identified under a stereomicroscope (Nikon SMZ 800; Nikon, Tokyo, Japan) up to species level according to Monserrat (2016), Duelli and Henry (2020) and (Canard and Thierry, 2017) keys, as well as

to the latest taxonomic review of the genus *Apertochrysa* (Breitkreuz et al., 2021).

2.3. Presence and infestation of P. Oleae

The presence of *P. oleae* adults was monitored over three generations using funnel traps (Econex TA027; Sanidad Agrícola Econex S.l., Santomera, Murcia, Spain), a pheromone lure and Snailnex® insecticide (Sanidad Agrícola Econex S.l., Santomera, Murcia, Spain). Ten funnel traps (two per site), placed at least 150 m apart, were inspected monthly from April to November 2016 and every-eight or ten days in June and July. *Prays oleae* adults collected was expressed as the number of adults collected per trap per day (ATD) index (Equation (1)). This is a well-known and commonly used index to express the presence of *P. oleae* adults (Civantos, 1999; Junta de Andalucía, 2014b; Ramos et al., 1998, 1984b).

$$ATD = \frac{Number\ of\ adults\ collected\ in\ both\ traps}{Number\ of\ traps \times number\ of\ days\ elapsed} \quad (1)$$

To measure the infestation of the phyllophagous, anthophagous and carpophagous generations of *P. oleae* in each olive orchard, damage to specific vegetative organs in each generation was examined under a stereomicroscope.

Phyllophagous generation (April-May; two samplings) – 10 randomly selected shoots from 10 randomly selected olive trees per site per sampling (100 shoots in total) were collected, the shoots attacked were counted and the percentage of shoots attacked per tree was calculated (Equation (2)).

$$\%shoots\ attacked = \frac{Number\ of\ shoots\ attacked}{Number\ of\ shoots\ observed} \times 100 \quad (2)$$

Anthophagous generation (May-June; two samplings) – two randomly selected inflorescences per shoot in each of the 50 shoots from five olive trees selected at random per site per sampling (100 inflorescences in total) were inspected; the eggs incubated, hatched and predated were counted in order to calculate the percentage of inflorescences attacked (Equation (3)) and eggs predated (Equation (4)) per tree.

$$\%inflorescences\ attacked = \frac{Number\ of\ inflorescences\ attacked}{Number\ of\ inflorescences\ observed} \times 100 \quad (3)$$

$$\%eggs\ predated = \frac{Number\ of\ eggs\ predated}{Total\ number\ of\ eggs\ counted} \times 100 \quad (4)$$

Carpophagous generation (July; two samplings) – two randomly selected fruits per shoot in each of the 50 shoots from five olive trees selected at random per site per sampling (100 fruits in total) were examined; the eggs incubated, hatched and predated were counted to calculate the percentage of fruits attacked (Equation (5)) and eggs predated (Equation (6)) per tree.

$$\%fruits\ attacked = \frac{Number\ of\ fruits\ attacked}{Number\ of\ fruits\ observed} \times 100 \quad (5)$$

$$\%eggs\ predated = \frac{Number\ of\ eggs\ predated}{Total\ number\ of\ eggs\ counted} \times 100 \quad (6)$$

Table 1
Site characteristics and number of tree species sampled in each site.

Site	Coordinates (datum: WGS 84)	Area (ha)	Number of trees sampled				
			Almond	Oak	Olive	Pine	Total
Norberto	37°19′5.96″N; 3°34′9.92″W	4.3	25	15	15	25	80
La Pedriza	37°20′17.44″N; 3°33′39.21″W	0.9	–	15	15	25	55
Los Almendros	37°22′24.76″N; 3°37′46.03″W	215	25–26	15	15	–	55–56
Píñar (right)	37°24′14.29″N; 3°29′14.13″W	58	–	15	15	25	55
Píñar (left)	37°24′40.93″N; 3°28′52.41″W	124	24–25	15	15	–	54–55
Total			**75**	**75**	**75**	**75**	**300**

2.4. Statistical analysis

We analysed the data using R version 3.5.0 (R Development Core Team, 2017) and R Studio software (RStudio Team, 2016) together with the packages *glmmTMB* (Brooks et al., 2017), *lme4* (Bates et al., 2014) and *vegan* (Oksanen et al., 2018). For each model, residuals were examined for model validation using the *DHARMa* package (Hartig, 2018). We checked fixed factors for significance using Wald tests with the aid of the *car* package (Fox and Weisberg, 2019), as well as multiple comparisons between fixed factor levels for significance using *lsmeans*, *emmeans* and *multcomp* packages (Hothorn et al., 2008; Lenth, 2020, 2016).

To investigate the effect of site and tree species on the number of the Chrysopidae adults and larvae collected, suction sampling data were analysed using generalized linear mixed models (GLMM) combined with a negative binomial (NB) distribution to correct for overdispersion. In each model, sampling date was established as a random effect to account for repeated measures on the same site and tree species at different times, as well as variations in population dynamics. Species richness, which was calculated as the number of Chrysopidae adult species collected per sample, was analysed using a Poisson GLMM to determine the effect of the tree species and site as a fixed factor and sampling date as a random factor. Species diversity was calculated using the Shannon-Wiener diversity index (hereafter referred to as Shannon diversity). During the preliminary data analysis stage, we noticed that data distribution was not normal. Thus, before calculating Shannon diversity, the numbers of Chrysopidae adults collected were grouped by tree species and sampling date. Shannon diversity was modelled using a linear mixed model (LMM) with a Gaussian distribution with tree species as a fixed factor and sampling date as a random factor. Following univariate analysis, principal response curve (PRC) analysis was used to explore both the temporal dynamics of the Chrysopidae adult community and the contribution of each Chrysopidae species to these dynamics for each tree species, according to the method described by Auber et al. (2017). A Hellinger transformation was applied to the Chrysopidae species count data to reduce the predominance of major Chrysopidae species values, as recommended by Borcard et al. (2011). PRC analysis is a multivariate method based on partial redundancy analysis developed by Van den Brink and Ter Braak (1999). The PRC is graphically represented by the canonical coefficient (C_{dt}) on the y axis against time on the x axis. C_{dt} was used to quantify the pattern of community responses relative to the control. The olive trees, which were designated as control and were represented by a horizontal line in the PRC graph, acted as a reference to evaluate its relationship with the other tree species. The sign of the C_{dt} indicates the type of community response and is interpreted by comparison with the signs of species weight (b_k) (Auber et al., 2017). A C_{dt} of up to zero indicates that abundance of Chrysopidae species is higher than that of the control (olive tree) in this period. Conversely, a C_{dt} of less than zero shows that Chrysopidae abundance is lower than that of the control (olive tree) in this period. In the same graph, b_k quantifies the contribution of each individual Chrysopidae species with respect to the overall community response. A b_k value of up to 0.5 indicates that the response of the species is likely to follow the pattern in the PRC graph, with b_k values of between −0.5 and 0.5 indicating a weak response, while high negative b_k values of up to −0.5 denote a reverse trend from that in the PRC graph (Auber et al., 2017). A Monte Carlo permutation test, with 999 permutations, was performed to test the significance of the y axis.

Prays oleae infestation was analysed in order to evaluate differences between the sampled sites by determining the percentage of shoots, inflorescences and fruits attacked, as well as eggs predated, in the phyllophagous, anthophagous and carpophagous generations using a GLMM with a beta-binomial distribution to correct for overdispersion. Models included site as a fixed factor and sampling date as a random effect in order to correct for repeated measures over time. To investigate the relationship between the number of Chrysopidae collected and the *P. oleae* infestation, the total Chrysopidae adults and larvae collected in the olive trees per site at the same period of *P. oleae* sampling date (anthophagous and carpophagous generations) were analysed in two different models using a GLMM with a NB distribution for Chrysopidae adults and a Poisson distribution for Chrysopidae larvae. The models included the percentage of eggs predated as a fixed factor in both models and as a random factor: sampling date in the model for Chrysopidae adults, as well as the sampling date and site in the model used for Chrysopidae larvae.

3. Results

3.1. Collection of Chrysopidae from tree species

A total of 3477 individual Chrysopidae (2918 adults as compared to 559 larvae) were collected between April and October 2016 (Table A.1). The smallest number of captures was in April (21 individuals), while the largest number of both adults and larvae were collected in September (800 individuals), with intermediate values being recorded in the other months (Table A.1).

Adult Chrysopidae vacuumed from the four tree species showed the following significant variations (GLMM, $\chi^2 = 541.34$, d.f. = 3, $P < 0.001$) (Fig. 1A, Table A.2): oak trees recorded by far the largest number of adult Chrysopidae (mean ± SE) (1.42 ± 0.07; 1381 adults), followed by olive trees (0.87 ± 0.05; 848 adults), almond trees (0.50 ± 0.04; 486 adults) and pine trees (0.21 ± 0.02; 203 adults). With respect to seasonal numbers of adult Chrysopidae associated with the different tree species (Fig. 2), oak trees reached a peak in early July (2.73 ± 0.32) and September (2.44 ± 0.37), while adult Chrysopidae in olive trees were abundant from May, decreased in early July, and reached a peak in late September (2.75 ± 0.29) and also in October (2.24 ± 0.24). On the other hand, the number of adult Chrysopidae in both pine and almond trees peaked at the beginning of June (0.87 ± 0.19 and 1.49 ± 0.21, respectively), while almond trees again reached a peak at the beginning of September (0.96 ± 0.22) (Fig. 2). The number of adult Chrysopidae collected also differed significantly between sites (GLMM, $\chi^2 = 127.25$, d.f. = 4, $P < 0.001$) (Fig. 1B, Table A.2), with the Norberto site (0.92 ± 0.05; 958 adults) recording the largest number of adult Chrysopidae as compared to the other sites. Oak trees clearly showed the highest values for Shannon diversity (mean ± SE) (1.80 ± 0.06) (LMM, $\chi^2 = 44.90$, d.f. = 3, $P < 0.001$) and species richness (mean ± SE) (0.99 ± 0.04) (GLMM, $\chi^2 = 681.61$, d.f. = 3, $P < 0.001$) (Fig. 3A and C, Table A.2). Species richness also differed significantly between sites (GLMM, $\chi^2 = 108.93$, d.f. = 4, $P < 0.001$) (Fig. 3B, Table A.2), with the Norberto site (0.62 ± 0.03) recording the highest richness compared to the other sites.

Although the sampling method was particularly oriented towards the capture of adult Chrysopidae, larvae were also collected, whose numbers in the tree species varied significantly (GLMM, $\chi^2 = 162.72$, d. f. = 3, $P < 0.001$) (Fig. 1, Table A.2): olive trees (0.27 ± 0.02; 259 larvae) had the largest number of larvae collected, with pine trees (0.06 ± 0.01; 62 larvae) showing an opposite trend, while almond and oak trees both recorded intermediate values without any significant statistical differences being observed. The seasonal number of larvae associated with oak trees peaked at the end of June (0.49 ± 0.08), while Chrysopidae larvae increased steadily in olive trees from the beginning of May, reached a maximum in early July (0.67 ± 0.12), diminished and did not increase again until the months of September and October (Fig. 2). In almond trees, the number of larvae increased from late May and peaked in early August (0.37 ± 0.09), and, from then on, began to decline. On the other hand, the number of larvae in pine trees remained almost flat during the study period (Fig. 2). Distribution among sites also varied significantly (GLMM, $\chi^2 = 95.64$, d.f. = 4, $P < 0.001$) (Fig. 1 and Table A.2): the Norberto site (0.23 ± 0.02; 235 larvae) presented the largest number of larvae as compared to La Pedriza, Los Almendros, Píñar (right) and Píñar (left), with no significant differences observed
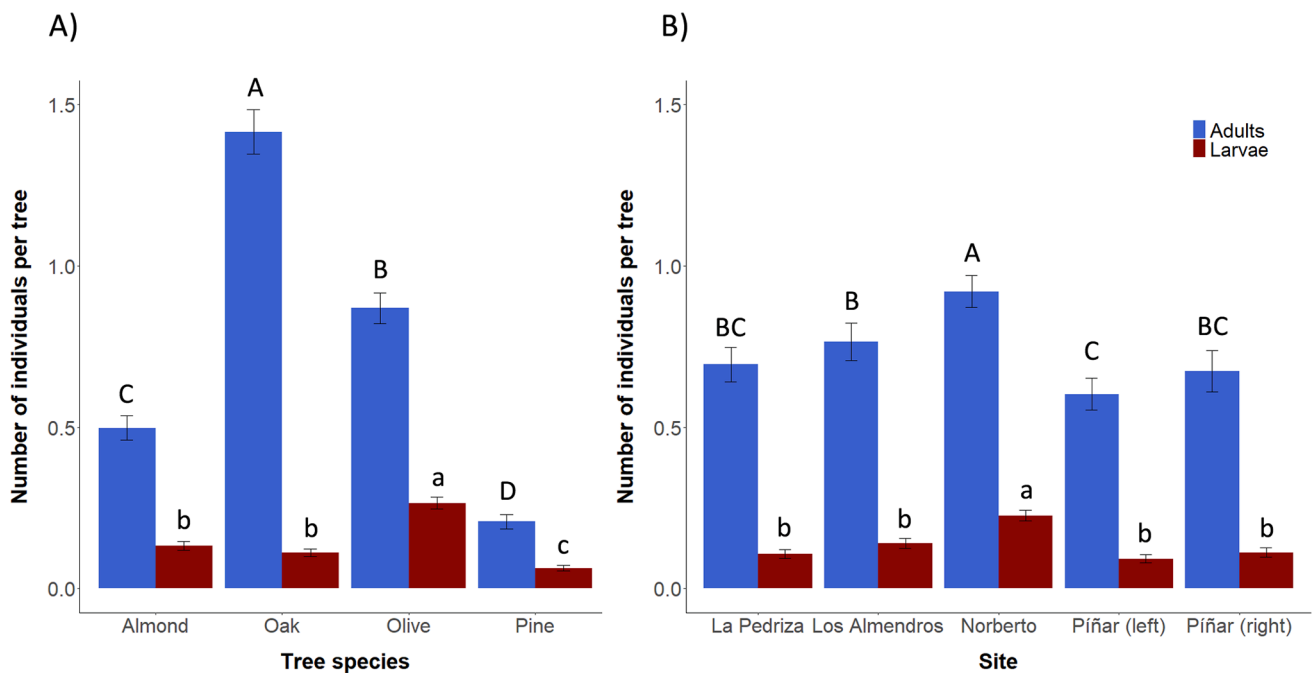
Fig. 1. Number of Chrysopidae adults and larvae collected per tree (mean ± SE) in A) each tree species and B) site. Different letters indicate statistically significant differences between Chrysopidae adults (capital letters) and larvae (lower case letters) (GLMM, Tukey's test, $P < 0.05$).
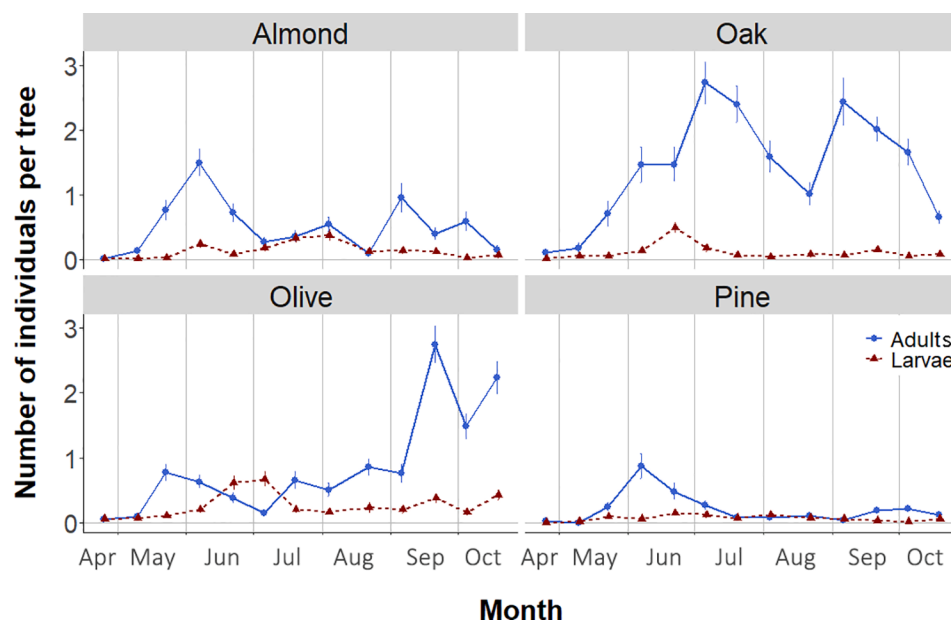

Fig. 2. Number of Chrysopidae adults and larvae (mean ± SE) collected from almond, oak, olive and pine trees on each sampling date.

between the latter four sites.

We collected the 2918 Chrysopidae adults belonging to 20 species from the following seven genera of the Chrysopidae family: *Apertochrysa* (six species), *Chrysopa* Leach, 1815 (four species), *Chrysoperla* (four species), *Pseudomallada* (three species), *Cunctochrysa* Hölzel, 1970 (one species), *Italochrysa* Principi, 1956 (one species), and *Rexa* Navás, 1920 (one species) (Table A.3).

The most abundant species were *Chrysoperla mutata* (McLachlan, 1898) (0.20 ± 0.01; 774 adults), followed by *Chrysoperla pallida* Henry et al., 2002 (0.13 ± 0.01; 520 adults), *Pseudomallada (prasinus) pp3* (Duelli and Henry, 2020) (0.12 ± 0.01; 460 adults), *Chrysoperla lucasina* (Lacroix, 1912) (0.11 ± 0.01; 424 adults), *Apertochrysa benedictae*

(Séméria, 1976) (0.04 ± 0.00; 168 adults) and *Pseudomallada (prasinus) pp2* (Duelli and Henry, 2020) (0.04 ± 0.00; 160 adults) (Table A.3). The following species, which ranged from 1 to 81 adults collected, were much less abundant: *Apertochrysa picteti* (McLachlan, 1880), *Pseudomallada (prasinus) pp1* (Duelli and Henry, 2020), *Cunctochrysa baetica* (Hölzel, 1972), *Apertochrysa granadensis* (Pictet, 1865), *Chrysoperla mediterranea* (Hölzel, 1972), *Apertochrysa flavifrons* (Brauer, 1851), *Chrysopa viridana* Schneider, 1845, *Chrysopa formosa* Brauer, 1851, *Apertochrysa ibericus* (Navás, 1903), *Rexa almerai* (Navás, 1919), *Apertochrysa subcubitalis* (Navás, 1901), *Chrysopa dorsalis* Burmeister, 1839, *Chrysopa pallens* (Rambur, 1838) and *Italochrysa italica* (Rossi, 1790) (Table A.3).
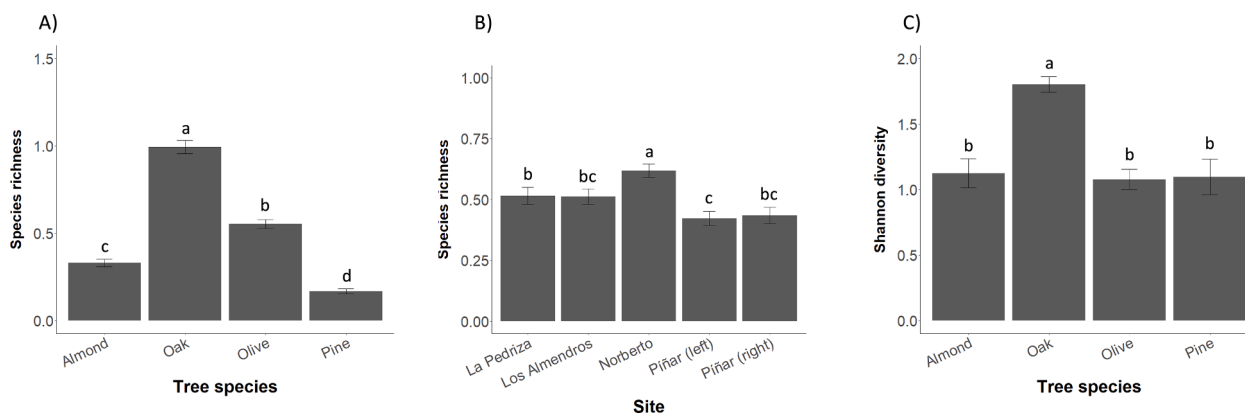
Fig. 3. Species richness (mean ± SE) in A) tree species and B) Site, and Shannon diversity in C) tree species. Different letters indicate statistically significant differences between tree species and site (GLMM to species richness and LMM to Shannon diversity, Tukey's test, $P < 0.05$).

PRC analysis of adults showed deviations from the olive tree species during the period of the study, which were especially marked from the end of June when the total number of adult Chrysopidae increased in the agroecosystems (Fig. 4). We observed positive deviations of oak trees from olive tree species during the end of June until the beginning of August, followed by slight or negative deviations (Fig. 4). Meanwhile almond trees showed a slight positive deviation at the end of June, followed by slight or negative deviations (Fig. 4). However, pine trees recorded negative deviations virtually throughout the whole period of the study. The species *Chrysoperla mutata*, *C. pallida*, *P. (prasinus) pp3*, *A. benedictae* and *P. (prasinus) pp2* were the principal contributors to the community deviations observed (Fig. 4). Although *C. mutata* was mainly collected from the almond, oak and olive trees, the number of adults mostly varied between oak and olive trees (Table A.3). The numbers of *Chrysoperla mutata* in oak tree species, which reached a peak in August, then diminished, especially with respect to olive tree species (Table A.3). *Chrysoperla pallida, P. (prasinus) pp3* and *P. (prasinus) pp2* reached a peak in July in oak trees and then diminished in favour of olive and almond tree species (Table A.3). On the other hand, *A. benedictae* was most commonly found in the oak tree species, with a peak in September and fewer captures from almond, olive and pine tree species (Table A.3).

With regard to the other Chrysopidae species, it has to be emphasized that *C. lucasina* specimens were collected from all tree species, particularly between May and July from almond, oak and pine trees, as well as from olive tree species in April and October (Table A.3). While not contributing to the deviations observed, *C. mediterranea, A. granadensis* and *A. picteti* were the Chrysopidae species most commonly found in pine trees (Table A.3).

3.2. Presence and infestation of P. Oleae

According to the ATD index, *P. oleae* adults appeared in April and continued to increase before reaching a peak at the end of June (mean ± SE) (217.43 ± 36.26), when they began to decrease drastically before disappearing altogether in August and then only reappeared in October (38.28 ± 14.59) (Figure A.1).

With respect to the infestation of the phyllophagous generation of *P. oleae*, the percentage of shoots attacked was significantly higher in Norberto (mean ± SE) (90.00 ± 2.29) than in the Los Almendros site (77.00 ± 2.91), although neither site differed significantly from the other sites (GLMM, $\chi^2 = 10.60$, d.f. = 4, $P < 0.05$) (Fig. 5A and Table A.2).
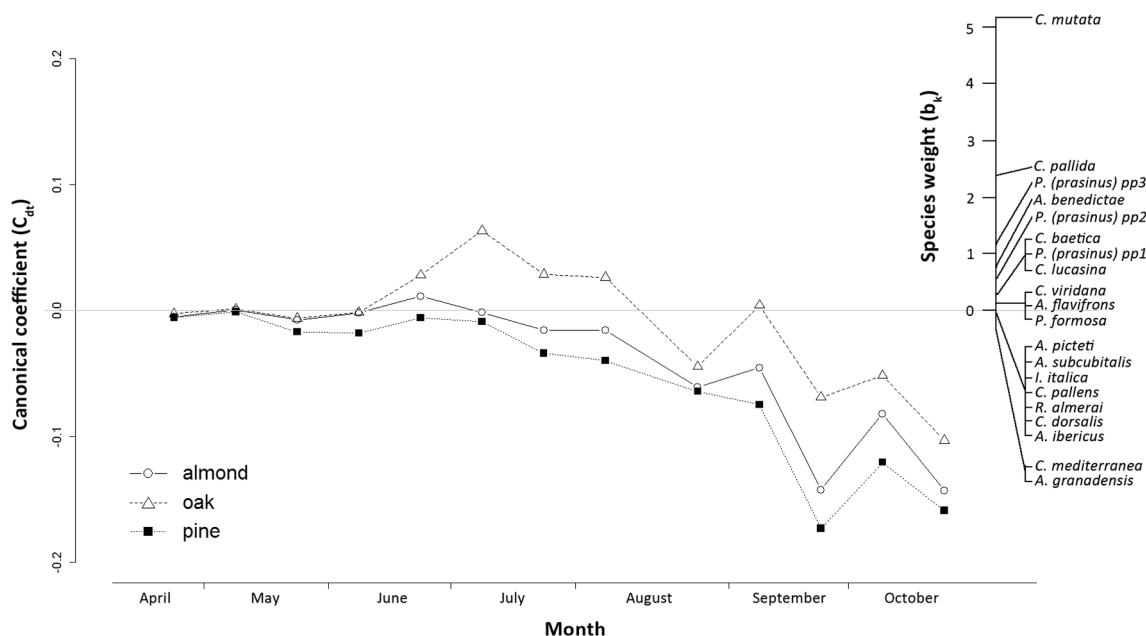

Fig. 4. PRC graph showing the effect of almond, oak, pine and olive trees on the Chrysopidae species composition collected from tree species on each sampling date by of suction sampling. The y axis was significant (Monte Carlo permutation test, $P < 0.05$).

With regard to the anthophagous generation, the percentage of inflorescences attacked varied significantly between the Píñar (left) (51.00 ± 4.64) and Norberto (31.00 ± 5.57) sites, neither of which differed from the other sites (GLMM, $\chi^2 = 17.28$, d.f. = 4, $P < 0.01$) (Fig. 5B and Table A.2). On the other hand, the percentage of eggs predated was significantly higher in La Pedriza (32.99 ± 7.59) and Norberto (25.45 ± 6.33) than in Píñar (left) (5.53 ± 1.72) and Píñar (right) (5.92 ± 2.74) (GLMM, $\chi^2 = 42.76$, d.f. = 4, $P < 0.001$) (Fig. 5B and Table A.2).

The carpophagous generation did not show any variations in the percentage of fruits attacked between the different sites (GLMM, $\chi^2 = 1.60$, d.f. = 4, $P = 0.900$) (Fig. 5C and Table A.2). On the other hand, the percentage of predated eggs was significantly higher in La Pedriza (84.21 ± 2.06) and Norberto (87.09 ± 2.23) than in the other sites (GLMM, $\chi^2 = 73.53$, d.f. = 4, $P < 0.001$) (Fig. 5C and Table A.2).

The number of Chrysopidae adults was unrelated to the percentage of predated eggs for the anthophagous and carpophagous generations (GLMM, $\chi^2 = 1.34$, d.f. = 1, $P = 0.250$) (Fig. 6A and Table A.2). However, the number of Chrysopidae larvae was significantly correlated with the percentage of predated eggs during the anthophagous and carpophagous generations (GLMM, $\chi^2 = 5.37$, d.f. = 1, $P < 0.05$) (Fig. 6B and Table A.2).

4. Discussion

Our study shows that the presence of almond, oak and pine trees adjacent to the olive orchard had a positive effect on the Chrysopidae community. The increased abundance of adult Chrysopidae in the different tree species translated into an increase in the abundance of larvae in olive trees, during the anthophagous and carpophagous generations of olive moths.

SNHs, which provide suitable refuge, oviposition and overwinter sites, as well as alternative food resources, are valuable structures for conserving and promoting Chrysopidae populations (Szentkirályi, 2001b). In vineyards, SNHs increase both the abundance and diversity of Chrysopidae on vine canopies (Serée et al., 2020). SNHs, such as hedgerows, windbreaks, shelterbelts, flower strips and cover vegetation, bordering and within cultivated crop areas, differ according to their floral composition and structure (Holland et al., 2016). Previous studies have reported that the presence of garrigue vegetation, legume fields or native vegetation, such as *Spartium*, *Cistus*, *Rosmarinus*, *Pistacia*, *Pinus* and *Quercus*, surrounding olive orchards, produces Chrysopidae assemblages displaying the largest number of species and highest abundance levels inside these orchards (Alrouechdi et al., 1980; Campos and Ramos, 1983; Canard et al., 1979). Furthermore, Porcel et al. (2017) have demonstrated that spontaneous vegetation cover could play an important role in enhancing the abundance and diversity of Chrysopidae

on olive tree canopies. Having simultaneously collected samples from tree species in SNHs and from the olive trees, we found that adult Chrysopidae were most attracted to oak trees and least attracted to pine trees. This appears to corroborate the results of González et al. (2008), who observed that olive orchards bordering oak trees (*Q. rotundifolia*) have higher Chrysopidae abundance than those next to pine trees (*P. halepensis*). We found that Chrysopidae species richness levels in our organic olive orchards were higher than those reported by Porcel et al. (2013) for olive orchards subjected to conventional agronomic management. This could be explained by the use of pesticides which have a negative impact on species richness and diversity (Porcel et al., 2013). Furthermore, we showed that oak trees had higher Shannon diversity and species richness than the other tree species. This could be explained by the specificity of the Chrysopidae community in relation to the vegetation (Monserrat and Marín, 1994), the suitability of the food resources, as well as the refuge and reproduction sites of each tree species (Alcalá Herrera et al., 2019a).

Regarding the Chrysopidae larvae collected, olive trees recorded significantly higher number of Chrysopidae larvae than other tree species, which reached peak levels between late June and early July. We found that the number of Chrysopidae larvae significantly correlated with the percentage of predated eggs during the anthophagous and carpophagous generations of *Prays oleae*. On the other hand, the number of Chrysopidae adults was unrelated to the percentage of predated eggs, as most of the Chrysopidae adult species collected were non-predatory. Previous studies have reported that *C. carnea s.l.* are attracted by the carpophagous generation of *P. oleae*, during which their highest egg predation rates have been recorded (Ramos et al., 1984a), while serological tests have confirmed that *C. carnea s.l.* feed on *P. oleae* eggs (Morris et al., 1999). Furthermore, the biological control of *P. oleae* is also driven by other predators such as Formicidae, Heteroptera and Arachnida (Álvarez et al., 2021; Morris et al., 1999), which were not investigated in our study. Tree species in SNHs are invaluable, and further studies of the temporal dynamics of Chrysopidae and intraguild predator communities need to be carried out in order to measure *P. oleae* egg consumption in relation to conservation biological control in olive orchards.

On the other hand, Chrysopidae abundance levels were very similar at site level except for Norberto and Píñar (left), which had the highest and lowest abundance, respectively, thus showing that the Chrysopidae community in the area covered by the study is quite stable. The highest abundance and species richness levels were observed in the Norberto site, which might be due to the presence of the almond, oak and pine tree species in the areas surrounding the olive orchard. Thus, a broad diversity of habitats and food sources might attract a large number of adult Chrysopidae. This situation has also been described when spontaneous
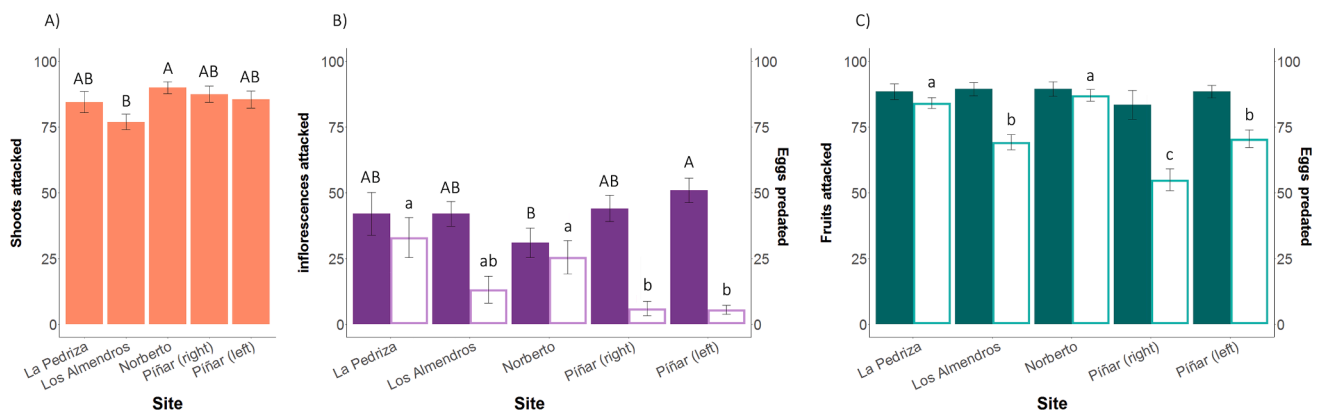

Fig. 5. *Prays oleae* infestation per tree (mean ± SE) in A) the phyllophagous generation (percentage of shoots attacked), B) anthophagous generation; percentage of inflorescences attacked (left axis) and eggs predated (right axis) and C) the carpophagous generation; percentage of fruits attacked (left axis) and eggs predated (right axis) in each site. Different letters indicate statistically significant differences between sites with lower case letters to indicate shoots, inflorescences and fruits attacked and capital letters for eggs predated (GLMM, Tukey's test, $P < 0.05$).
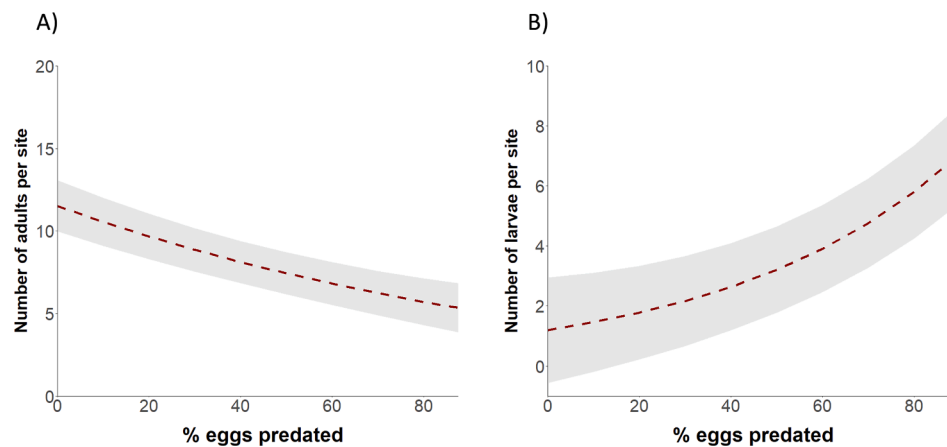
Fig. 6. Predicted GLMM values ($\pm$95 % CI) for the number of (A) Chrysopidae adults ($\chi^2 = 1.34$, d.f. $= 1$, $P = 0.250$) and (B) Chrysopidae larvae ($\chi^2 = 5.37$, d.f. $= 1$, $P < 0.05$) relative to the percentage of predated *Prays oleae eggs*.

vegetation cover was established in olive orchards (Porcel et al., 2017) and when different types of SNHs (vegetation cover and hedgerows) were combined, as Sorribas et al. (2016) have reported in relation to citrus orchards. In vineyards, Serée et al. (2020) found that Chrysopidae abundance is more affected by the proportion of SNHs than by the landscape configuration, which is influenced by factors such as patch size and connectivity. Furthermore, Serée et al. (2020) have shown the impact of a positive interaction between landscape context and sampling period on Chrysopidae population dynamics. Meanwhile, Alves et al. (2021) have reported that land uses such as shrublands, grasslands and vineyards, as well as pine and oak forests surrounding olive orchards, do not affect *C. carnea s.l.* populations. Alves et al. (2021) have attributed their results to the impact of meteorological parameters on *C. carnea s.l.* dispersal strategies.

Despite their uniform morphological traits, Chrysopidae have different biological and ecophysiological characteristics (Canard, 1998). It is therefore important to increase our knowledge of their temporal dynamics at species level in order to better understand the factors that influence their spatial cycles and their availability to contribute to biological control (Paulian, 2001). Most of the 20 Chrysopidae species collected in our study were previously found in Spanish olive orchards (Campos and Ramos, 1983; González et al., 2008; Monserrat, 2016; Porcel et al., 2017), except to *A. benedictae*, *P. (prasinus) pp1*, *pp2* and *pp3*, which, to the best of our knowledge, were identified for the first time in Spanish olive orchards. Our study shows that tree species plays an important role in Chrysopidae temporal dynamics. Monserrat and Marín (1994) have reported that different types of vegetation, herbaceous, shrubs and tree species are specifically associated with Iberian Chrysopidae species. Between the months of April and October, we collected the species *C. mutata*, *C. pallida*, *P. (prasinus) pp3*, *A. benedictae* and *P. (prasinus) pp2,* which were mainly responsible for the differences between the tree species. As with *C. mediterranea* and pine trees, *A. benedictae* was found to be markedly specific to oak trees. Meanwhile, *C. mutata*, *C. pallida*, *P. (prasinus) pp3* and *P. (prasinus) pp2* were recorded in almond, oak and olive trees, with slight differences between the tree species, which may be indicative of differing behaviour patterns. Except for the genus *Chrysopa*, most Chrysopidae species collected from almond, oak, pine and olive tree species are basically palynoglycophagous. This indicates that the tree species sampled could be used for refuge, feeding and reproduction purposes as most of the Chrysopidae community was shared by all the tree species studied. In a previous study, we confirmed that the most abundant adult Chrysopidae, *C. pallida*, *C. mutata*, *C. lucasina* and *P. prasinus,* collected in our current study use mainly almond, oak and olive trees for reproduction (Alcalá Herrera et al., 2019a). Furthermore, Villa et al. (2019) have reported that *C. carnea s.l.* collected from olive orchards feed on pollen

grains from trees, shrubs and herbaceous species such as *O. europaea*, *Fabaceae*, *Pinaceae*, *Cistaceae* and *Ericaceae*, as well as on pollen settled on vegetation surfaces. As also reported by Villa et al. (2019) adult Chrysopidae collected from olive trees in September and October in our study may consume olive pollen grains on olive tree surfaces and complement their diet with other pollen grains from surrounding plant species.

Unfortunately, according to field observations by Szentkirályi (1991) and (Alcalá Herrera et al., 2022) with regard to arable crops, SNHs adjacent to crops could prevent female Chrysopidae from laying their eggs in the crop. The weak response of Chrysopidae oviposition to pests may be a consequence of the non-predatory nature of most of the Chrysopidae species collected; egg laying by these species does not appear to be related to pest abundance, and there is a time-lag between the migratory flight of Chrysopidae and oviposition (Duelli, 1984; Rácz et al., 1986; Sakuratatani, 1986; Szentkirályi, 1991). With regard to Chrysopidae movement in the agroecosystem, Lefebvre et al., (2017) observed that Chrysopidae prefer to frequently move from adjacent SNHs to the orchard. Furthermore, Duelli (2001) found that Chrysopidae, which return to the field crop following the winter diapause, behave nomadically during the reproductive period in order to reduce the risk to the offspring in unpredictable, temporary and patchy habitats. Unlike Lefebvre et al., (2017), we did not mark individual Chrysopidae in the SNHs in order to confirm their movements between the olive tree and SNHs. However, based on the Chrysopidae captured, in our study, *Chrysoperla* sp. and *Pseudomallada* sp. may have been involved in the movements between the tree species in SNHs and the olive orchard.

Although *C. lucasina* was mainly captured between May and July (a total of 424 individuals), its contribution to global changes in the Chrysopidae community structure was limited according to the b_k value in the PRC. *Chrysoperla lucasina* is an opportunistic species attracted by herbaceous vegetation (Alcalá Herrera et al., 2020; Villenave et al., 2005). All olive orchards in our study have spontaneous vegetation cover, which can provide food resources such as pollen, nectar and honeydew in spring and summer (Alcalá Herrera et al., 2020; Gonzalez et al., 2016; Villenave et al., 2005). Furthermore, *C. lucasina* use the tree species studied for the purposes of oviposition (Alcalá Herrera et al., 2019a) and possibly also for refuge (Duelli 2001). This could explain the captures of *C. lucasina* in almond, oak, pine and olive trees up to the month of July due to the removal of vegetation cover between the months of April and May.

5. Conclusions

We showed that adult Chrysopidae had the highest levels of

abundance, species richness and diversity in oak trees and the lowest abundance, richness and diversity levels in pine trees; olive trees recorded the most abundance of Chrysopidae larvae, with pine trees recording the lowest levels. Regarding sites, Norberto had the largest number of Chrysopidae adults and larvae, probably due to the presence of all the tree species studied. In our study area, a total of 20 Chrysopidae species were collected, with a predominance of the species *C. mutata, C. pallida, P. (prasinus) pp3, A. benedictae* and *P. (prasinus) pp2,* which were responsible for the temporal deviations in the Chrysopidae community among the different tree species. *Chrysoperla mutata* and *C. pallida* had a preference for olive trees, while *A. benedictae, P. (prasinus)* pp2 and pp3 preferred oak trees. Furthermore, we observed a positive relationship between the number of Chrysopidae larvae and the percentage of predated eggs in the anthophagous and carpophagous generations of *Prays oleae*. Our study has important implications for the protection and promotion of SNHs in agricultural landscapes aimed at conserving and maintaining Chrysopidae in olive orchards. We recommend planting oaks and almond trees around olive orchards. Both these tree species attract Chrysopidae species which are predominant in olive agroecosystems. However, further research is required to investigate the connection between the effect of temporal variations in the Chrysopidae community on *P. oleae* pest control in olive orchards and their interaction with the SNH design.

CRediT authorship contribution statement

Rafael Alcalá Herrera: Conceptualization, Methodology, Formal analysis, Visualization, Supervision, Funding acquisition, Writing – original draft, Writing – review & editing. **Francisca Ruano:** Funding acquisition, Conceptualization, Methodology, Supervision, Writing – review & editing.

Acknowledgments

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocontrol.2022.105003.

References

Albertini, A., Pizzolotto, R., Petacchi, R., 2017. Carabid patterns in olive orchards and woody semi-natural habitats: first implications for conservation biological control against *Bactrocera oleae*. Biocontrol 62 (1), 71–83. https://doi.org/10.1007/s10526-016-9780-x.

Alcalá Herrera, R., Campos, M., González-Salvadó, M., Ruano, F., 2019a. Abundance and population decline factors of chrysopid juveniles in olive groves and adjacent trees. Insects 10, 134. https://doi.org/10.3390/insects10050134.

Alcalá Herrera, R., Ruano, F., Gálvez Ramírez, C., Frischie, S., Campos, M., 2019b. Attraction of green lacewings (Neuroptera: Chrysopidae) to native plants used as ground cover in woody Mediterranean agroecosystems. Biol. Control 139, 104066. https://doi.org/10.1016/j.biocontrol.2019.104066.

Alcalá Herrera, R., Fernández Sierra, M.L., Ruano, F., Saunders, M.E., 2020. The suitability of native flowers as pollen sources for *Chrysoperla lucasina* (Neuroptera:

Chrysopidae). PLoS ONE 15 (10), e0239847. https://doi.org/10.1371/journal.pone.0239847.

Alcalá Herrera, R., Cotes, B., Agustí, N., Tasin, M., Porcel, M., 2022. Using flower strips to promote green lacewings to control cabbage insect pests. J Pest Sci 95 (2), 669–683.

Alrouechdi, K., Lyon, J.P., Canard, M., Fournier, D., 1980. Les chrysopids (Neuroptera) récoltés dans une oliveraie du sud-est de la France. Acta Oecologica-Oecologia Appl. 1, 173–180.

Álvarez, H.A., Jiménez-Muñoz, R., Morente, M., Campos, M., Ruano, F., 2021. Ground cover presence in organic olive orchards affects the interaction of natural enemies against *Prays oleae*, promoting an effective egg predation. Agric. Ecosyst. Environ. 315, 107441. https://doi.org/10.1016/j.agee.2021.107441.

Alves, J.F., Mendes, S., da Silva, A.A., Sousa, J.P., Paredes, D., 2021. Land-use effect on olive groves pest *Prays oleae* and on its potential biocontrol agent *Chrysoperla carnea*. Insects 12, 1–13. https://doi.org/10.3390/insects12010046.

Aspöck, H., Aspöck, U., Hölzel, H., 1980. Die Neuropteren Europas: eine zusammenfassende Darstellung der Systematik, Ökologie und Chorologie der Neuropteroidea (Megaloptera, Raphidioptera, Planipennia) Europas. Goecke & Evers, Krefeld, AT.

Auber, A., Travers-Trolet, M., Villanueva, M.C., Ernande, B., 2017. A new application of principal response curves for summarizing abrupt and cyclic shifts of communities over space. Ecosphere 8 (12), e02023. https://doi.org/10.1002/ecs2.2023.

Barbosa, P., 1998. Conservation biological control. Academic Press, Elsevier, San Diego, CA, US.

Bates, D., Mächler, M., Bolker, B.B.M., Walker, S.C.S., 2014. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Begg, G.S., Cook, S.M., Dye, R., Ferrante, M., Franck, P., Lavigne, C., Lovei, G.L., Mansion-Vaquie, A., Pell, J.K., Petit, S., Quesada, N., Ricci, B., Wratten, S.D., Birch, A.N.E., 2017. A functional overview of conservation biological control. Crop Prot. 97, 145–158. https://doi.org/10.1016/j.cropro.2016.11.008.

Bianchi, F.J.J.A., Schellhorn, N.A., Cunningham, S.A., 2013. Habitat functionality for the ecosystem service of pest control: reproduction and feeding sites of pests and natural enemies. Agric. For. Entomol. 15, 12–23. https://doi.org/10.1111/j.1461-9563.2012.00586.x.

Borcard, D., Gillet, F., Legendre, P., 2011. Numerical Ecology with R. Springer-Verlag Wien, New York, US. https://doi.org/10.1007/978-1-4419-7976-6.

Breitkreuz, L., Duelli, P., Oswald, J., 2021. *Apertochrysa* Tjeder, 1966, a new senior synonym of *Pseudomallada* Tsukaguchi, 1995 (Neuroptera: Chrysopidae: Chrysopinae: Chrysopini). Zootaxa 4966, 215–225. https://doi.org/10.11646/zootaxa.4966.2.8.

Brook, A.J., Woodcock, B.A., Sinka, M., Vanbergen, A.J., 2008. Experimental verification of suction sampler capture efficiency in grasslands of differing vegetation height and structure. J. Appl. Ecol. 45, 1357–1363. https://doi.org/10.1111/j.1365-2664.2008.01530.x.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. 9, 378–400.

Campos, M., 1989. Observaciones sobre la bioecologia de *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae) en el sur de España. Neuroptera Int. 5, 159–164.

Campos, M., Ramos, P., 1983. Crisópidos (Neuroptera) capturados en un olivar del sur de España. Neuroptera Int. 2, 219–227.

Canard, M., Thierry, D., 2017. Une Chrysope contestée et réhabilitée: *Pseudomallada benedictae* (Séméria, 1976) (Neuropterida, Chrysopidae). Rev. l'Association Roussillonnaise d'Entomologie XXVI, 97–102.

Canard, M., Neuenschwander, P., Michelakis, S., 1979. Les Névroptères capturés au piège de McPhail dans les oliviers en Grèce. 3. La Crète occidentale. Ann. La Soc. Entomol. Fr. 15, 607–615.

Canard, M., 1998. Life history strategies of green lacewings in temperate climates: a review (Neuroptera, Chrysopidae). in: Panelius, S. P. (ed.). Neuropterology 1997. Proceedings of the Sixth International Symposium on Neuropterology (13-16 July 1997, Helsinki, Finland). Acta Zool. Fenn. 209, 65–74.

Civantos, M., 1999. Control de plagas y enfermedades del olivar. Consejo Oleícola Internacional, Madrid, ES.

Cordero-Rivera, A., Galicia-Mendoza, D.I., 2017. The relevance of Ethology in insect conservation. Ecosistemas 26, 13–20. https://doi.org/10.7818/ECOS.2017.26-3.03.

Dathe, H.H., 1999. Das erste Insekt des Jahres: die Florfliege *Chrysoperla carnea* (Stephens, 1836) (Neur., Chrysopidae). Entomol. Nachr. Ber. 43, 1–3.

Devetak, D., Klokocovnik, V., 2016. The feeding biology of adult lacewings (Neuroptera): a review. Trends Entomol. 12, 29–42.

Doxon, E.D., Davis, C.A., Fuhlendorf, S.D., 2011. Comparison of two methods for sampling invertebrates: vacuum and sweep-net sampling. J. F. Ornithol. 82, 60–67. https://doi.org/10.1111/j.1557-9263.2010.00308.x.

Duelli, P., Henry, C.S., 2020. A species continuum exists between *Pseudomallada prasinus* and *P. abdominalis* (Neuroptera, Chrysopidae). Zootaxa 4845, 357–374. https://doi.org/10.11646/zootaxa.4845.3.3.

Duelli, P., Obrist, M.K., 2003. Regional biodiversity in an agricultural landscape: the contribution of seminatural habitat islands. Basic Appl. Ecol. 4, 129–138. https://doi.org/10.1078/1439-1791-00140.

Duelli, P., Obrist, M.K., 2019. In search of the real *Pseudomallada prasinus* (Neuroptera, Chrysopidae). Zootaxa 4571, 510–530. https://doi.org/10.11646/zootaxa.4571.4.4.

Duelli, P., Obrist, M.K., Fluckiger, P.F., 2002. Forest edges are biodiversity hotspots - Also for Neuroptera. Acta Zool. Acad. Sci. Hungaricae 48, 75–87.

Duelli, P., 1984. Dispersal and oviposition strategies in *Chrysoperla carnea*, in: Gepp, J. (Ed.), Progress in World's Neuropterology. Proceedings of the 1st International

Symposium on Neuropterology, 22-26 September 1980, Graz, Austria. Osterreichischen Akademie der Wissenschaften, Vienna, AT, pp. 133–145.

Duelli, P., 2001. Lacewings in field crops, in: Whittington, A.E., McEwen, P.K., New, T.R. (Eds.), Lacewings in the Crop Environment. Cambridge University Press, Cambridge, UK, pp. 158–171. https://doi.org/DOI: 10.1017/CBO9780511666117.010.

European Union, 2008. Reglamento (CE) no. 889/2008 de la Comisión, de 5 de septiembre de 2008, por el que se establecen disposiciones de aplicación del Reglamento (CE) no. 834/2007 del Consejo sobre producción y etiquetado de los productos ecológicos, con respecto a la producción ecológica, su etiquetado y su control.

Fox, J., Weisberg, S., 2019. An R Companion to Applied Regression, Third. ed. Sage, Thousand Oaks, CA, US.

Franin, K., Barić, B., Kuśtera, G., 2016. The role of ecological infrastructure on beneficial arthropods in vineyards. Spanish J. Agric. Res. 14, 1–10. https://doi.org/10.5424/sjar/2016141-7371.

González, R., Al-Asaad, S., Bozsik, A., 2008. Influencia de las masas forestales en la diversidad y abundancia de los crisópidos (Neur. Chrysopidae) del olivar. Cuad. la Soc. Española Ciencias For. (Actas la I Reun. sobre Sanid. For. 26, 33–38.

Gonzalez, D., Nave, A., Gonçalves, F., Nunes, F.M., Campos, M., Torres, L., 2016. Effects of ten naturally occurring sugars on the reproductive success of the green lacewing, *Chrysoperla carnea*. Biocontrol 61, 57–67. https://doi.org/10.1007/s10526-015-9694-z.

Gúzman-Alvarez, J.R., Gómez, J.A., Rallo, L., 2009. Sostenibilidad de la producción de olivar en Andalucía, Olivicultura y Elaiotecnia. Consejería de Agricultura y Pesca, Sevilla, ES.

Hartig, F., 2018. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R package version 0.2.0.

Hatt, S., Uyttenbroeck, R., Lopes, T., Mouchon, P., Chen, J.L., Piqueray, J., Monty, A., Francis, F., 2017. Do flower mixtures with high functional diversity enhance aphid predators in wildflower strips? Eur. J. Entomol. 114, 66–76. https://doi.org/10.14411/eje.2017.010.

Holland, J.M., Bianchi, F.J.J.A., Entling, M.H., Moonen, A.-C., Smith, B.M., Jeanneret, P., 2016. Structure, function and management of semi-natural habitats for conservation biological control: a review of European studies. Pest Manag. Sci. 72, 1638–1651. https://doi.org/10.1002/ps.4318.

Holland, J.M., Douma, J.C., Crowley, L., James, L., Kor, L., Stevenson, D.R.W., Smith, B.M., 2017. Semi-natural habitats support biological control, pollination and soil conservation in Europe. A review. Agron. Sustain. Dev. 37, 23. https://doi.org/10.1007/s13593-017-0434-x.

Holland, J., Fahrig, L., 2000. Effect of woody borders on insect density and diversity in crop fields: a landscape-scale analysis. Agric. Ecosyst. Environ. 78, 115–122.

Hossain, Z., Gurr, G.M., Wratten, S.D., 1999. Capture efficiency of insect natural enemies from tall and short vegetation using vacuum sampling. Ann. Appl. Biol. 135, 463–467. https://doi.org/10.1111/j.1744-7348.1999.tb00875.x.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biometrical J. 50, 346–363. https://doi.org/10.1002/bimj.200810425.

Junta de Andalucía, 2014a. Caracterización agraria del territorio de la OCA "Montes Orientales", provincia de Granada.

Junta de Andalucía, 2014b. Protocolo de campo para el seguimiento del cultivo: Olivar.

Landis, D.A., Wratten, S.D., Gurr, G.M., 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. Annu. Rev. Entomol. 45, 175–201. https://doi.org/10.1146/annurev.ento.45.1.175.

Lefebvre, M., Papaix, J., Mollot, G., Deschodt, P., Lavigne, C., Ricard, J.M., Mandrin, J.F., Franck, P., 2017. Bayesian inferences of arthropod movements between hedgerows and orchards. Basic Appl. Ecol. 21, 76–84. https://doi.org/10.1016/j.baae.2017.05.002.

Lenth, R.V., 2016. Least-squares means: The R package lsmeans. J. Stat. Softw. 69 https://doi.org/10.18637/jss.v069.i01.

Lenth, R., 2020. emmeans: Estimated Marginal Means, aka Least-Squares Means.

Macleod, A., Wratten, S.D., Harwood, R.W.J., 1994. The efficiency of a new lightweight suction sampler for sampling aphids and their predators in arable land. Ann. Appl. Biol. 124, 11–17. https://doi.org/10.1111/j.1744-7348.1994.tb04110.x.

McEwen, P.K., Ruiz, J., 1994. Relationship between non-olive vegetation and green lacewing eggs in a Spanish olive orchard. Antenna 18, 148–150.

McEwen, P.K., Senior, L.J., 1998. The use of common green lacewings in environmentally friendly pest control. Agric. Equip. Int. 50, 132–134.

Mignon, J., Colignon, P., Haubruge, E., Francis, F., 2003. Impact of field borders on lacewing populations (Neuroptera: Chrysopidae) in vegetable open fields. Phytoprotection 84, 121–128.

Monserrat, V.J., 2016. Los crisópidos de la Península Ibérica y Baleares (Insecta, Neuropterida, Neuroptera: Chrysopidae). Graellsia 72, 1–123. https://doi.org/10.3989/graellsia.2016.v72.143.

Monserrat, V.J., Marín, F., 2001. Comparative plant substrate specificity of Iberian Hemerobiidae, Coniopterygidae, and Chrysopidae, in: Whittington, A.E., McEwen, P.K., New, T.R. (Eds.), Lacewings in the Crop Environment. Cambridge University Press, Cambridge, UK, pp. 424–434. https://doi.org/DOI: 10.1017/CBO9780511666117.026.

Monserrat, V.J., Marín, F., 1994. Plant substrate-specifity of Iberian Chrysopidae (Insecta, Neuroptera). Acta Oecologica-International J. Ecol. 15, 119–131.

Morris, T.I., Campos, M., Kidd, N.A.C., Symondson, W.O.C., 1999. What is consuming *Prays oleae* (Bernard) (Lep.: Yponomeutidae) and when: a serological solution? Crop Prot. 18, 17–22.

New, T.R., 1975. Lacewings (Neuroptera) as biological control agents. Vic. Entomol. 5, 102–103.

Nicoli Aldini, R., 2002. Insetti predatori di interesse agrario. Not. sulla Prot. delle Piante 14, 81–106.

Nielsen, S.E., 1977. Studies on lacewings (Neuroptera s. str.) in a Danish beech stand. Entomol. Meddelelser 45, 45–64.

Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., Wagner, H., 2018. vegan: Community Ecology Package.

Paulian, M., 2001. The green lacewings of Romania, their ecological patterns and occurrence in some agricultural crops, in: Whittington, A.E., McEwen, P.K., New, T.R. (Eds.), Lacewings in the Crop Environment. Cambridge University Press, Cambridge, UK, pp. 498–512. https://doi.org/DOI: 10.1017/CBO9780511666117.033.

Pfister, S.C., Schirmel, J., Entling, M.H., 2017. Aphids and their enemies in pumpkin respond differently to management, local and landscape features. Biol. Control 115, 37–45.

Porcel, M., Cotes, B., Castro, J., Campos, M., 2017. The effect of resident vegetation cover on abundance and diversity of green lacewings (Neuroptera: Chrysopidae) on olive trees. J. Pest Sci. (2004). 90, 195–196. https://doi.org/10.1007/s10340-016-0748-5.

Porcel, M., Ruano, F., Pena, A., Campos, M., 2013. Agricultural management systems affect the green lacewing community (Neuroptera: Chrysopidae) in olive orchards in southern Spain. Environ. Entomol. 42, 97–106. https://doi.org/10.1603/EN11338erratum.

R Development Core Team, 2017. R: A Language and Environment for Statistical Computing.

Rácz, V., Szentkirályi, F., Visnyovszky, É., 1986. Study of aphid-aphidophage connections in maize. Pp. 318-322, in: Hodek, I. (Ed.), Ecology of Aphidophaga: Proceedings of the 2nd Symposium Held at Zvíkovské Podhradí, September 2-8, 1984. Series Entomologica. Vol. 35. W. Junk, Zvíkovské Podhradí, Czech Republic, p. 562.

Ramos, P., Campos, M., Ramos, J.M., 1984a. Estabilización del ataque de *Prays oleae* Bern. y de la actividad de los depredadores oófagos sobre el fruto del olivo. Boletín Sanid. Veg. Plagas 10, 239–243.

Ramos, P., Campos, M., Ramos, J.M., 1984b. Four years of observations on the relationship between the captures of adult *Prays oleae* Bern. in pheromone traps and the resulting level of infestation. Redia 67, 157–163.

Ramos, P., Campos, M., Ramos, J.M., 1998. Long-term study on the evaluation of yield and economic losses caused by Prays oleae Bern. in the olive crop of Granada (southern Spain). Crop Prot. 17, 645–647. https://doi.org/10.1016/S0261-2194(98)00065-9.

Reddy, P.P., 2017. Agro-ecological approaches to pest management for sustainable agriculture. Springer Nature Singapore, SG.

Ridgway, R.L., Murphy, W.L., 1984. Biological control in the field, in: Canard, M., Séméria, Y., New, T.R. (Eds.), Biology of Chrysopidae. Dr. W. Junk Publishers, The Hague, NL, pp. 220–227.

Rieux, R., Simon, S., Defrance, H., 1999. Role of hedgerows and ground cover management on arthropod populations in pear orchards. Agric. Ecosyst. Environ. 73, 119–127.

RStudio Team, 2016. RStudio: Integrated Development Environment for R.

Ruano, F., Lozano, C., Garcia, P., Peña, A., Tinaut, A., Pascual, F., Campos, M., 2004. Use of arthropods for the evaluation of the olive-orchard management regimes. Agric. For. Entomol. 6, 111–120. https://doi.org/10.1111/j.1461-9555.2004.00210.x.

Sakuratatani, Y., 1986. Behavioral response aphidophagous insects to the prey distribution with special reference to quadrat size, in: XVI International Congress of Entomology. Kyoto, Japan, pp. 1–3.

Samu, F., Sarospataki, M., 1995. Design and use of a hand-hold suction sampler, and its comparison with sweep net and pitfall trap sampling. Folia Entomol. Hungarica 56, 195–203.

Sanders, D., Entling, M.H., 2011. Large variation of suction sampling efficiency depending on arthropod groups, species traits, and habitat properties. Entomol. Exp. Appl. 138, 234–243. https://doi.org/10.1111/j.1570-7458.2010.01094.x.

Santos, S.A.P., Pereira, J.A., Torres, L.M., Nogueira, A.J.A., 2007. Evaluation of the effects, on canopy arthropods, of two agricultural management systems to control pests in olive groves from north-east of Portugal. Chemosphere 67, 131–139. https://doi.org/10.1016/j.chemosphere.2006.09.014.

Serée, L., Rouzes, R., Thiéry, D., Rusch, A., 2020. Temporal variation of the effects of landscape composition on lacewings (Chrysopidae: Neuroptera) in vineyards. Agric. For. Entomol. 22, 274–283. https://doi.org/10.1111/afe.12380.

Sorribas, J., González, S., Domínguez-Gento, A., Vercher, R., 2016. Abundance, movements and biodiversity of flying predatory insects in crop and non-crop agroecosystems. Agron. Sustain. Dev. 36, 34. https://doi.org/10.1007/s13593-016-0360-3.

Szentkirályi, F., 1991. Reproductive numerical response of chrysopids and hemerobiids (Neuropteroidea) to aphids on the common thistle, *Carduus acanthoides*. In: Polgár, L., Chambers, R., Dixon, A.F.G., Hodek, I. (Eds.), Behaviour and Impact of Aphidophaga. SPB Academic, The Hague, NL, pp. 273–280.

Szentkirályi, F., 2001a. Lacewings in vegetables, forests, and other crops, in: Whittington, A.E., McEwen, P.K., New, T.R. (Eds.), Lacewings in the Crop Environment. Cambridge University Press, Cambridge, UK, pp. 239–292. https://doi.org/DOI: 10.1017/CBO9780511666117.012.

Szentkirályi, F., 2001b. Ecology and habitat relationships, in: Whittington, A.E., McEwen, P.K., New, T.R. (Eds.), Lacewings in the Crop Environment. Cambridge University Press, Cambridge, UK, pp. 82–115. https://doi.org/DOI: 10.1017/CBO9780511666117.006.

Sziraki, G., 1996. Ecological investigations of the Neuropteroidea of oak forests in Hungary (Insecta: Raphidioptera, Neuroptera), in: Canard, M., Aspock, H., Mansell, M.W. (Eds.), Pure and Applied Research in Neuropterology: Proceedings of the 5th

International Symposium on Neuropterology 2-6 May 1994, Cairo, Egypt. Toulouse, FR, pp. 229–232.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R. D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H., Westphal, C., 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biol. Rev. 87, 661–685. https://doi.org/10.1111/j.1469-185X.2011.00216.x.

Tscharntke, T., Karp, D.S., Chaplin-Kramer, R., Batáry, P., DeClerck, F., Gratton, C., Hunt, L., Ives, A., Jonsson, M., Larsen, A., Martin, E.A., Martínez-Salinas, A., Meehan, T.D., O'Rourke, M., Poveda, K., Rosenheim, J.A., Rusch, A., Schellhorn, N., Wanger, T.C., Wratten, S., Zhang, W., 2016. When natural habitat fails to enhance biological pest control – Five hypotheses. Biol. Conserv. 204, 449–458. https://doi.org/10.1016/j.biocon.2016.10.001.

Valle Tendero, F., Navarro Reyes, F.B., Jiménez Morales, M.N., Algarra Ávila, J.A., Arrojo Agudo, E., Asensi Marfil, A., Cabello Piñar, J., Cano Carmona, E., Cañadas Sánchez, E.M., Cueto Romero, M., Dana Sánchez, E.D., De Simón Navarrete, E., Díez Garretas, B., García Fuentes, A., Giménez Luque, E., Gómez Mercado, F., Linares Cuesta, J.E., Lorite Moreno, J., Melendo Luque, M., Montoya Fernández, M.C., Mota Poveda, J.F., Peñas De Giles, J., Salazar Mendías, C., Torres Cordero, J.A., 2005.

Datos botánicos aplicados a la gestión del medio natural andaluz I: Bioclimatología y Biogeografía. Consejería de Medio Ambiente, Junta de Andalucía, Sevilla, ES.

Van den Brink, P.J., Ter Braak, C.J.F., 1999. Principal response curves: Analysis of time-dependent multivariate responses of biological community to stress. Environ. Toxicol. Chem. 18, 138–148. https://doi.org/10.1897/1551-5028(1999)018<0138:Prcaot>2.3.Co;2.

Villa, M., Somavilla, I., Santos, S.A.P., López-Sáez, J.A., Pereira, J.A., 2019. Pollen feeding habits of *Chrysoperla carnea* s.l. adults in the olive grove agroecosystem. Agric. Ecosyst. Environ. 283, 106573 https://doi.org/10.1016/j.agee.2019.106573.

Villenave, J., Thierry, D., Al Mamun, A., Lode, T., Rat-Morris, E., 2005. The pollens consumed by common green lacewings *Chrysoperla spp.* (Neuroptera: Chrysopidae) in cabbage crop environment in western France. Eur. J. Entomol. 102, 547–552.

Villenave, J., Deutsch, B., Lode, T., Rat-Morris, E., 2006. Pollen preference of the *Chrysoperla* species (Neuroptera: Chrysopidae) occurring in the crop environment in western France. Eur. J. Entomol. 103, 771–777.

Villenave-Chasset, J., Denis, A., 2013. Study of pollen consumed by lacewings (Neuroptera, Chrysopidae) and hoverflies (Diptera, Syrphidae) in western France. Symbioses 29, 17–20.

Wilson, S.W., Smith, J.L., Purcell, A.H., 1993. An inexpensive vacuum collector for insect sampling. Entomol. News 104, 203–208.