

*Intraguild predation or spatial separation?  
the efficacy and interactions of two natural  
enemy species for the biological control of  
Pear Psyllid (Cacopsylla pyri)*

Article

Published Version

Creative Commons: Attribution 4.0 (CC-BY)

Open Access

Reeves, L. A., Fountain, M. T., Garratt, M. P. D. ORCID: <https://orcid.org/0000-0002-0196-6013> and Senapathi, D. ORCID: <https://orcid.org/0000-0002-8883-1583> (2024) Intraguild predation or spatial separation? the efficacy and interactions of two natural enemy species for the biological control of Pear Psyllid (*Cacopsylla pyri*). *Journal of Insect Behavior*, 37 (3-4). pp. 200-219. ISSN 1572-8889 doi: 10.1007/s10905-024-09863-w Available at <https://centaur.reading.ac.uk/118960/>

It is advisable to refer to the publisher's version if you intend to cite from the work. See [Guidance on citing](#).

To link to this article DOI: <http://dx.doi.org/10.1007/s10905-024-09863-w>

Publisher: Springer

copyright holders. Terms and conditions for use of this material are defined in the [End User Agreement](#).

[www.reading.ac.uk/centaur](http://www.reading.ac.uk/centaur)

## **CentAUR**

Central Archive at the University of Reading

Reading's research outputs online



# Intraguild Predation or Spatial Separation? The efficacy and Interactions of Two Natural Enemy Species for the Biological Control of Pear Psyllid (*Cacopsylla pyri*)

Laura A. Reeves · Michelle T. Fountain · Michael P. D. Garratt ·  
Deepa Senapathi

Received: 16 February 2024 / Revised: 27 August 2024 / Accepted: 12 September 2024  
© The Author(s) 2024

**Abstract** Pear psyllid (*Cacopsylla pyri*) is a persistent pest to the pear industry; with an estimated cost of £5 million per annum in the UK alone. This phloem feeding insect is resistant to a large proportion of approved pesticides, necessitating the use of alternative control strategies. Many pear growers practice integrated pest management (IPM) of pear psyllid, focusing on maximizing natural enemy populations, whilst minimizing the use of agrochemical sprays. The anthocorid *Anthocoris nemoralis* and the European earwig *Forficula auricularia* are particularly effective at controlling pear psyllid populations during the summer months. Despite the effectiveness of both natural enemies, there is a lack of understanding on whether both species should be promoted together or separately, due to the risk of intraguild predation (IGP) or interference competition. Furthermore, abiotic factors including temperature may influence both behaviors, altering activity level and niche overlap. Although IGP and interference

competition have been documented between multiple species of natural enemies neither have been studied between these two specific predators. Using microcosm experiments, olfactometer assays and survival analyses this study demonstrated whether *A. nemoralis* and *F. auricularia* can be used in synchrony to control pear psyllid. Results indicated that IGP is present; *F. auricularia* will consume *A. nemoralis* when predators are not spatially separate and in absence of psyllid prey. There was no evidence for interference competition, although both predators consumed more prey at higher temperatures. This confirms that pear growers can encourage both predators for the control of pear psyllid without losing predation efficacy.

**Keywords** Pear psyllid · *Cacopsylla pyri* · Natural enemies · Interference competition · Temperature · Survival analysis · Olfactometry · Intraguild predation · Anthocorids · Earwigs

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10905-024-09863-w>.

L. A. Reeves (✉) · M. P. D. Garratt · D. Senapathi  
School of Agriculture, Policy and Development, Centre for Agri-Environmental Research, University of Reading, Reading, Berkshire RG6 6AR, UK  
e-mail: l.reeves@pgr.reading.ac.uk

M. T. Fountain  
NIAB, New Road, East Malling, Kent ME19 6BJ, UK

## Introduction

Pear psyllid (*Cacopsylla pyri*), is the dominant pest of UK pears, with an estimated cost of £5 million per annum (AHDB 2012). These phloem feeding pests are resistant to a number of commonly available pesticides (Erler 2004; Sek Kocourek and Stará 2006); furthermore multiple insecticides used in psyllid control have been withdrawn for UK usage in the past decade (Hertfordshire University 2023;

HSE 2023). Therefore, integrated pest management (IPM) has become more widespread for controlling psyllid in pear orchards (DuPont and John Strohm 2020; Nottingham et al. 2022), focusing on keeping pest populations below economic threshold, whilst minimizing chemical input and disruption to agroecosystems (Moorthy and Kumar 2004). Biological control is a common technique used in pear psyllid IPM (Civolani 2012; DuPont and John Strohm 2020). Biocontrol can be augmentative; where a predator or parasitoid is usually commercially reared and mass released in order to manage pest populations (Collier and Van Steenwyk 2004; Van Lenteren 2012). The anthocorid *Anthocoris nemoralis* is a key biocontrol agent reared and available for mass release (Bioplanet 2023; Koppert 2023), helping to control *C. pyri* populations when wild populations are slow to build up in orchards. By contrast conservation biocontrol promotes the preservation and enhancement of wild populations of natural enemies (Naranjo 2001). The enhancement of natural enemies such as the European earwig (*Forficula auricularia*), has been recommended to improve pest control in orchards (Belien et al. 2012; Fountain et al. 2013; Hanel et al. 2023; Solomon et al. 2000), with Wignests (wooden shelters for earwigs) commercially available to growers within the UK, which encourage earwigs to forage in the tree canopy where pear psyllids are present (Shaw et al. 2021).

Increased predator diversity has been shown to enhance prey suppression in several agroecosystem studies (Snyder et al. 2008, 2006; Tylianakis and Romo 2010), especially if predators show spatial or temporal niche separation or respond differently to abiotic factors (Snyder et al. 2008); as the pest population can be controlled throughout the year, with other predator guilds continuing to control pests when some species are less abundant. However, high natural enemy diversity is not always beneficial (Snyder and Wise 2001); if species occupy similar niches then interference competition (when one predatory species reduces prey capture for a second predator species) (Stiling and Cornelissen 2005) or intraguild predation (IGP, where different predators consume each other, in addition to their target prey) is more likely (Jonsson et al. 2017). Furthermore, abiotic factors such as temperature can increase the likelihood of IGP or interference competition due to increased niche

overlap (Barton and Schmitz 2009; Schmitz and Barton 2014).

With summer temperatures predicted to increase by as much as 5.1 °C under the high emissions scenario by 2070 (MetOffice 2022) climate change is likely to impact insect behavior, activity and prey consumption (Karuppaiah and Sujayanad 2012). Prey consumption may increase under higher temperatures due to an elevated metabolism (Yuan et al. 2009); increasing demand for energy and nutrients (Frances and McCauley 2018; Schmitz and Barton 2014), this could also increase the risk of IGP if alternative prey sources aren't available. Climate change can also alter predator behavior; Barton and Schmitz (2009) investigated the niche overlap of two predatory spiders *Phidippus rimator*, and *Pisaurina mira* and their grasshopper prey (*Melanoplus femurrubrum*). Under ambient temperatures spiders filled spatially separate niches but under elevated temperatures (+3 °C) *P. mira*, moved downwards in the plant canopy, whereas *P. rimator* did not shift spatially, leading to niche overlap and IGP. *Phidippus rimator* was consumed by *P. mira* in all elevated temperature replicates. This led to a higher grasshopper density and reduced biomass of herbs in the +3 °C treatment compared to the control. Thus, it is important to consider how predator interactions may change with respect to climatic warming, helping us to predict whether current biological control agents will still be effective predators under future temperature scenarios.

In pear orchards both *A. nemoralis* and *F. auricularia* are key biological control agents; *F. auricularia* has a maximal consumption rate of approximately 10 mg of psyllid eggs or nymphs per day (Lenfant et al. 1994), whilst an average *A. nemoralis* female has a maximum consumption rate of 14.5 nymphs per day (Reeves et al. 2023) or 5000 *C. pyri* eggs in its lifetime (Yanik and Ugur 2004). However, a key question is whether both *A. nemoralis* and *F. auricularia* can be used in combination within an agroecosystem, or if IGP or interference competition will reduce their efficacy as natural enemies. This will allow growers to decide whether to release *A. nemoralis* and enhance *F. auricularia* populations, or if only one species should be encouraged, to optimize pest management. Both *A. nemoralis* and *F. auricularia* show temporal overlap; adult anthocorids migrate into orchards in April–May from surrounding hedgerows (Nagy et al. 2008; Reeves et al. 2023), eggs are laid

and anthocorid populations peak mid-summer (Nagy et al. 2008; Scutareanu et al. 1999). European earwigs start to appear in pear trees in May; stage three and four earwig nymphs are arboreal and show population peaks in June, whilst adults peak in mid-July (Gobin et al. 2008; Moerkens et al. 2009, 2011). Thus, there is the potential for niche overlap in late spring and throughout the summer when effective pear psyllid control is most importance.

IGP is likely to be unidirectional (only one predator consumes the other) rather than bidirectional between these two species, as larger natural enemies often predate on those with smaller body sizes (Yano 2006). Adult earwigs (length 13–14 mm) and all arboreal nymph stages (9–11 mm) are significantly larger than adult *A. nemoralis* (3.5–4 mm) (Capinera 2008; Reeves et al. 2023). *Forficula auricularia*, has a varied diet of insect, animal and plant material (Helsen et al. 1998), thus there is potential for earwigs to consume other natural enemies. Weak IGP has been documented between *F. auricularia* and young ladybird larvae (*H. axyridis*) when pest density was low (Dib et al. 2020), and between *A. nemoralis* and several coccinellid species (Batuecas et al. 2022). IGP has yet to be studied between *F. auricularia* and *A. nemoralis*. However, earwigs are nocturnal foragers (Kölliker 2007; Suckling et al. 2006), demonstrating diurnal sheltering behavior when other natural enemies are active (Lame 1974), so it may be less likely that earwigs and anthocorids interact directly, due to differences in activity period.

Natural enemies often rely on “infochemicals”; chemical compounds which carry information and can be used to help locate prey (Hatano et al. 2008; Vet and Dicke 1992). These chemical signals can be HIPVs (herbivore-induced plant volatiles) emitted from herbivorized plants (Allison and Daniel Hare 2009; Valle et al. 2023) or kairomones emitted by pests themselves, on which natural enemies eavesdrop (Ayelo et al. 2021). Infochemicals may also play a role in IGP and interference competition; they may allow predators to actively avoid areas with hetero-specific predators or be attracted to them if alternative prey sources are scarce (Gnanvossou et al. 2003; Tapia et al. 2010). Moreover, temperature can alter signal composition, transmission and perception (Becker et al. 2015; Yuan et al. 2009), as the volatility and diffusion rates of VOCs (Volatile organic compounds) are temperature dependent (Niinemet

et al. 2004; Yuan et al. 2009). Earwigs are dependent on olfactory cues and signals; *F. auricularia* relies on chemical signals in offspring care (Mas 2011) and also release an aggregation pheromone (Hehar et al. 2008; Walker et al. 1993). Whilst the earwig species *Doru luteipes* Scudder, responds to HIPVs released by herbivorized maize plants (Naranjo-Guevara et al. 2017). However, the use of infochemicals in the location of psyllid prey by *F. auricularia* has not been investigated.

Combining microcosm experiments, olfactometry assays and survival analyses, this study aims to assess whether *F. auricularia* and *A. nemoralis* in combination could deliver better control of pear psyllid, or if IGP or interference competition is likely to disrupt biological control, all experiments took place at two temperature regimes based on current summer temperatures and those predicted under the high emissions scenario (RCP8.5) for 2080. Our study tested four hypotheses: (1) *F. auricularia* demonstrates unidirectional IGP for *A. nemoralis* when alternative prey is absent, (2) *F. auricularia* and *A. nemoralis* show similar rates of psyllid consumption in the same microcosm, compared to total prey consumption of *F. auricularia* and *A. nemoralis* in separate microcosms (additive), demonstrating the absence of interference competition, (3) the likelihood of IGP is dependent on sex and stage of *F. auricularia*, and (4) *F. auricularia* shows a positive olfactory response to *C. pyri* prey but not to *A. nemoralis*, highlighting a preference for psyllid prey.

## Materials and methods

### Pear psyllid, earwig and anthocorid husbandry

Pear psyllid hardshell nymphs (L4–L5, the fourth or fifth nymph stage in a pear psyllid’s life history) were collected from cv. Conference pear trees (*Pyrus communis*) at NIAB East Malling (51.2885° N, 0.4383° E). Nymphs were removed from trees daily, using a soft, fine tipped paintbrush, to minimize damage. Prior to nymph collection the orchard was sampled for psyllid adults for several weeks via beat tray sampling of 30 trees; to check whether the majority of pear psyllids were *C. pyri*. Adult psyllids were identified, based on genitalia using a light microscope. A large proportion of individuals were

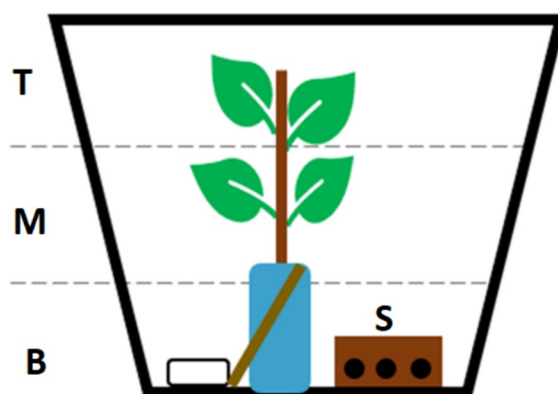
*C. pyri* (95.92%) but *C. pyricola* were also present but in small numbers. Hence, the majority of the nymphs used within experiments were likely *C. pyri*, but it is difficult to distinguish between the two species at juvenile stage. For beat tray sampling a pear tree branch was tapped with a foam-covered stick, with a white tray (260 mm by 460 mm) held underneath. Adult *C. pyri* were kept in ventilated Tupperware pots (diameter 105 mm, height 75 mm) containing pear shoots (70 mm in length) in water tubes (40 mm height, 15 mm diameter) to keep moist. Individuals were kept in a controlled temperature (CT) cabinet at 12.1 °C during dark and 22.0 °C during light conditions. Semi-mature pear psyllid eggs (yellow-white in color) were collected from the Tupperware pots daily, these were used for feeding anthocorids. Earwigs were fed dry cat food and mealworms; water was available in a small plastic dish. *Cacopsylla pyri* adults and nymphs were identified to species level using the Psyllid key from RLP Agrosience (Agrosience 2022).

A batch of 500 *A. nemoralis* adults were ordered from the biocontrol company Koppert each week (Anthobug) of the study. These were approximately 4–10 days after their final molt, when used in all experiments. Anthocorids were kept in a ventilated plastic container, with the carrier material they arrived in and fed *C. pyri* eggs daily. These were kept in a CT cabinet at 12.1 °C during dark and 22.0 °C during light conditions. Five batches of anthocorids were used for survival analyses and microcosm experiments, 4 were used for olfactometer assays. Female anthocorids were identified using a light microscope based on differences in genitalia. Third and fourth instar *F. auricularia* nymphs and adults were collected from NIAB East Malling at the beginning of each week from orchard Wignests (Russel-IPM 2023) and using beat trays. Third and fourth instar nymphs and adults were chosen as these are the arboreal stages (Moerkens et al. 2009), thus are more important for *C. pyri* predation in pear orchards. Earwigs were housed in Tupperware containers (diameter 105 mm, height 75 mm) at 12.1 °C during dark and 22.0 °C during light conditions in CT cabinets, which also contained a pear shoot in a water tube to keep moist, a small water dish and a wooden wignest (59 mm, length 48 mm width, 14 mm height) for shelter.

## Microcosm experiments

Microcosms consisted of a ventilated Tupperware pot (diameter 105 mm, height 75 mm), containing a pear shoot with four leaves collected from cv. Conference pear trees (*Pyrus communis*), kept moist in a plant holder (20 mm diameter, 57 mm height), with a small stick attached so that natural enemies could crawl to the top of the holder, a wignest for earwigs to shelter in (59 mm, length 48 mm width, 14 mm height) and a small dish of distilled water (20 mm diameter, 10 mm height) (Fig. 1). For the purposes of recording whether there was spatial overlap between earwigs and anthocorids, the microcosm was divided into four different zones: top (T), middle (M), bottom (B) and wignest shelter (S).

Adult anthocorid females and earwigs were starved for 24 h at one of the two temperature regimes, current (12.1 °C during dark and 22.0 °C during light conditions) or RCP8.5 (15.9 °C during dark and 26.4 °C during light conditions) in a microcosm, within a controlled temperature cabinet. There were seven treatments: 1. earwig, anthocorid and *C. pyri* nymphs, 2. earwig and *C. pyri* nymphs, 3. anthocorid and *C. pyri* nymphs, 4. earwig, anthocorid no prey, 5. earwig no prey, 6. anthocorid no prey and 7. control with no predators, each treatment only contained one individual of the species to avoid the impacts of



**Fig. 1** A ventilated microcosm containing a wignest (brown box) and a pear tree shoot with four leaves collected from cv. Conference pear trees (*Pyrus communis*), kept moist in a plant holder (blue tube), with a small stick attached so that natural enemies can crawl to the top of the holder. The white dish contained distilled water. Four different areas were labelled within the microcosm; top (T), middle (M), bottom (B) and wignest shelter (S)



intraspecific competition. After 24 h, 100 L4-5 stage *C. pyri* nymphs and anthocorids were added to the required treatments. The prey density was above the combined natural enemies' saturation points for maximal prey intake, so prey consumption could be compared between treatments. Microcosms were monitored after 2 h dark and 2 h light for two minutes to check the position of the earwig or anthocorid (top, middle, bottom or shelter) and the behavior demonstrated (Antennating, Cleaning, Feeding, Interacting, Moving and Stationary). A red-light torch was used during behavioral observations to minimize disturbance. After 24 h natural enemies were removed and whether they were alive was recorded. The number of live *C. pyri* nymphs was also recorded. Each treatment was replicated ten times.

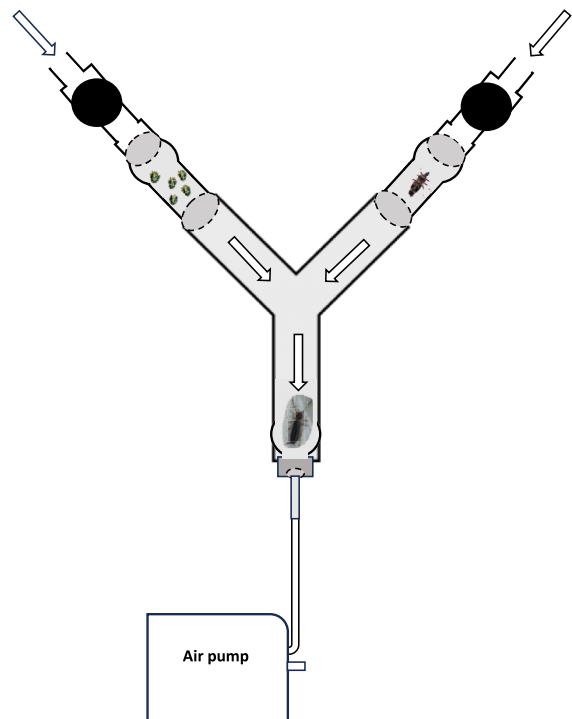
### Survival analyses

For survival analyses, *F. auricularia* and adult *A. nemoralis* were starved for approximately 24 h at either Current (12.1 °C during dark and 22.0 °C during light conditions) or RCP8.5 (15.9 °C during dark and 26.4 °C during light conditions) temperature regimes in controlled temperature (CT) cabinets, in separate triple vented Petri dishes (55 mm in diameter) containing a leaf disk of *P. communis* 'Conference' (20 mm in diameter) and moist kitchen towel. The Petri dish was sealed with plastic paraffin film to prevent insects escaping and returned to the CT cabinet. After 24 h the earwig was added to the Petri dish containing the anthocorid and resealed, each treatment only contained one individual of each predator species to avoid the impacts of intraspecific competition. There were five different treatments (stage 3 nymph, stage 4 nymph, adult female, adult male *F. auricularia* and a control where no earwig was added). The Petri dish was checked after 6 h, 12 h and then at 12 h intervals, to see if anthocorid and earwig were still alive or had been consumed, over a period of 10 days. The petri dish was sprayed with distilled water every 24 h, to keep the leaf disc moist. There was a total of 10 replicates for each treatment and temperature, giving a total of 100 observations.

### Olfactometer assays

For olfactometer assays, female earwigs were starved for 24 h in CT cabinets at Current and RCP 8.5

temperature treatments. Glass chambers at the end of each arm contained either *C. pyri* nymphs and adult *A. nemoralis*, *C. pyri* nymphs and nothing and adult *A. nemoralis* and nothing, as control treatments. Experimental set-up of the glass Y-tube olfactometer (main arm, 15 cm long; side arms: 10 cm long; 0.9 cm internal diameter) is as shown in Fig. 2. Air was pumped through for 10 min prior to releasing the earwig, using a Dymax 8 vacuum pump, average air flow was 1.6 L/min. Each arm had an activated carbon filter to remove other odors and VOCs from the air. The earwig was then added to the base of the olfactometer, whilst air was still being circulated. This was videoed in darkness with a red-light torch over the equipment, in the CT cabinet to minimize disturbance. After 10 min video footage was viewed and the time taken for the earwig to reach the end of one of the arms was recorded, as well as the choice made (Left or Right arm). Any individuals that did



**Fig. 2** Experimental set-up for the Y-tube olfactometer assays, earwigs were placed at the start of the tube and given a binary choice between two prey types (*Cacopsylla pyri* nymphs and adult *Anthocoris nemoralis*, *Cacopsylla pyri* nymphs and nothing and adult *Anthocoris nemoralis* and nothing). Arrows represent the direction of air flow, black dots are activated carbon filters and dashed circles are mesh to stop prey escaping

not make a choice after 10 min were disregarded; 2 individuals were disregarded during the experiment. After each replicate, the equipment was washed using 70% ethanol and distilled water, then dried. The position of prey on the left or right arm was randomized. There were 20 replicates for each treatment and temperature giving a total of 120 observations.

### Temperature regimes

The two temperature treatments were determined based on the current average minimum and maximum June–August temperature (1990–2020) and the average minimum and maximum June–August temperatures predicted in 2080, based on the RCP8.5 (high emissions) scenario (Table. S1). A 2080 timeframe was chosen as this year is commonly used in studies predicting future trophic interactions (Aartsma et al. 2019; Duffy 2014; South et al. 2018), thus the results of this paper can be compared to others. June–August temperatures were chosen as this is when anthocorids and earwigs are most abundant in pear orchards (Fields and Beirne 1973; Scutareanu et al. 1999). The current temperature was calculated using the average minimum and maximum June–August temperatures (1990–2020) from East Malling weather station (51.288° N, 0.448° E) in Kent. To calculate future temperatures for 2080, data was extracted using the UK Climate Projections User Interface, based on UKCP18 projections (UKCP 2021). The predicted increase for minimum and maximum air temperature at 1.5 m for 2080 was calculated for June to August (baseline scenario 1981–2000) for a 25 km×25 km region in Kent, surrounding East Malling, this temperature was calculated for the RCP8.5 scenario and added to the average minimum and maximum 1981–2000 June–August temperature.

The first CT cabinet was set at 12.1 °C during dark and 22.0 °C during light conditions (Current temperature treatment) and the second was set at 15.9 °C during dark and 26.4 °C during light conditions (RCP8.5 temperature treatment). The CT cabinets had two containers half-filled with water to keep humidity constant. Temperature and humidity were monitored using OM EL USB 2 dataloggers (OMEGA 2023). The daylight cycle within the cabinets was 8 h dark followed by 16 h light, based on average summer day length in the UK.

Data analyses.

### Intraguild predation and prey consumption

To compare prey consumption between natural enemy treatments the total prey eaten for single earwigs and anthocorids in the same batch were added together (additive), then compared to the corresponding treatment containing both earwigs and anthocorids (combination) in the same batch. To account for natural mortality in each treatment, average mortality from the control treatment (for each temperature) was subtracted from all other treatments. Any microcosms where a predator had died during the experiment were removed from the analysis. As data was normally distributed a Two-way ANOVA was carried out to test if there was a significant difference in prey mortality depending on treatment, temperature and interaction between temperature and treatment. For pairwise comparisons between treatments a Tukey HSD test was done, all statistical analysis were done using base R version 4.3.0 (R 2023), plots were generated using the package ‘ggplot2’ (Wickham et al. 2016).

### Behavioral observations, activity and position within the microcosm

For behavioral observations, stacked bar charts were created using the ‘ggplot2’ package in R. These show the percentage of time *A. nemoralis* and *F. auricularia* spent exhibiting certain behaviors (feeding, moving, interacting, cleaning, stationary and antennating) over the 2-min time period, for both light and dark observations. Stacked bar charts also show time spent at different heights within the microcosm (top, middle, bottom or shelter). For statistical analysis a Linear discriminant analysis occurred (LDA) to define the positional and behavioral profiles of earwigs and anthocorids during the night and day. Discriminant function analyses are commonly used in behavioral studies to demonstrate whether species show different behavioral profiles or niches, or whether there is overlap between groups (Kramer et al. 2009; Martha and Jones 2002). In an LDA the probability of individuals belonging to the different groups is calculated; individuals are then assigned to groups with the highest probability score. The LDA was performed using the “MASS” package (Ripley et al. 2013) and biplots were created using the “ggord” package (Beck 2017). The predictor variables for the analysis were the behaviors “Antennating,



Cleaning, Feeding, Moving and Stationary” and positions in the microcosm “Shelter, Bottom, Middle and Top”, with time of day and predator species as dependent variables. The interacting behavior was excluded due to the low frequency of observations. The data were split and 80% of it were used for training the model and 20% were used to test the model, the `preProcess()` function was used to center and scale the data, in order to standardize it. The `lda()` function was used to perform the analysis, producing coefficients of linear discriminants. The `predict()` function was used to predict classes for observations within the training dataset, so that model accuracy could be calculated. Activity of each predator was calculated by adding the total time spent (s) “Antennating, Cleaning, Feeding, Interacting, Moving and Stationary”. As variables were normally distributed, a multi-way ANOVA was carried out to observe if there was a significant difference in predator activity depending on treatment, temperature and time of day (after 2 h dark or after 2 h light), or an interaction between the variables. For pairwise comparisons between treatments a Tukey HSD test was done.

#### Olfactometry assays and survival analysis

Differences in choice number by *F. auricularia* between 1) the control odor source and *A. nemoralis*, control odor source and 2) *C. pyri* nymphs and 3) *A. nemoralis* and *C. pyri* nymphs were tested using a two-sided binomial exact test with  $H_0=0.5$ , using the `binom.test()` function (R 2023), as this analysis is commonly used on binary count data from two-arm olfactometers (Meza et al. 2020; Roberts et al. 2023). Differences in choice number depending on temperature was analyzed using a  $\chi^2$  goodness of fit test. Differences in time taken to make a decision depending on temperature and odor source were analyzed using a Two-way ANOVA, as data were normally distributed.

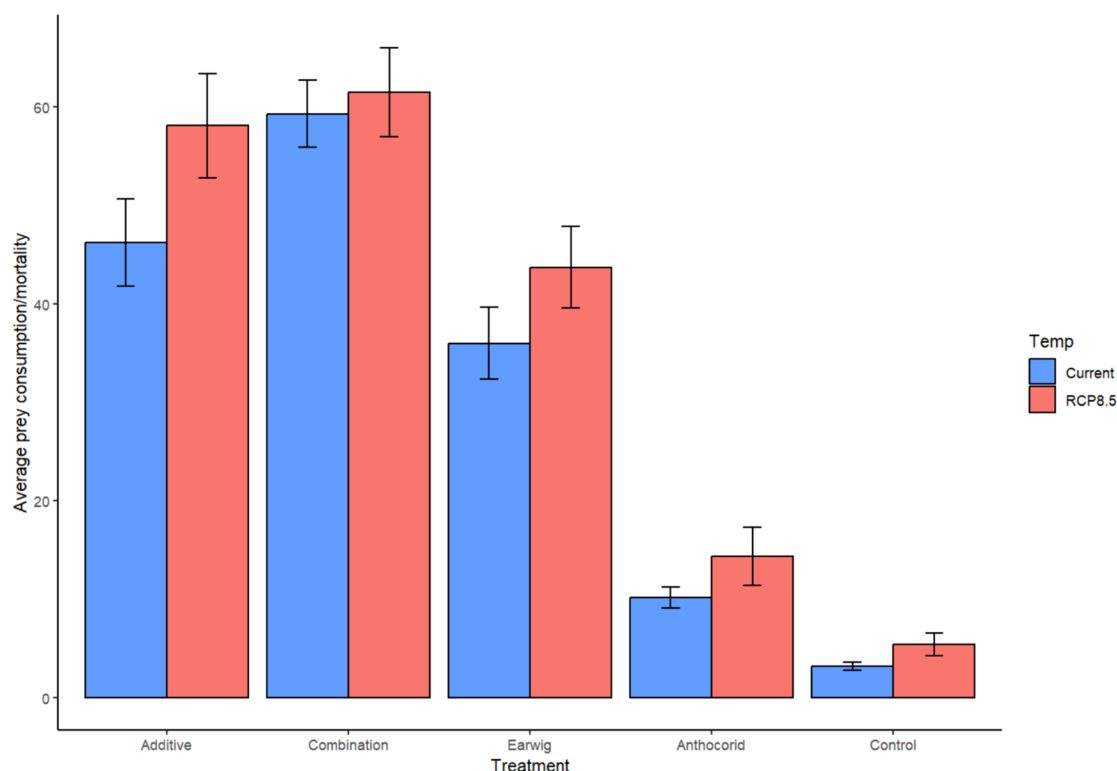
Survival analyses were performed using the “survival” and “survminer” packages (Kassambara et al. 2017; Therneau and Lumley 2013). This method of analysis is common in insect survival studies (Boff et al. 2021; Hüftlein et al. 2023; Pal et al. 2022). By means of the `survfit()` function a survival analysis was conducted, using the Kaplan–Meier estimate of survival probability at a given time (hrs), depending on temperature (current or RCP8.5) and stage of earwig

(stage 3, stage 4, adult female, adult male or control). Significant between-group differences were tested using a log-rank test, using the `survdiff()` function to highlight whether there was a significant difference in survival time depending on temperature or stage of earwig. For pairwise comparisons the function `pairwise_survdiff()` was used, with the Benjamini–Hochberg correction to account for multiple testing. For plotting survival curves the function `ggsurvplot()` from the “survminer” package was used.

## Results

### Prey consumption and Interference competition

The number of nymphs consumed significantly differed depending on treatment ( $F_{(4,79)}=71.61$ ,  $p<0.001$ ), a Tukey HSD test demonstrated that earwigs consumed significantly more *C. pyri* nymphs than anthocorids ( $p<0.001$ ), that earwigs and anthocorids combined consumed more than single Earwig ( $p<0.001$ ) or Anthocorid ( $p<0.001$ , Fig. 3). However, the number of *C. pyri* nymphs consumed in the combined treatment (earwig and anthocorids in the same microcosm) did not significantly differ from earwig+anthocorid in separate microcosms (additive),  $p=0.171$ , suggesting that interference competition is unlikely at high prey density. The interaction between temperature and treatment was non-significant ( $F_{(4,79)}=0.581$ ,  $p=0.677$ ). For natural mortality without predators present there was an average of  $3.20 \pm 0.84$  (SD) dead *C. pyri* nymphs per sample at Current temperatures and  $5.40 \pm 2.61$  (SD) at RCP8.5 temperatures. These averages were subtracted from all treatments to account for natural mortality. One anthocorid died during the course of this experiment, therefore these data were removed from the analysis. Significant differences between treatments and temperatures were found using a Two-way ANOVA; results indicated that there was a significant difference in prey consumption depending on temperature ( $F_{(1,79)}=5.12$ ,  $p=0.0264$ ), with an average of  $43.70 \pm 13.15$  (SD) nymphs consumed by earwigs at the higher temperature (RCP8.5) compared to the lower temperature (Current) with an average of  $36.0 \pm 11.67$  (SD) nymphs consumed (Fig. 3). Higher numbers of nymphs were also consumed by anthocorids at the high temperature ( $14.4 \pm 9.33$ ,



**Fig. 3** The mean ( $\pm$  SE) number of *Cacopsylla pyri* nymphs consumed by natural enemies in Earwig, Anthocorid and Combination (an earwig and anthocorid in the same microcosm) treatments, as well as the average prey consumption of earwig + anthocorid in separate microcosms (Additive) and a con-

trol treatment representing average natural mortality. Error bars represent the  $\pm$  SE for each treatment. The control treatment for each temperature was subtracted from each of the predator treatments to account for natural mortality,  $n=80$

SD) compared to the lower temperature treatment ( $10.2 \pm 3.37$ , SD).

#### Intraguild predation and survival analysis

After 8.5 days all anthocorids were dead at all temperatures and treatments. For treatments containing earwigs, 45.0% of the anthocorids were eaten, no earwigs were consumed or injured by anthocorids during this timeframe. The survival rate of anthocorids differed depending on treatment and temperature ( $\chi^2=25.06$ , d.f.=5,  $p<0.001$ ), in all treatments anthocorids in combination with earwigs had a significantly lower survival rate than those alone ( $p=0.0448$ , Table 1) and anthocorid survival rate significantly differed depending on temperature ( $p=0.001$ ), with higher temperatures leading to lower average survival rates, however this was dependent on stage (Table 1, Fig. 4). Pairwise comparison tests

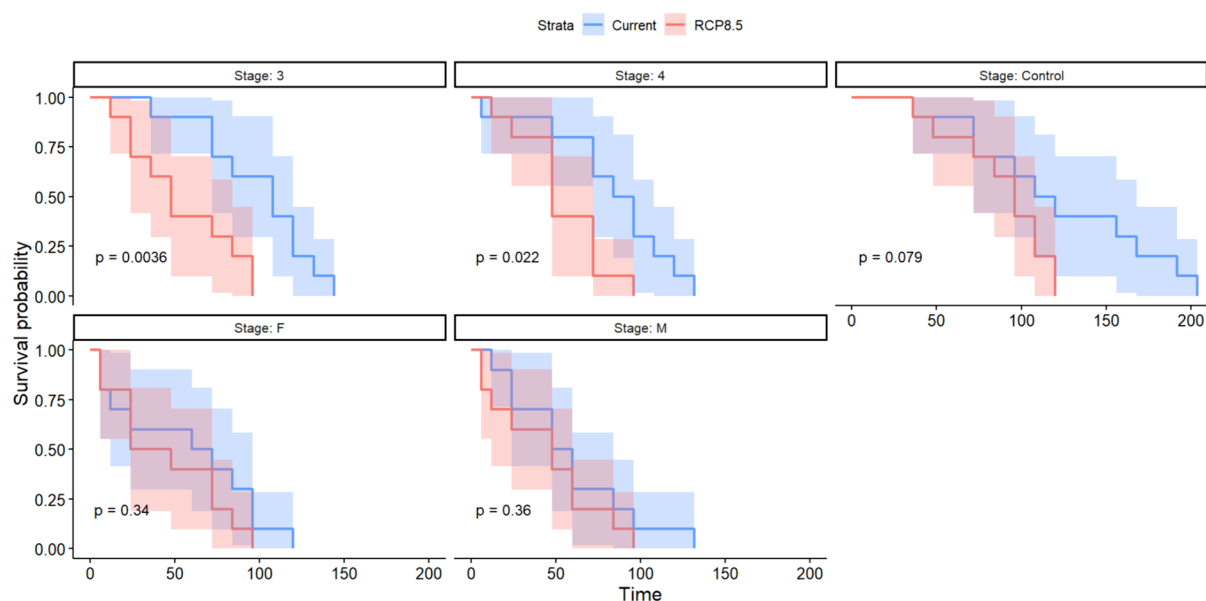
with the BH correction applied found that Current and RCP8.5 control treatments significantly differed from all other treatments containing both anthocorids and earwigs. Mortality rates of anthocorids did not significantly differ depending on sex of earwig at Current ( $p=0.952$ ) or RCP8.5 ( $p=0.909$ ) temperature treatments, based on pairwise comparison tests.

#### Activity, behavior and position within the microcosm

Predator activity significantly differed depending on the interaction between treatment and time of day (Two-way ANOVA:  $F_{(3,144)}=29.97$ ,  $p<0.001$ , Fig. 5); a Tukey HSD test demonstrated that earwigs were significantly more active at night compared to during the day ( $p<0.001$ ); conversely, anthocorids were significantly more active during the day compared to at night ( $p=0.030$ ). However, no significant differences were found between time spent

**Table 1** Average and median survival times (hrs) for anthocorids *Anthocoris nemoralis* depending on temperature and stage of earwig *Forficula auricularia* (control with no earwig present, stage 3, stage 4 juvenile, adult male and adult female). Standard error (SE) and upper and lower 95% confidence intervals are also provided

Stage	Temperature	Mean survival	SE	Median survival	LCL	UCL
Control	Current	122.4	16.78	114	72	168
	RCP8.5	88.8	8.69	96	72	108
Stage 3	Current	99.6	9.90	108	72	120
	RCP8.5	54.0	9.33	48	24	84
Stage 4	Current	83.4	11.01	90	72	108
	RCP8.5	54.0	7.45	48	48	72
Adult F	Current	57.6	12.76	66	12	96
	RCP8.5	45.6	9.98	36	24	72
Adult M	Current	58.8	11.06	54	24	84
	RCP8.5	44.4	9.57	48	12	60

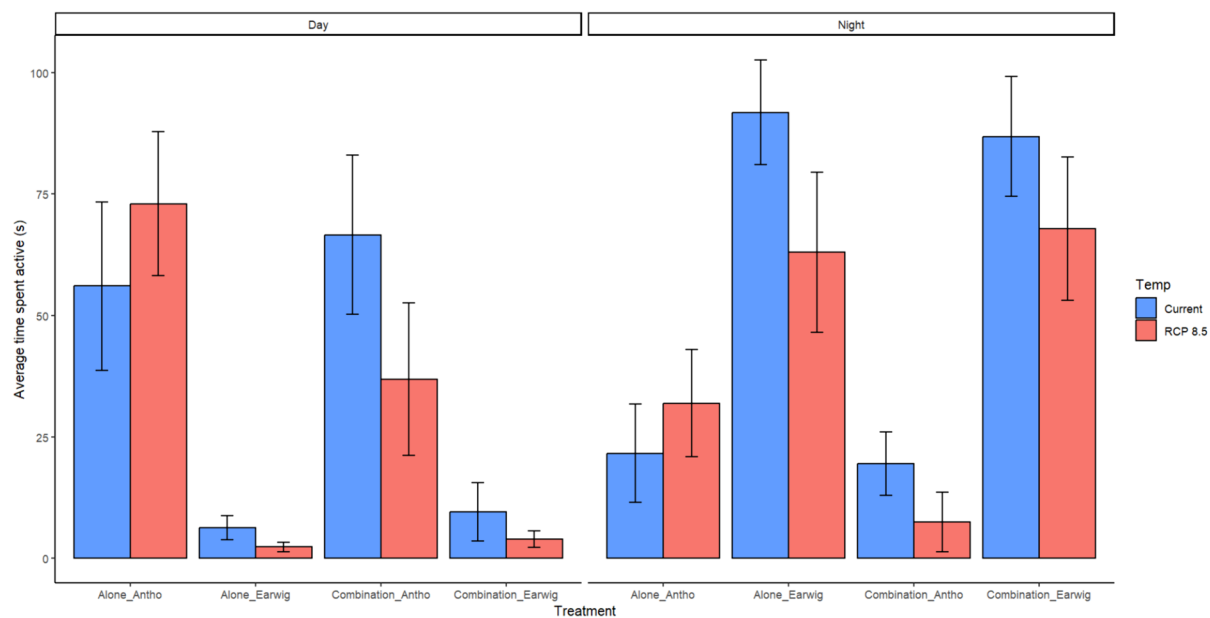


**Fig. 4** Probability of survival over time (hrs) depending on temperature (Current or RCP8.5) and stage of earwig *Forficula auricularia* (stage 3, stage 4, adult female, adult male and control with no earwig). Red (RCP8.5) and blue lines (Cur-

rent) represent the mean proportion of surviving anthocorids *Anthocoris nemoralis*, with shaded areas representing the confidence intervals

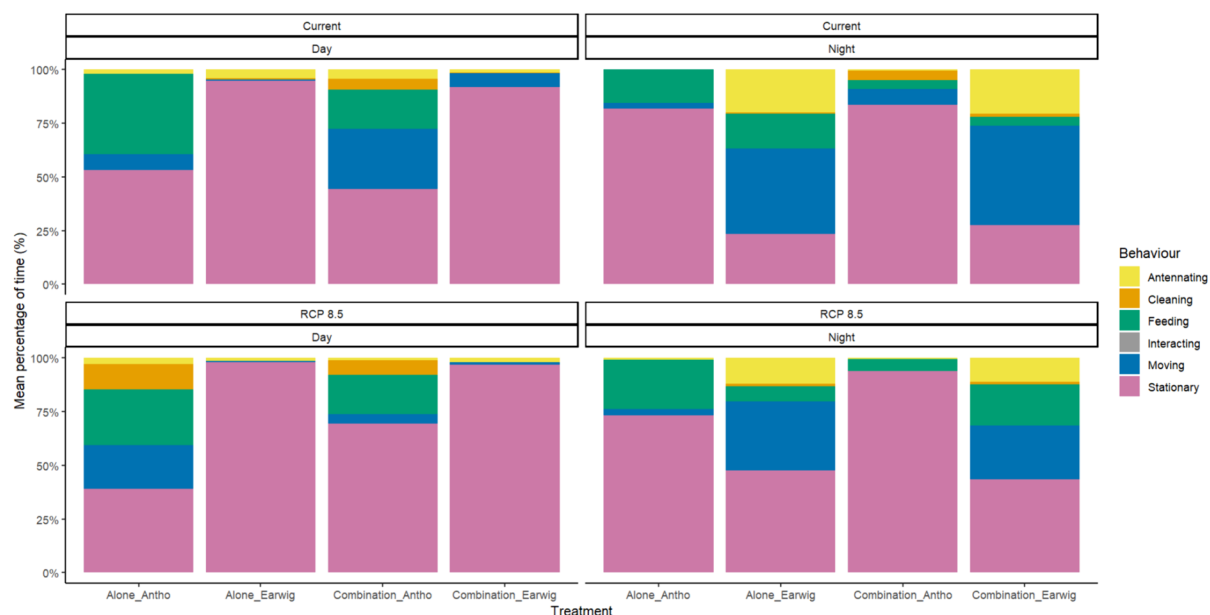
active for earwigs alone or in combination during the night ( $p=1.000$ ) or for anthocorids alone or in combination during the day ( $p=0.955$ ), indicating that the presence of another predator is unlikely to interfere with their activity level. Furthermore, temperature (Two-way ANOVA:  $F_{(1,144)}=2.417$ ,  $p=0.122$ ) or the interaction between treatment and temperature (Two-way ANOVA:  $F_{(1,144)}=2.417$ ,  $p=0.152$ ) did not significantly impact time spent active.

The time spent stationary significantly differed depending on predator and time of day (Fig. 6, Kruskal Wallis:  $\chi^2=52.70$ ,  $p<0.001$ ); earwigs spent more time stationary during the day than at night (Pairwise Wilcoxon:  $p<0.001$ ), and more time stationary than anthocorids during the day ( $p<0.001$ ). However, time spent stationary did not significantly differ depending on temperature (Kruskal Wallis:  $\chi^2=1.45$ ,  $p=0.229$ ) or whether the predator was alone or in combination (Kruskal Wallis:  $\chi^2=0.872$ ,



**Fig. 5** The mean activity levels (total time spent feeding, cleaning, interacting, moving and antennating in seconds) of anthocorid (*Anthocoris nemoralis*) and earwig (*Forficula auricularia*) predators in combination (both earwig and

anthocorid in the same microcosm) and alone (a microcosm containing only one predator), for predators provided with *Cacopsylla pyri* nymphs (food treatment),  $n=80$ . Error bars represent the  $\pm$ SE for each treatment



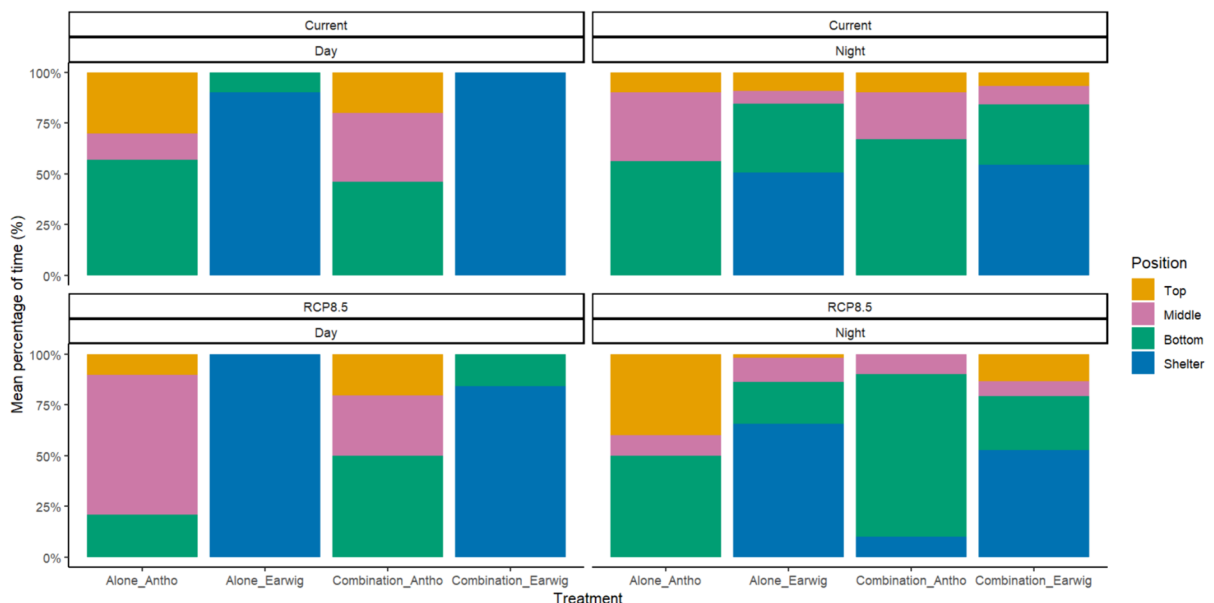
**Fig. 6** Mean percentage of time spent feeding, cleaning, interacting, moving and antennating for anthocorid (*Anthocoris nemoralis*) and earwig (*Forficula auricularia*) predators in combination (both earwig and anthocorid in the same micro-

cosm) and alone (a microcosm containing only one predator), depending on temperature, for predators provided with *Cacopsylla pyri* nymphs (food treatment),  $n=80$

$p=0.350$ ). Interactions between predators were very uncommon with only two brief interactions observed between earwigs and anthocorids across the entire experiment. Feeding behavior also differed depending on treatment (Fig. 6, Kruskal Wallis:  $\chi^2=20.33$ ,  $p<0.001$ ), earwigs spent significantly more time feeding at night compared to daytime (Pairwise Wilcoxon:  $p<0.001$ ). Time spent feeding did not significantly differ depending on temperature (Kruskal Wallis:  $\chi^2=0.0030$ ,  $p=0.956$ ), or a significant difference in feeding depending on whether the predator was alone or in combination (Kruskal Wallis:  $\chi^2=3.94$ ,  $p=0.051$ ). Time spent antennating also differed depending on treatment (Fig. 6, Kruskal Wallis:  $\chi^2=66.64$ ,  $p<0.001$ ), earwigs spent significantly more time antennating at night compared to daytime (Pairwise Wilcoxon:  $p=0.038$ ), whereas anthocorids spent more time antennating in the day than at night. Time spent antennating did not significantly differ depending on temperature (Kruskal Wallis:  $\chi^2=0.268$ ,  $p=0.605$ ), or a significant difference in antennating depending on whether the predator was alone or in combination (Kruskal Wallis:  $\chi^2=0.0004$ ,  $p=0.985$ ). Findings were similar for no food treatments (Fig S1), except no feeding behavior

was demonstrated by anthocorids or earwigs. Once again temperature and whether the predator was alone or in combination did not significantly affect time spent demonstrating these behaviors.

The time spent in the shelter within the microcosm differed significantly depending on predator and time of day (Fig. 7, Kruskal Wallis:  $\chi^2=129.58$ ,  $p<0.001$ ), earwigs spent significantly more time in the shelter than anthocorids during the night and day (Pairwise Wilcoxon:  $p<0.001$ ) compared to night-time. The temperature regime (Kruskal Wallis:  $\chi^2=0.107$ ,  $p=0.743$ ) and whether the predators were alone or in combination (Kruskal Wallis:  $\chi^2=0.0441$ ,  $p=0.834$ ) did not significantly impact the time spent within the shelter. Time spent in different locations for anthocorids was far more variable, on average anthocorids spent the majority of time at the bottom of the microcosm during the night and day (Fig. 7), this was significantly higher than earwigs (Kruskal Wallis:  $\chi^2=55.55$ ,  $p<0.001$ ). Time spent at the bottom did not significantly differ depending on temperature (Kruskal Wallis:  $\chi^2=1.05$ ,  $p=0.306$ ), time of day (Kruskal Wallis:  $\chi^2=55.55$ ,  $p=1.00$ ) or whether the predator was



**Fig. 7** Average percentage of time spent in different locations within the microcosm (top, middle, bottom and shelter) for anthocorid (*Anthocoris nermoralis*) and earwig (*Forficula auricularia*) predators in combination (both earwig and

anthocorid in the same microcosm) and alone (a microcosm containing only one predator), depending on temperature, for predators provided with *Cacopsylla pyri* nymphs (food treatment),  $n=80$

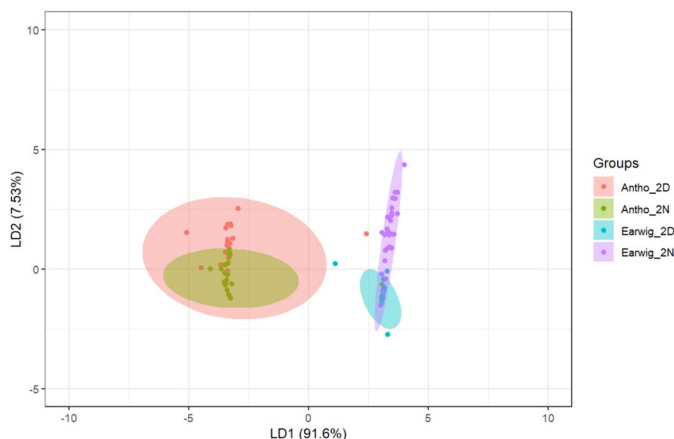
alone or in combination (Kruskal Wallis:  $\chi^2=0.136$ ,  $p=0.712$ ). Both predators spent a very low proportion of time in the middle of the microcosm, earwigs spent significantly more time in the middle during the night compared to the day (Kruskal Wallis:  $\chi^2=10.31$ ,  $p=0.0067$ ). However, all other variables were non-significant. Time spent at the top of the microcosm significantly differed depending on predator and time of day (Fig. 7, Kruskal Wallis:  $\chi^2=13.39$ ,  $p=0.004$ ), earwigs spent significantly more time at the top during the night than the day (Pairwise Wilcoxon:  $p=0.019$ ). Once again, temperature and predator combination did not significantly impact behavior. Findings were similar for no food treatments (Fig S2), earwigs spent a large proportion of time in the shelter whilst anthocorids spent most time in the bottom of the microcosm. Temperature and whether the predator was alone or in combination with another predator did not significantly affect time spent in a position.

For the behavioral analysis a linear discriminant analysis was undertaken; groups were significantly different from each other based on the behavioral and positional predictor variables (Wilk's  $\lambda=0.0665$ ,  $F=24.52$ ,  $df=3,156$ ,  $p<0.001$ ). With respect to model accuracy 78.13% of the observations within the test dataset were assigned to the correct group when using the predict function. However, despite the high model accuracy the

95% confidence intervals overlapped between groups (Fig. 8); there was overlap between earwigs at night and earwigs during the day, as well as anthocorids at night and anthocorids during the day. However, confidence levels for earwigs and anthocorid groups did not show any overlap with each other, suggesting a distinct spatial and behavioral niche for each species. The first linear discriminant (LD1) explained a large proportion (91.60%) of all between-class variance, whilst the second and third linear discriminants explained a much lower proportion of variance (Table 2). The predictor variables with the highest linear discriminant scores for LD1 were strong positive scores for stationary, and feeding behavior (Table 2).

#### Olfactometer assays.

For olfactometer assays there was a significant preference by earwigs for arms containing *C. pyri* nymphs compared to the control treatment (Binomial exact test:  $p=0.038$ ,  $N=40$ , Fig S3), 67.5% of the choices were for *C. pyri*. However, the preference for arms containing *C. pyri* nymphs compared to *A. nemoralis* was not quite significant (Binomial exact test:  $p=0.081$ ,  $N=40$ ), the preference between arms containing *A. nemoralis* compared to the control treatment was non-significant (Binomial exact test:  $p=0.430$ ,  $N=40$ ). There was no significant preference for left or right arms of the olfactometer (Binomial exact test:  $p=0.235$ ,  $N=120$ ).



**Fig. 8** A linear discriminant analysis based on position and behavior of predators; for anthocorids (*Anthocoris nemoralis*) during the day (Antho\_2D), anthocorids at night (Antho\_2N), earwigs (*Forficula auricularia*) during the day (Earwig\_2D) and earwigs at night (Earwig\_2N). Axes represent the first

(LD1) and second (LD2) linear discriminants, percentages show the proportion of between-class variance that is explained by the discriminant functions. Ellipses represent 95% confidence levels,  $n=80$



**Table 2** Results from the linear discriminant analysis, displaying the first 3 linear discriminants, based on five behavioral variables and four positional variables measured for anthocorid (*Anthocoris nemoralis*) and earwig (*Forficula auricularia*) predators. Proportion of trace represents the proportion of between-class variance explained by discriminant functions, whilst the coefficients of linear discriminants is the linear combination of predictor variables used within the LDA decision rule

Linear discriminant	LD1	LD2	LD3
Proportion of trace	0.916	0.0753	0.0087
Coefficients of linear discriminants			
Antennating	2.83	-16.35	-11.49
Cleaning	2.70	-18.54	-13.99
Feeding	7.17	-45.51	-33.03
Moving	6.30	-39.67	-28.81
Stationary	10.60	-68.29	-48.23
Shelter	2.96	-0.360	-0.450
Bottom	-0.240	0.0707	0.0358
Middle	-0.0863	-0.103	0.158
Top	-0.203	0.0736	-0.0821

There was no significant difference in arm choice depending on temperature for *A. nemoralis* and control ( $\chi^2=0.1023$ , d.f.=1,  $p=0.749$ ), *A. nemoralis* and *C. pyri* ( $\chi^2=0.440$ , d.f.=1,  $p=0.507$ ) and *C. pyri* and control ( $\chi^2=0.114$ , d.f.=1,  $p=0.736$ ). Temperature did not have a significant effect on time taken to choose an arm (Two-way ANOVA:  $F_{(1,114)}=0.182$ ,  $p=0.671$ ), neither did the odor source within the arm (Two-way ANOVA:  $F_{(2,114)}=0.546$ ,  $p=0.581$ ), or the interaction between temperature and odor source (Two-way ANOVA:  $F_{(2,114)}=1.561$ ,  $p=0.214$ ). On average, it took earwigs approximately  $26.14 \pm 47.07$  (SD) to make a decision at the low temperature treatment and  $22.81 \pm 38.06$  (SD) at the high temperature treatment.

## Discussion

We found unidirectional intraguild predation (IGP) between earwigs and anthocorids, as *A. nemoralis* was eaten by *F. auricularia* during survival analyses. IGP was exhibited by adult male and female *F. auricularia* and stage 3 and 4 juveniles. This was anticipated as larger generalist natural enemies usually predate on those with smaller body sizes (Yano 2006), and all earwig stages used were larger than

adult *A. nemoralis*. However, it is probable that IGP is only likely to occur if both predators are in close proximity, when alternative food sources are unavailable. This is evident in behavioral analyses, as there were few interactions observed between *A. nemoralis* and *F. auricularia*, within microcosms. Both predators occupy different behavioral niches with little positional overlap, as highlighted in the LDA analysis. Earwigs were more active at night and spent most of the day stationary in the Wignest shelter, whilst anthocorids were far more active during the day spending a large proportion of time at the bottom of the microcosm. This is supported by the scientific literature that earwigs are nocturnal (Kölliker 2007; Suckling et al. 2006), spending their free-foraging phase active during the night, whilst during the day they are inactive, hidden within shelters (Lame 1974). However, it is important to note that these were laboratory-based experiments containing a single individual of each species and only one prey density (100 nymphs) within the microcosm. Thus, the interactions between predator and prey species are likely to be far more complex in field experiments, with the potential for intraspecific competition, increased search times, increased habitat complexity, and variable prey density.

Niche separation may explain the reason for IGP within the petri dish but lack of predator-predator interaction within the microcosm. Niche separation is when species have a distinct niche due to using the environment differently from others, this may be temporal, spatial or behavioral so that coexistence can occur (Hurlbert 1978; Lear et al. 2021; Schirmer et al. 2020). Thus, in a simplified arena (Petri dish) *F. auricularia* may exhibit IGP due to niche overlap, however when predators occupy different levels within more complex plant canopy niche separation occurs. This supports the experiment by Barton and Schmitz (2009) where two spider species were spatially segregated within the vegetation canopy, however as *P. mira*, shifted downwards in the plant canopy in response to temperature resulting in spatial overlap IGP occurred. However, unlike Barton and Schmitz (2009), there is no evidence for spatial shifts with respect to temperature in our study.

Anthocorids and earwigs did respond differently under the two temperature regimes; both predator species consumed significantly more *C. pyri* prey under the RCP8.5 scenario compared to the current

temperature scenario. One explanation for differences in feeding rate is due to altered metabolism (Yuan et al. 2009); metabolic rate increases exponentially with temperature up to a certain threshold, increasing demand for both energy and nutrients (Frances and McCauley 2018; Schmitz and Barton 2014). Furthermore, other studies on *F. auricularia* (Quach 2019) and *Anthocoris* spp. (Simonsen et al. 2009; Yanik and Unlu 2011), also found that temperature significantly impacts prey consumption and functional response. In our study prey consumption of earwigs was higher than anthocorids, at the current temperature regime compared to anthocorids. The number of nymphs consumed by anthocorids are supported by Reeves et al., (2023) who found that on average *A. nemoralis* consumed  $9.90 \pm 2.99$  *C. pyri* nymphs at 21 °C in functional response experiments in 24 h. However, it is more difficult to find studies confirming prey consumption by *F. auricularia*, as few involve *C. pyri* prey. Experiments by Quach (2019) found *F. auricularia* had a maximum prey consumption rate of 46.0 rosy apple aphid *Dysaphis plantaginea* per day, in similar temperatures to our regimes during the night. As *D. plantaginea* is of similar size to *C. pyri* this supports our findings.

There was little evidence for interference competition between predators, as additive and combination treatments showed no significant difference in the number of *C. pyri* nymphs eaten, furthermore few behavioral interactions were observed between the two predators within the microcosm. A study on *F. auricularia* and *Episyrphus balteatus* predators consuming rosy apple aphid nymphs *D. plantaginea*, also found no evidence for interference competition; microcosms containing stage three *F. auricularia* and *E. balteatus* had an additive effect on *D. plantaginea* consumption rather than a negative one (Yanik and Unlu 2011). Furthermore, no evidence for IGP was observed between predators within these microcosms; as both *F. auricularia* and *E. balteatus* are nocturnal predators, it is likely due to spatial or behavioral niche separation rather than temporal.

*Forficula auricularia* did not show a significant positive response to anthocorids olfactometry assays. This suggests that earwigs do not show a preference for *A. nemoralis* based on their volatile kairomones. Earwigs do rely on olfactory cues and signals for prey location and detection of conspecifics (Naranjo-Guevara et al. 2017; Walker et al. 1993). *F. auricularia*

relies on chemical signals in offspring care (Mas 2011) and also releases an aggregation pheromone (Hehar et al. 2008; Walker et al. 1993). Whilst the earwig species *Doru luteipes* Scudder, has been shown to respond to HIPVs released by herbivorised maize plants (Naranjo-Guevara et al. 2017). Therefore, the fact that *F. auricularia* does have a preference for *C. pyri* nymphs over a control treatment but shows no preference for *A. nemoralis*, may suggest it does not actively seek out anthocorids as prey. For *C. pyri* nymphs, earwigs may potentially be responding to kairomones on the insect or in its honeydew. Adult pear psyllid females have been shown to produce higher levels of a pheromone (13-Me C27) (Guédot et al. 2009; Yuan et al. 2021), which attracts *C. pyri* males (Ganassi et al. 2018). However, there is currently little research on infochemicals produced by *C. pyri* nymphs or how predators respond to them.

Predators and parasitoids could also be attracted to VOCs within nymphal honeydew. A study on *Vespula vulgaris* wasps found that they responded to kairomones from sooty scale insect honeydew (*Ultracoelostoma*) (Brown et al. 2015). Wasps were more attracted to baited traps containing 8 different compounds found within *Ultracoelostoma* honeydew compared to controls. Anthocorids show significant responses to HIPVs produced from psyllid infested trees (Drukker et al. 1995). Honeydew has the potential to act as a attractant and a defense mechanism for pear psyllids; natural enemies can be attracted to honeydew due to the VOCs emitted; however, predators can be slowed down due to honeydew's viscosity, so they take longer to find prey items (Ge et al. 2020; Tougeron et al. 2021). Furthermore, the parasitoid *Trechnites insidiosus*, has been found to oviposit in honeydew drops, in the absence of pear psyllid hosts (Tougeron et al. 2021); this could reduce parasitoid search time for other psyllid nymphs. Thus, other natural enemies may be attracted to infested foliage or nymphal honeydew containing similar compounds, highlighting an area of further research.

These results have a significant implication on biological control in pear orchards, as both *F. auricularia* and *A. nemoralis* can be used in synchrony without concerns about reduced efficiency due to IGP or interference competition. Relying on more than one predator may be more efficient due to efficacy backup (Lawson et al. 2017); if one predator species is less prevalent then there are others that can act as

a back-up for effective biological control, reducing variability of biological control (Snyder et al. 2008). This is supported by Stiling and Cornelissen (2005), in a meta-analysis comparing single species and multi-species releases of biological control agents. Results indicated that releasing multiple biocontrol agents was 27.2% more effective in decreasing pest abundance than single species releases. Natural enemy populations can be enhanced in a variety of ways, including the use of natural refugia; these can provide shelter and resources before migration into nearby orchard trees (Nagy et al. 2008; Scutareanu et al. 1999). Nagy et al. (2008), found high numbers of adult *A. nemoralis* on hawthorn, goat willow and stinging nettle surrounding orchards during spring. Artificial refuges can also be especially beneficial for earwig populations (Solomon et al. 1999), this includes corrugated cardboard in a bottle (Hansen et al. 2005; Solomon et al. 1999) or commercially available wooden Wignests (Russel-IPM 2023; Shaw et al. 2021).

Anthocorids are also commercially available for mass release (Sigsgaard et al. 2006; Bioplanet 2023; Koppert 2023), when wild populations are slow to build up in orchards. Sigsgaard et al. (2006), suggest between 1000–1500 adult *A. nemoralis* should be released hectare at 5–6 points within a pear orchard during the spring. *F. auricularia* is currently not available commercially for mass release; however, Hanel et al. (2023) recommends sourcing earwigs from stone fruit crops (where they are a notable pest) and mass releasing them into pear orchards as a biocontrol agent. The study found that mass release of 500 earwigs annually, significantly decreases pear psyllid populations, for 5 replicates within each of the two pear orchards, with a plot size of 9 trees (in a 3×3 square). It should also be noted that earwigs are particularly sensitive to pesticide usage and soil tillage (Le Navenant et al. 2021; Moerkens et al. 2012), therefore avoiding tilling soil to > 5 cm depth during the underground nesting period and not applying certain insecticides during the earwig's arboreal phase is advised (Orpet et al. 2019).

The response of both natural enemy species to temperature is also notable within our study. The fact that earwigs and anthocorids ate a significantly higher number of *C. pyri* nymphs, without changing other behaviors or position within the mesocosm under the high temperature regime, suggests they will still be

effective pear psyllid predators under future climate scenarios. However, experiments were undertaken in a small microcosm, so there is unlikely to be significant differences in temperature depending on height. In a tree canopy this is very different; the microclimate can vary significantly depending on position within the canopy with differences in humidity, temperature and exposure to solar radiation (Pangga et al. 2011, 2013). Thus, if studies were undertaken in a plant canopy with height dependent temperature differences, there may be more distinct changes in predator position. Moreover, we did not look at pear psyllid position; the spatial distribution of pear psyllid varies within the canopy throughout the year (Horton 1994; Stratopoulou and Kapatos 1992). Stratopoulou and Kapatos (1992a) monitored the spatial distribution of *C. pyri* (eggs and nymphs); during the spring psyllid density was higher in the upper canopy, however later in the year, numbers increased in the lower canopy. This could suggest areas exposed to more sunlight were actively chosen to meet temperature requirements for development earlier in the year, however later in the year it may be more optimal to oviposit lower down in the canopy to reduce desiccation of eggs. Therefore, predators may move to match the spatial distribution of their prey source, highlighting the need to observe predator behavior in situ, alongside their prey.

## Conclusion

To conclude, *F. auricularia* and *A. nemoralis* are likely to be suitable in combination for pear psyllid management, both are effective predators of *C. pyri* nymphs, with no evidence of interference competition and little IGP when a habitat is spatially complex. Furthermore, *F. auricularia* does not show a preference for *A. nemoralis* based on olfaction. However, there was a significant preference for psyllid prey in olfactometry assays, highlighting an area of further research. Temperature had a significant impact on prey consumption for both earwigs and anthocorids, with higher prey consumption at the RCP8.5 temperature regime compared to current climatic temperatures. Behavior, position and activity were not significantly influenced by temperature treatment, although results were based on 2-min observations, perhaps observations using EthoVision tracking software over

longer time periods would be a more viable approach to analyze this behavior. It is also worth noting that these studies were laboratory based, in small microcosms and petri dishes. Interactions in field-based studies are likely to be far more complex with the potential for intraspecific competition and increased search-times, especially at low prey density. We recommend that future field studies compare single and combined predator treatments in psyllid infested orchards, alongside DNA analysis of *F. auricularia* gut contents to determine whether IGP or interference competition is prevalent at a larger spatial scale.

**Acknowledgements** Our thanks to NIAB East Malling for the use of their controlled temperature cabinets and laboratory facilities for this project. Thank you to Celine Silva (NIAB) for her help on the set up of olfactometry assays.

**Author Contributions** Laura A. Reeves, Michael P. D. Garratt, Michelle T. Fountain and Deepa Senapathi conceived and designed the study. Laura A. Reeves carried out the lab work, data analyses and drafted the manuscript. Michael P. D. Garratt, Michelle T. Fountain and Deepa Senapathi provided feedback on multiple drafts prior to submission.

**Funding** This project was funded by BBSRC and Waitrose Agronomy Group as part of the Waitrose Collaborative Training Partnership (WCTP) (BB/V509747/1).

**Data Availability** Dataset accessible from the University of Reading Research Data Archive. DOI: <https://doi.org/https://doi.org/10.17864/1947.001341>.

## Declarations

**Conflicts of Interest** The authors declare no competing interests.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

## References

- Aartsma Y, Cusumano A, De Bobadilla MF, Rusman Q, Vosteen I, Poelman EH (2019) Understanding insect foraging in complex habitats by comparing trophic levels: insights from specialist host-parasitoid-hyperparasitoid systems. *Curr Opin Insect Sci* 32:54–60. <https://doi.org/10.1016/j.cois.2018.11.001>
- AHDB. (2012). Final report-exploiting semiochemicals, conservation biocontrol and selective physical controls in integrated management of pear sucker. <https://projectbluearchive.blob.core.windows.net/media/Default/Research%20Papers/Horticulture/TF%20181%20final%202012%20psg.pdf> Accessed 30 July 2024
- Agroscience (2022) Pictorial key of central European *Cacopsylla* species which are associated with Rosaceae <https://www.dlr.rlp.de/Psylliden-english/Key/Adults/families> Accessed 23 May 2023
- Allison JD, Daniel HJ (2009) Learned and naive natural enemy responses and the interpretation of volatile organic compounds as cues or signals. *New Phytol* 184:768–782. <https://doi.org/10.1111/j.1469-8137.2009.03046.x>
- Ayelo PM, Pirk CW, Yusuf AA, Chailleux A, Mohamed SA, Deletre E (2021) Exploring the kairomone-based foraging behavior of natural enemies to enhance biological control: A review. *Front Ecol Evo* 9:641974. <https://doi.org/10.3389/fevo.2021.641974>
- Barton BT, Schmitz OJ (2009) Experimental warming transforms multiple predator effects in a grassland food web. *Ecol Lett* 12:1317–1325. <https://doi.org/10.1111/j.1461-0248.2009.01386.x>
- Batuecas I, Alomar O, Castañe C, Piñol J, Boyer S, Gallardo-Montoya L, Agustí N (2022) Development of a multiprimer metabarcoding approach to understanding trophic interactions in agroecosystems. *Insect Sci* 29:1195–1210. <https://doi.org/10.1111/1744-7917.12992>
- Beck MW (2017) ggord: ordination plots with ggplot2. R package version 1.0.0. <https://zenodo.org/badge/latestdoi/10.5281/zenodo.135334615> Accessed 27 November 2023
- Becker C, Desneux N, Monticelli L, Fernandez X, Michel T, Lavoie AV (2015) Effects of abiotic factors on HIPV-mediated interactions between plants and parasitoids. *Biomed Res Int* 2015:342982. <https://doi.org/10.1155/2015/342982>
- Belien T, Moerkens R, Leirs H, Peusens G (2012) Earwig management tool: a practical software application to predict and optimize the development of earwig populations in pip fruit orchards. <https://www.ecofruit.net/wpcontent/uploads/2020/04/67-belien-415-419.pdf>. Accessed 15 Sept 2024
- Bioplanet (2023) *Anthocoris nemoralis* predator of psyllids. <https://bioplanet.eu/it/anthocoris-nemoralis/> Accessed 19 May 2023
- Boff S, Scheiner R, Raizer J, Lupi D (2021) Survival rate and changes in foraging performances of solitary bees exposed to a novel insecticide. *Ecotoxicol Environ Saf* 211:111869. <https://doi.org/10.1016/j.ecoenv.2020.111869>
- Brown RL, El-Sayed AM, Unelius CR, Beggs JR, Suckling DM (2015) Invasive *Vespula* wasps utilize kairomones to exploit honeydew produced by sooty scale insects, *Ultra-coelostoma*. *J Chem Ecol* 41:1018–1027. <https://doi.org/10.1007/s10886-015-0635-1>
- Capinera J (2008) European earwig, *Forficula auricularia* Linnaeus (Dermaptera: *Forficulidae*). *Encyclopædia*



- of Entomology; Springer, Dordrecht, The Netherlands. <https://doi.org/10.32473/edis-in875-2010>
- Civolani S (2012) The past and present of pear protection against the pear psylla, *Cacopsylla pyri* L. Insecticides, Pest Eng (ed. by F Perveen), Intech, pp 385–408.
- Collier T, Van Steenwyk R (2004) A critical evaluation of augmentative biological control. *Biol Control* 31:245–256. <https://doi.org/10.1016/j.biocontrol.2004.05.001>
- Dib H, Siegwart M, Delattre T, Perrin M, Lavigne C (2020) Does combining *Forficula auricularia* L. (Dermaptera: Forficulidae) with *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) enhance predation of rosy apple aphid, *Dysaphis plantaginea* Passerini (Hemiptera: Aphididae)? *Biol Control* 151:104394. <https://doi.org/10.1016/j.biocontrol.2020.104394>
- Drukker B, Scutareanu P, Sabelis M (1995) Do anthocorid predators respond to synomones from Psylla-infested pear trees under field conditions? *Entomol Exp App* 77:193–203. <https://doi.org/10.1111/j.1570-7458.1995.tb02001.x>
- Duffy C (2014) Developing a temperature-dependent simulation model for impacts of climate change for spring barley in Ireland. Thesis, National University of Ireland, Maynooth. <https://www.proquest.com/dissertations-theses/developingtemperature-dependent-simulation-model/docview/2175884482/se-2?accountid=13460>. <http://mural.maynoothuniversity.ie/10381/>. Accessed 15 Sept 2024
- DuPont ST, John Strohm C (2020) Integrated pest management programmes increase natural enemies of pear psylla in Central Washington pear orchards. *J Appl Entomol* 144:109–122. <https://doi.org/10.1111/jen.12694>
- Erlor F (2004) Natural enemies of the pear psylla *Cacopsylla pyri* in treated vs untreated pear orchards in Antalya, Turkey. *Phytoparasitica* 32:295–304. <https://doi.org/10.1007/BF02979824>
- Fields G, Beirne B (1973) Ecology of anthocorid (Hemiptera: Anthocoridae) predators of the pear psylla (Homoptera: Psyllidae) in the Okanagan Valley, British Columbia. *J Entomol Soc BC* 70:18–19
- Fountain M, Nagy C, Harris A, Cross J (2013) Importance of naturally occurring predators for pear sucker control. *IOBC-WPRS Bull* 91:117–125
- Frances DN, McCauley SJ (2018) Warming drives higher rates of prey consumption and increases rates of intraguild predation. *Oecologia* 187:585–596. <https://doi.org/10.1007/s00442-018-4146-y>
- Ganassi S, Germinara GS, Pati S, Civolani S, Cassanelli S, Sabatini MA, De Cristofaro A (2018) Evidence of a female-produced sex pheromone in the European pear psylla, *Cacopsylla pyri*. *Bull Insectology* 71:57–64
- Ge Y, Liu P, Zhang L, Snyder WE, Smith OM, Shi W (2020) A sticky situation: honeydew of the pear psylla disrupts feeding by its predator *Orius sauteri*. *Pest Manag Sci* 76:75–84. <https://doi.org/10.1002/ps.5498>
- Gnanvossou D, Hanna R, Dicke M (2003) Infochemical-mediated intraguild interactions among three predatory mites on cassava plants. *Oecologia* 135:84–90. <https://doi.org/10.1007/s00442-002-1120-4>
- Gobin B, Peusens G, Moerkens R, Leirs H (2008) Understanding earwig phenology in top fruit orchards. Ecofruit-13th international conference on cultivation technique and phytopathological problems in organic fruit-growing, Weinsberg, Germany. pp 208–212
- Guédot C, Millar JG, Horton DR, Landolt PJ (2009) Identification of a sex attractant pheromone for male winterform pear psylla, *Cacopsylla pyricola*. *J Chem Ecol* 35:1437–1447. <https://doi.org/10.1007/s10886-009-9725-2>
- Hanel A, Orpet RJ, Hilton R, Nottingham L, Northfield TD, Schmidt-Jeffris R (2023) Turning a pest into a natural enemy: removing earwigs from stone fruit and releasing them in pome fruit enhances pest control. *Insects* 14:906. <https://doi.org/10.3390/insects14120906>
- Hansen MR, Sigsgaard L, Braun P (2005) Earwig in pome fruit production—a beneficial? DIAS Report 1:279
- Hatano E, Kunert G, Michaud J, Weisser WW (2008) Chemical cues mediating aphid location by natural enemies. *Eur J Entomol* 105:797–806. <https://doi.org/10.14411/eje.2008.106>
- Hehar G, Gries R, Gries G (2008) Re-analysis of pheromone-mediated aggregation behavior of European earwigs. *Can Entomol* 140:674–681. <https://doi.org/10.4039/n08-026>
- Helsen H, Vaal F, Blommers L (1998) Phenology of the common earwig *Forficula auricularia* L. (Dermaptera: Forficulidae) in an apple orchard. *Int J Pest Manag* 44:75–79. <https://doi.org/10.1080/096708798228356>
- Hertfordshire University (2023) PPDB: Pesticide properties database. <http://sitem.herts.ac.uk/aeru/ppdb/en/Reports/424.htm> Accessed 23 November 2023
- Horton DR (1994) Relationship among sampling methods in density estimates of pear psylla (Homoptera: Psyllidae): implications of sex, reproductive maturity, and sampling location. *Ann Entomol Soc Am* 87:583–591
- HSE (2023) Modified plant protection products, including products which have been withdrawn. <https://secure.pesticides.gov.uk/pestreg/PMSearch.asp> Accessed 23 November 2023
- Hüftlein F, Seidenath D, Mittereder A, Hillenbrand T, Brüggemann D, Otti O, Feldhaar H, Laforsch C, Schott M (2023) Effects of diesel exhaust particles on the health and survival of the buff-tailed bumblebee *Bombus terrestris* after acute and chronic oral exposure. *J Hazard Mater* 131905. <https://doi.org/10.1016/j.jhazmat.2023.131905>
- Hurlbert SH (1978) The measurement of niche overlap and some relatives. *Ecology* 59:67–77. <https://doi.org/10.2307/1936632>
- Jonsson M, Kaartinen R, Straub CS (2017) Relationships between natural enemy diversity and biological control. *Curr Opin Insect Sci* 20:1–6. <https://doi.org/10.1016/j.cois.2017.01.001>
- Karuppaiah V, Sujayanad G (2012) Impact of climate change on population dynamics of insect pests. *World J Agric Sci* 8:240–246
- Kassambara A, Kosinski M, Biecek P, Fabian S (2017) Package ‘survminer’. Drawing survival curves using ‘ggplot2’ (R package version 03.1). <https://cir.nii.ac.jp/crid/13603/00776601012224>. Accessed 15 Sept 2024

- Kölliker M (2007) Benefits and costs of earwig (*Forficula auricularia*) family life. *Behav Ecol Sociobiol* 61:1489–1497. <https://doi.org/10.1007/s00265-007-0381-7>
- Koppert. (2023). Anthobug. <https://www.koppert.it/anthobug/> Accessed 12 May 2023
- Kramer M, Weldon P, Carroll JF (2009) Composite scores for concurrent behaviors constructed using canonical discriminant analysis. *Anim Behav* 77:763–768. <https://doi.org/10.1016/j.anbehav.2008.12.011>
- Lame RJ (1974) Earwig travel in relation to habitat. Dissertation, University of British Columbia. <https://open.library.ubc.ca/soa/cIRcle/collections/ubctheses/831/items/1.0100004>. Accessed 15 Sept 2024
- Lawson DA, Whitney HM, Rands SA (2017) Colour as a backup for scent in the presence of olfactory noise: testing the efficacy backup hypothesis using bumblebees (*Bombus terrestris*). *R Soc Open Sci* 4:170996. <https://doi.org/10.1098/rsos.170996>
- Le Navenant A, Brouchoud C, Capowiez Y, Rault M, Suchail S (2021) How lasting are the effects of pesticides on earwigs? A study based on energy metabolism, body weight and morphometry in two generations of *Forficula auricularia* from apple orchards. *Sci Total Environ* 758:143604. <https://doi.org/10.1016/j.scitotenv.2020.143604>
- Lear KO, Whitney NM, Morris JJ, Gleiss AC (2021) Temporal niche partitioning as a novel mechanism promoting co-existence of sympatric predators in marine systems. *Proc R Soc B* 288:20210816. <https://doi.org/10.1098/rspb.2021.0816>
- Lenfant C, Lyoussoufi A, Chen X, D'Arcier FF, Sauphanor B (1994) Potentialités prédatrices de *Forficula auricularia* sur le psylle du poirier *Cacopsylla pyri*. *Entomol Exp Appl* 73:51–60. <https://doi.org/10.1111/j.1570-7458.1994.tb01838.x>
- Martha K, Jones M (2002) Behavioral overlap in six Caribbean labrid species: intra- and interspecific similarities. *Environ Biol Fishes* 65:71–81. <https://doi.org/10.1023/A:1019675323053>
- Mas F (2011) Maternal behavior and the evolution of chemical signalling by offspring in the European earwig (*Forficula auricularia*). Thesis, University of Basel, Switzerland. <https://edoc.unibas.ch/1298/>. Accessed 15 Sept 2024
- Meza FC, Roberts JM, Sobhy IS, Okumu FO, Tripet F, Bruce TJ (2020) Behavioral and electrophysiological responses of female *Anopheles gambiae* mosquitoes to volatiles from a mango bait. *J Chem Ecol* 46:387–396. <https://doi.org/10.1007/s10886-020-01172-8>
- Moerkens R, Gobin B, Peusens G, Helsen H, Hilton R, Dib H, Suckling DM, Leirs H (2011) Optimizing biocontrol using phenological day degree models: the European earwig in pipfruit orchards. *Agric for Entomol* 13:301–312. <https://doi.org/10.1111/j.1461-9563.2011.00525.x>
- Moerkens R, Leirs H, Peusens G, Belien T, Gobin B (2012) Natural and human causes of earwig mortality during winter: temperature, parasitoids and soil tillage. *J Appl Entomol* 136:490–500. <https://doi.org/10.1111/j.1439-0418.2011.01676.x>
- Moerkens R, Leirs H, Peusens G, Gobin B (2009) Are populations of European earwigs, *Forficula auricularia*, density dependent? *Entomol Exp Appl* 130:198–206. <https://doi.org/10.1111/j.1570-7458.2008.00808.x>
- Moorthy PK, Kumar NK (2004) Integrated pest management in vegetable crops. [https://www.researchgate.net/publication/352257410\\_Integrated\\_pest\\_management\\_in\\_vegetable\\_crops](https://www.researchgate.net/publication/352257410_Integrated_pest_management_in_vegetable_crops). Accessed 15 Sept 2024
- Nagy C, Cross J, Luton M, Ashdown C (2008) Mixed deciduous hedgerows as sources of anthocorids and other predators of pear psyllids in the UK. 7th IOBC conference, Avignon. pp 395
- Naranjo-Guevara N, Peñaflores MFG, Cabezas-Guerrero MF, Bento JMS (2017) Nocturnal herbivore-induced plant volatiles attract the generalist predatory earwig *Doru luteipes* Scudder. *Sci Nat* 104:1–11. <https://doi.org/10.1007/s00114-017-1498-9>
- Naranjo SE (2001) Conservation and evaluation of natural enemies in IPM systems for *Bemisia tabaci*. *Crop Prot* 20:835–852. [https://doi.org/10.1016/S0261-2194\(01\)00115-6](https://doi.org/10.1016/S0261-2194(01)00115-6)
- Niinemets Ü, Loreto F, Reichstein M (2004) Physiological and physicochemical controls on foliar volatile organic compound emissions. *Trends Plant Sci* 9:180–186. <https://doi.org/10.1016/j.tplants.2004.02.006>
- Nottingham LB, Orpet RJ, Beers EH (2022) Integrated pest management programs for pear psylla, *Cacopsylla pyricola* (Förster)(Hemiptera: Psyllidae), using kaolin clay and reflective plastic mulch. *J Econ Entomol* 115:1607–1619. <https://doi.org/10.1093/jee/toac121>
- OMEGA (2023) USB temperature, humidity, process voltage or current data loggers. <https://www.omega.co.uk/pptst/OM-EL-USB-1.html> Accessed 12 May 2023
- Orpet RJ, Crowder DW, Jones VP (2019) Biology and management of European earwig in orchards and vineyards. *J Integr Pest Manag* 10:21. <https://doi.org/10.1093/jipm/pnz019>
- Pal E, Almasri H, Paris L, Diogon M, Pioz M, Cousin M, Sené D, Tchamitchian S, Tavares DA, Delbac F (2022) Toxicity of the pesticides imidacloprid, difenoconazole and glyphosate alone and in binary and ternary mixtures to winter honey bees: effects on survival and antioxidative defenses. *Toxics* 10:104. <https://doi.org/10.3390/toxics10030104>
- Pangga IB, Hanan J, Chakraborty S (2011) Pathogen dynamics in a crop canopy and their evolution under changing climate. *Plant Pathol* 60:70–81. <https://doi.org/10.1111/j.1365-3059.2010.02408.x>
- Pangga IB, Hanan J, Chakraborty S (2013) Climate change impacts on plant canopy architecture: implications for pest and pathogen management. *Eur J Plant Pathol* 135:595–610. <https://doi.org/10.1007/s10658-012-0118-y>
- Quach D (2019) Efficacy of the European Earwig (*Forficula auricularia*) as a generalist biocontrol agent. Thesis, Simon Fraser University, Canada. <https://summit.sfu.ca/item/19923>. Accessed 15 Sept 2024
- R (2023) R: a language and environment for statistical computing. *R foundation for statistical computing*, Vienna, Austria. <https://www.R-project.org>
- Reeves LA, Garratt MP, Fountain MT, Senapathi D (2023) Functional and behavioral responses of the natural



- enemy *Anthocoris nemoralis* to *Cacopsylla pyri*, at different temperatures. J Insect Behav 36:222–238. <https://doi.org/10.1007/s10905-023-09836-5>
- Ripley B, Venables B, Bates DM, Hornik K, Gebhardt A, Firth D, Ripley MB (2013) Package ‘mass.’ Cran r 538:113–120
- Roberts JM, Clunie BJ, Leather SR, Harris WE, Pope TW (2023) Scents and sensibility: best practice in insect olfactometer bioassays. Entomol Exp Appl 171:808–820. <https://doi.org/10.1111/eea.13351>
- Russel-IPM (2023) Wignest. <https://russellipm.com/product/11622-2/> Accessed 12 May 2023
- Schirmer A, Hoffmann J, Eccard JA, Dammhahn M (2020) My niche: individual spatial niche specialization affects within- and between-species interactions. Proc R Soc B 287:20192211
- Schmitz OJ, Barton BT (2014) Climate change effects on behavioral and physiological ecology of predator-prey interactions: Implications for conservation biological control. Biol Control 75:87–96. <https://doi.org/10.1016/j.biocontrol.2013.10.001>
- Scutareanu P, Lingeman R, Drukker B, Sabelis MW (1999) Cross-correlation analysis of fluctuations in local populations of pear psyllids and anthocorid bugs. Ecol Entomol 24:354–363. <https://doi.org/10.1046/j.1365-2311.1999.00199.x>
- Sek Kocourek F, Stará J (2006) Management and control of insecticide-resistant pear psylla (*Cacopsylla pyri*). J Fruit Ornament Plant Res 14:167–174
- Shaw B, Nagy C, Fountain MT (2021) Organic control strategies for use in IPM of invertebrate pests in apple and pear orchards. Insects 12:1106. <https://doi.org/10.3390/insects12121106>
- Sigsgaard L, Esbjerg P, Philipsen H (2006) Controlling pear psyllids by mass-releasing *Anthocoris nemoralis* and *A. nemorum* (Heteroptera: Anthocoridae). J Fruit Ornament Plant Res 14:89. <https://agro.icm.edu.pl/agro/element/bwmeta1.element.agro-article-765ab1fe-5bad-48ca-b243-6026ec9401cf>. Accessed 15 Sept 2024
- Simonsen ML, Enkegaard A, Bang C, Sigsgaard L (2009) Temperature effect on the predation rate of *Anthocoris nemorum* (Het.: Anthocoridae) on cabbage aphids (Hom.: Aphididae). J Appl Entomol 133:198–200. <https://doi.org/10.1111/j.1439-0418.2008.01327.x>
- Snyder GB, Finke DL, Snyder WE (2008) Predator biodiversity strengthens aphid suppression across single- and multiple-species prey communities. Biol Control 44:52–60. <https://doi.org/10.1016/j.biocontrol.2007.09.006>
- Snyder WE, Snyder GB, Finke DL, Straub CS (2006) Predator biodiversity strengthens herbivore suppression. Ecol Lett 9:789–796. <https://doi.org/10.1111/j.1461-0248.2006.00922.x>
- Snyder WE, Wise DH (2001) Contrasting trophic cascades generated by a community of generalist predators. Ecology 82:1571–1583. <https://doi.org/10.1111/j.1461-0248.2006.00922.x>
- Solomon M, Cross J, Fitzgerald J, Campbell C, Jolly R, Olszak R, Niemczyk E, Vogt H (2000) Biocontrol of pests of apples and pears in northern and central Europe-3. Predators Biocontrol Sci Technol 10:91–128. <https://doi.org/10.1080/09583150029260>
- Solomon M, Fitzgerald J, Jolly R (1999) Artificial refuges and flowering plants to enhance predator populations in orchards. IOBC WPRS Bull 22:31–38
- South J, Welsh D, Anton A, Sigwart J, Dick J (2018) Increasing temperature decreases the predatory effect of the intertidal shanny *Lipophrys pholis* on an amphipod prey. J Fish Biol 92:150–164. <https://doi.org/10.1111/jfb.13500>
- Stiling P, Cornelissen T (2005) What makes a successful bio-control agent? A meta-analysis of biological control agent performance. Biol Control 34:236–246. <https://doi.org/10.1016/j.biocontrol.2005.02.017>
- Stratopoulou E, Kapatos E (1992) Distribution of population of immature stages of pear psylla, *Cacopsylla pyri*, within the Tree and Development of Sampling Strategy. Entomol Hell 10:5–10. <https://doi.org/10.12681/eh.13997>
- Suckling D, Burnip G, Hackett J, Daly J (2006) Frass sampling and baiting indicate European earwig (*Forficula auricularia*) foraging in orchards. J Appl Entomol 130:263–267. <https://doi.org/10.1111/j.1439-0418.2006.01064.x>
- Tapia D, Morales F, Grez A (2010) Olfactory cues mediating prey-searching behavior in interacting aphidophagous predators: are semiochemicals key factors in predator-facilitation? Entomol Exp Appl 137:28–35. <https://doi.org/10.1111/j.1570-7458.2010.01034.x>
- Therneau T, Lumley T (2013) R survival package. R Core Team. <https://rweb.webapps.cla.umn.edu/R/library/survival/doc/survival.pdf>. Accessed 15 Sept 2024
- Tougeron K, Iltis C, Renoz F, Albittar L, Hance T, Demeter S, Le Goff GJ (2021) Ecology and biology of the parasitoid *Trechmites insidiosus* and its potential for biological control of pear psyllids. Pest Manag Sci 77:4836–4847. <https://doi.org/10.1002/ps.6517>
- Tylianakis JM, Romo CM (2010) Natural enemy diversity and biological control: making sense of the context-dependency. Basic Appl Ecol 11:657–668. <https://doi.org/10.1016/j.baae.2010.08.005>
- UKCP (2021) UK climate projections user interface data: anomalies for probabilistic projections (25km) over UK, 1961–2100. [https://ukclimateprojections-ui.metoffice.gov.uk/products/form/LS1\\_Sample\\_01](https://ukclimateprojections-ui.metoffice.gov.uk/products/form/LS1_Sample_01) Accessed 10 May 2023
- Valle D, Mujica V, Gonzalez A (2023) Herbivore-dependent induced volatiles in pear plants cause differential attractive response by lacewing larvae. J Chem Ecol 23:1–14. <https://doi.org/10.1007/s10886-023-01403-8>
- Van Lenteren JC (2012) The state of commercial augmentative biological control: plenty of natural enemies, but a frustrating lack of uptake. Biocontrol 57:1–20. <https://doi.org/10.1007/s10526-011-9395-1>
- Vet LE, Dicke M (1992) Ecology of infochemical use by natural enemies in a tritrophic context. Annu Rev Entomol 37:141–172. <https://doi.org/10.1146/annurev.en.37.010192.001041>
- Walker KA, Jones TH, Fell RD (1993) Pheromonal basis of aggregation in European earwig, *Forficula auricularia* L. (Dermaptera: Forficulidae). J Chem Ecol 19:2029–2038. <https://doi.org/10.1007/BF00983805>
- Wickham H, Chang W, Wickham MH (2016) Package ‘ggplot2’. create elegant data visualisations using the grammar of graphics. Version 2:1–189

- Yanik E, Ugur A (2004) Avcı böcek *Anthocoris nemoralis* (F.)(Heteroptera: Anthocoridae)'in laboratuvar ve doğa şartlarında *Cacopsylla pyri* (L.)(Homoptera: Psyllidae) ve *Ephestia kuehniella* Zell. (Lepidoptera: Pyralidae) yumurta tüketimi. Plant Prot Bull 44:47–67
- Yanik E, Unlu L (2011) Influences of temperature and humidity on the life history parameters and prey consumption of *Anthocoris minki* Dohrn (Heteroptera: Anthocoridae). Appl Entomol Zool 46:177–184. <https://doi.org/10.1007/s13355-011-0029-y>
- Yano E (2006) Ecological considerations for biological control of aphids in protected culture. Popul Ecol 48:333–339. <https://doi.org/10.1007/s10144-006-0008-2>
- Yuan G, Yang Y, Liu J, Bian Q, Wang M, Zhong J (2021) Synthesis of the enantiomers of 13-methylheptacosane, the sex pheromone of pear psylla, *Cacopsylla pyricola*. Chirality 33:274–280. <https://doi.org/10.1002/chir.23307>
- Yuan JS, Himanen SJ, Holopainen JK, Chen F, Stewart CN Jr (2009) Smelling global climate change: mitigation of function for plant volatile organic compounds. Trends Ecol Evol 24:323–331. <https://doi.org/10.1016/j.tree.2009.01.012>

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.