

Can pollen provision mitigate competition interactions between three phytoseiid predators of *Tetranychus urticae* under future climate change conditions?

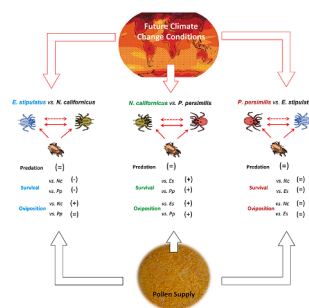
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HIGHLIGHTS

- Climate change (CC) may enhance competition between *T. urticae* predators.
- As a consequence, CC may disrupt *T. urticae* biological control.
- Pollen could compensate negative effects of CC on omnivores like *E. stipulatus*.
- But cannot on specialists like *N. californicus* and *P. persimilis*.

GRAPHICAL ABSTRACT



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ABSTRACT

Biological control can be severely disrupted by hot and dry environmental conditions associated with climate change. These conditions may alter the food web configuration of arthropod communities through their effects on species interactions. They could disrupt the competition between the phytoseiid predators *Euseius stipulatus*, *Neoseiulus californicus*, and *Phytoseiulus persimilis*, which are the key natural enemies of *Tetranychus urticae* in citrus in Spain. Because the provision of alternative food could compensate for such a situation, we studied in laboratory conditions whether pollen supply could modify competition among these predatory species under different climatic conditions. Our results show that access to high-quality pollen may enhance the performance of *E. stipulatus* and *N. californicus*. However, when the phytoseiids considered in our study were forced to compete, pollen provision had contrasting effects depending on the competing pair. Overall, climate change did not affect predation when pollen was available. Predation, though, was lower than expected except when the competing pair was *P. persimilis* and *E. stipulatus*. Therefore, pollen provision can partially mitigate the adverse effects of climate change on some of the biological parameters of the three main predators of *T. urticae* when competing in the system. This has important implications for the future success of biological pest control.

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1. Introduction

Ecologists have commonly documented climate change to alter species distributions, phenology, and interactions (Parmesan and Yohe, 2003; Tylianakis et al., 2008). An increasing amount of studies indicates that global warming affects a broad range of species and ecosystems (Hooper et al., 2012; Deutsch et al., 2018; Thierry, Hrček, & Lewis, 2019; Agathokleous et al., 2020; González-Tokman et al., 2020; Schleuning et al., 2020), including agricultural systems through thermal and osmotic stresses (Luedeling et al., 2011; Sykes, 2009; Uleberg et al., 2014). In the Mediterranean region, temperature increases of 1.5 and 2.0 °C in winter and summer, respectively, and 5–15% lower relative humidity values coupled with a 5% decrease in rainfall are forecasted for the mid-21st century (Diffenbaugh et al., 2007; Giorgi and Lionello, 2008; Gualdi et al., 2012; Jacob et al., 2014; Navarra and Tubiana, 2013). These changes, together with increasingly frequent extreme events (IPCC, 2018) such as drought and heatwaves (Hansen et al., 2012), can have detrimental effects on ecosystem dynamics (Ummenhofer and Meehl, 2017).

Citrus is an important crop grown throughout the world, including the Mediterranean region (FAO 2017). This crop is especially susceptible to the effects of climate change through drought stress (Anderson et al., 2004; García-Tejero et al., 2012; Rodríguez-Gamir et al., 2010). Moreover, global warming may profoundly affect the control of citrus pests (Urbaneja-Bernat et al., 2019; Urbaneja-Bernat and Jaques, 2020), generating pest outbreaks, which may be mediated by their natural enemies (Cock et al., 2013; Evans et al., 2013; Gillespie et al., 2012; Hance et al., 2007; Jeffs and Lewis, 2013; Stireman et al., 2005; Thomson et al., 2010). Arthropod species with the highest specializations in lifestyle or habitat are most vulnerable to climate change (Aguilar-Fenollosa and Jacas, 2014). Trophic cascades could be dampened, and biological control jeopardized (Araújo and Luoto, 2007; Hegland et al., 2009). Predatory phytoseiid mite communities (Mesostigmata: Phytoseiidae) controlling the pest *Tetranychus urticae* Koch (Prostigmata: Tetranychidae) in citrus could be affected (Urbaneja-Bernat et al., 2019; Urbaneja-Bernat and Jaques, 2020). *Tetranychus urticae* is a key pest of clementine mandarins, *Citrus clementina* Tanaka (Rutaceae), in the Mediterranean (Aguilar-Fenollosa et al., 2011a; Martínez-Ferrer et al., 2006; Pascual-Ruiz et al., 2014). Its main natural enemies, phytoseiid mites, have different diet specializations (Mcmurtry et al., 2013). The omnivorous *Euseius stipulatus* (Athias-Henriot) and the Tetranychidae-specialist *Neoseiulus californicus* (McGregor) are the most abundant predatory mites in citrus orchards in Spain (Abad-Moyano et al., 2009; Aguilar-Fenollosa et al., 2011b; Vela et al., 2017). However, these phytoseiids are not the most efficient predators of *T. urticae*. This role is played by the *T. urticae*-specialist *Phytoseiulus persimilis* (Athias-Henriot), which preys on this herbivore almost five times more frequently than *E. stipulatus* (Pérez-Sayas et al., 2015).

Contrary to the progressive increase in average temperature, which is a long-term process, extreme climatic events, such as heatwaves, can induce immediate consequences for poikilothermic animals, as mites, with different effects at higher organizational levels (i.e., population, community) (Bannerman et al., 2011; Ciais et al., 2005; De Boeck et al., 2010; Gillespie et al., 2012; Jentsch et al., 2007; Sentis et al., 2013; Urbaneja-Bernat and Jaques, 2020). Recent research (Urbaneja-Bernat et al., 2019) studied the interactions between *T. urticae* and its predators *E. stipulatus*, *N. californicus*, and *P. persimilis* under climate change scenarios in citrus semi-field assays. Under hotter and drier spring and summer semi-field conditions representative of future climate change in the Mediterranean region, the efficacy of these phytoseiids decreased, resulting in a deficient control of *T. urticae*. The most abundant *E. stipulatus* was the most severely impacted phytoseiid, mainly in combinations with *N. californicus*. Additional laboratory assays showed that at the species level, these adverse effects could be partly compensated by the addition of alternative food to the system (Urbaneja-Bernat and Jaques, 2020), as observed for other generalist predators in similar

cases (Beltrà et al., 2017; González-Fernández et al., 2009; Janssen and Sabelis, 2015; Maoz et al., 2011; Mcurmtry et al., 2013; Pozzebon et al., 2009; Etienne et al., 2021). However, the effect of pollen supply on each predatory species individually did not seem enough to restore the efficacy of biological control (Urbaneja-Bernat and Jaques, 2020). Although *E. stipulatus* is presumed to behave as a superior intraguild predator relative to *N. californicus* and *P. persimilis* under laboratory, semi-field, and field conditions (Abad-Moyano et al., 2010a, 2010b; Pérez-Sayas et al., 2015), the question of whether pollen supply could mitigate the negative interactions between these predators (i.e., competition, intra-guild predation) remains unsolved.

The objective of the present study is to assess the effect of alternative food (pollen) provision on competition between predators under controlled conditions. Results should help explain some of the results obtained in previous studies (Urbaneja-Bernat et al., 2019; Urbaneja-Bernat and Jaques, 2020). Our hypothesis assumes that pollen supply may modulate the strength of competition between *E. stipulatus*, *N. californicus*, and *P. persimilis* at hot and dry environmental conditions associated with climate change (IPCC, 2018). These experiments, which are commonly used to assess the effect of extreme climatic events such as heatwaves (Ciais et al. 2005; Jentsch et al. 2007; De Boeck et al. 2010; Bannerman et al. 2011; Gillespie et al. 2012; Sentis et al. 2013), should allow us to explore how hotter and drier abiotic conditions may affect the key biological parameters (i.e., survival, oviposition, and predation) of these predators under different co-occurrence combinations, and whether the addition of pollen could mitigate any negative effect on the physiology and/or the behavioral responses of these predators. On the one hand, competition in co-occurrence with alternative food and prey may promote the abundance of the omnivorous predator *E. stipulatus* relative to the other two phytoseiids, *N. californicus* and *P. persimilis*, which could further prey on it (i.e., increased intra-guild predation). On the other hand, it may result in increased competition between phytoseiids, which, together with apparent competition between pollen and *T. urticae*, could disrupt existing biological control, as observed in avocado by Montserrat et al. (2013a). In addition to explaining semi-field results previously observed (Urbaneja-Bernat et al. 2019), the present study should shed light on whether pollen supply could be an effective tactic for conserving these natural enemies in a rapidly approaching warmer future.

2. Material and methods

2.1. Plant material

In the experiments, we used leaves obtained from potted clementine plants (*Citrus clementina* Tanaka cv. Clementina de Nules (Rutaceae) grafted on citrange Carrizo). Five weeks before the beginning of each experiment, 75 plants were defoliated and kept in a greenhouse at Universitat Jaume I (UTM: 39°59'10.883 "N 0°3'4.769 "W) maintained at 22 ± 2 °C, 55 ± 10% relative humidity (RH) and natural photoperiod. Pesticide-free clementine plants were grown on vermiculite and peat (1:3; vol: vol) in 320 ml pots and fertilized twice per week using a standard N-P-K (10-10-10) solution. Bean leaves (*Phaseolus vulgaris* L. (Fabaceae)), lemon fruits (*Citrus lemon* Burm. f. (Rutaceae)), and *Carbobrotus edulis* (L.) (Aizoaceae) pollen (dried at 37 °C, sieved, and frozen until use) were used to rear phytoseiid mites. *C. edulis* pollen is considered high-quality for phytoseiids (Pina et al., 2012).

2.2. Mite colonies

Four different mite species were used in this study: the two-spotted spider mite (*T. urticae*) and the Phytoseiidae *E. stipulatus*, *N. californicus*, and *P. persimilis*. Each mite colony was maintained in a separate climatic chamber set at 25 ± 1 °C, 65 ± 5% RH, and a 16-hour light photoperiod. The same photoperiod applies to the experiments below.

Tetranychus urticae were initially collected in a clementine orchard at Les Alqueries (UTM: 39°59'15.1 "N 0°03'02.0"W), and were maintained on detached leaves of clementines using standard procedures (Aguilar-Fenollosa et al., 2012), and, in some cases (see below), on pesticide-free lemon fruits (Abad-Moyano et al., 2010a). *Tetranychus urticae* were used to feed the Phytoseiidae stock colonies and to start new cohorts for our experiments. When used to feed Phytoseiids, bean leaflets were infested by exposure to *T. urticae* colonies on lemon fruits. New cohorts were established by transferring 100 females to new rearing arenas on clementine leaves. Females were removed one day later, and these leaves, which contained less than 24-hour old eggs, were held separately in a climatic chamber (25 °C, 65% RH) and constituted the cohorts used in our experiments.

Individuals of *N. californicus* used to initiate the laboratory colony were obtained from Koppert Biological Systems (SPICAL®). *Phytoseiulus persimilis* and *E. stipulatus* were collected in 2012 from two clementine orchards in Les Alqueries (same location as *T. urticae*) and Montcada (UTM: 39° 32' 42.906" N 0° 23' 45.699" W), respectively.

Phytoseiid stock colonies were maintained on detached leaf arenas. These arenas consisted of a single bean leaflet placed upside down on moistened filter paper and placed on a water-saturated foam cube (3–4 cm thick) in an open plastic box (L × W × H: 300 × 150 × 50 mm) half-filled with water. Phytoseiid colonies received detached bean leaflets infested with *T. urticae* and *C. edulis* pollen as food twice a week.

2.3. Experimental setup

Arenas used for the experiments consisted of a Petri dish (5 cm in diameter) with a 3 cm-diameter hole in the cover (Fig. 1). The base of the dish was filled with agar (2.5% weight). As soon as the agar solidified, a fully expanded clementine leaf was placed upside down on top of the agar to maintain its turgor. The arena was subsequently closed with the cover; The upper and lower parts of the dishes were then sealed with a strip of Parafilm® (Pechiney Plastic Packaging, Menasha, WI, USA). To prevent mites escaping from the arenas, permanent glue (Tree Tanglefoot®; Grand Rapids, MI, USA) was applied along the rim of the hole in the cover (Guzmán et al., 2016).

2.4. Experimental procedure

We considered each predator species alone (*E. stipulatus*, *N. californicus*, and *P. persimilis*) and the competition treatments in pairs of two heterospecific females: *E. stipulatus* and *N. californicus*,

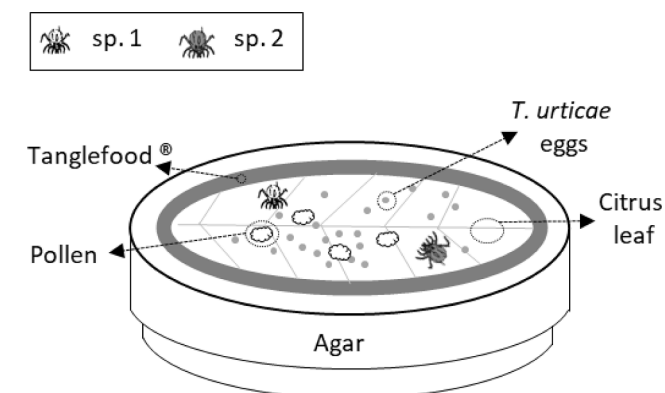


Fig. 1. Experimental setup for competition experiments, designed to confine two abiotic environments isolated from each other: the agar was kept humid to help maintain turgidity of the citrus leaf; the experimental treatments defined the upper environment (Actual and future abiotic conditions), and it incorporated the area containing the two tested phytoseiid species in competition (or alone = control) with different diet treatments (unfed, pollen, *T. urticae* eggs, and *T. urticae* eggs + pollen).

E. stipulatus and *P. persimilis*, and *N. californicus* and *P. persimilis*. For each combination, we studied four different diet treatments: control (unfed), pollen (P), *T. urticae* eggs (T), and *T. urticae* eggs plus pollen (TP). In the pollen treatments, pollen was supplied *ad libitum* to each arena immediately before introducing the phytoseiid.

For the experiments, we created phytoseiid cohorts from eggs. First, a fully expanded healthy clementine leaf was introduced onto a *T. urticae*-infested lemon stock colony. Twenty-four hours later, the infested leaf was moved to an *N. californicus* or a *P. persimilis* colony and left there for an additional 24 h period. Since this method did not work for *E. stipulatus*, the eggs of this species were obtained by exposing a few cotton threads to an existing colony. Then, leaves were inspected under a binocular microscope to remove all motile stages. A separate colony was started with each leaf, and they constituted the phytoseiid cohorts used in our assays.

We used gravid adult females at their peak oviposition rate (12–14 days from egg hatch) (Aucejo-Romero et al., 2004; Janssen and Sabelis, 1992). Gravid females were randomly selected from the cohort and placed individually in plastic arenas on top of sponges in water-containing trays without food for 24 h. This ensured the same level of satiety in all females tested. Before introducing the phytoseiid into the experimental arena, 15 *T. urticae* females were placed in each arena to feed, oviposit, and produce web for 48 h. The mean number of *T. urticae* eggs per arena was 75 ± 2.1 . Subsequently, we removed all mobile forms of *T. urticae*, and only ≤ 48 h old eggs were left. Then, the 24-h starved phytoseiid females were introduced into the experimental arena in the different combinations mentioned above (i.e., one single female or two heterospecific females).

Arenas were checked 24 h after the onset of the assay (i.e., 48 h after the beginning of the starvation period for adult phytoseiid females) under a binocular microscope. The reason for selecting this period was that *T. urticae* eggs used in the arenas could start hatching after 48 h, especially at high temperatures (>30 °C). When predators were placed individually in the arena, we checked for predation (number of *T. urticae* eggs eaten), oviposition (number of eggs deposited), and survival (i.e., alive and dead specimens and escapees). When predators competed (heterospecific pair), we checked the same parameters. However, in the case of predation, we checked the total number of eggs eaten by both phytoseiids in each arena (observed predation), which was compared with the expected predation (i.e., species 1 alone + species 2 alone). In the case of oviposition in the *E. stipulatus* vs. *N. californicus* treatment, because immature stages cannot be easily distinguished, the eggs of each replicate were isolated on leaf discs provided with *T. urticae* eggs and pollen and left to develop to adults at optimal conditions. Once they reached adulthood, they were identified to the species level under the microscope. A total of 15 replicates (five arenas repeated three times) were performed for each treatment combination.

2.5. Environmental conditions

Temperature and RH values during the summer season (25 ± 1 °C and $70 \pm 5\%$ RH) were chosen for the experiments as a proxy for the present average conditions in the Mediterranean region and called 'present abiotic conditions' (PAC). These climatic conditions were compared with predicted future temperature and RH conditions (IPCC, 2014), with an increase of 5 °C in temperature (30 °C) and a decrease of 20% in RH (50%), and called 'future abiotic conditions' (FAC). Stable RH conditions were obtained using desiccators (L × W × H: 250 × 320 × 355 mm) with different salt solutions (Winston and Bates, 1960). Experiments were carried out under laboratory conditions in a climate chamber (Sanyo Electric Co., Ltd., Japan) with 16:8h L:D.

2.6. Statistical analyses

To study the effects of the different factors included in our assays on survival, oviposition, and predation, we used Generalized Linear Mixed

Models (GLMM) assuming different probability distributions and different link functions depending on the characteristics of the data. We used a multinomial distribution of the error and a logit link function for survival, with three possible outputs (i.e., alive and dead specimens and escapees). For oviposition and predation, we used a Poisson distribution of the error and a logistic link function. In all cases, the factors ‘Phytoseiid sp. combination’, ‘diet’, and ‘abiotic conditions’ were used as fixed effects, and ‘time’ (replication through time) as a random factor.

Because our main goal was to evaluate the effects of abiotic conditions on the competitive interactions between phytoseiids and whether diet could modulate this response, we started our analyses by considering all combinations, including the factor ‘Phytoseiid sp. combination’. Once the significance of this factor was tested, we continued the analyses by studying the effect of the remaining factors sequentially. When necessary, we used the Bonferroni post-hoc test for mean separation. Chi-square tests (χ^2) were used to compare the observed and expected predation in the competition treatments. The SPSS 23.0 software was used for all statistical analyses.

3. Results

The effect of the factor ‘Phytoseiid sp. combination’ on survival and oviposition (Table 1), and predation (Table 4S) was significant in all cases except for survival of *P. persimilis* (Table 1). Consequently, further analyses of survival of *P. persimilis* considered all combinations including this species together.

3.1. Survival

Abiotic conditions, AC (i.e., PAC and FAC), did not affect the survival of *E. stipulatus* alone, which was highest when offered pollen only (Fig. 2a). However, the interaction of AC and diet was significant when this species competed with *N. californicus* and *P. persimilis* (Table 1S). When competing with *N. californicus*, highest survival occurred at PAC both when there was no food supply and when offered the mixed diet of *T. urticae* eggs and pollen. Pollen increased survival at FAC but was neutral when *T. urticae* eggs were also available (Fig. 2b). When competing with *P. persimilis*, highest survival occurred at PAC when the diet consisted of *T. urticae* eggs only. Same as before, pollen supply did not affect the survival of *E. stipulatus* at FAC when *T. urticae* eggs were available. However, it slightly decreased survival at FAC when this was the only food source available (Fig. 2c).

The interaction between AC and diet significantly affected the survival of *N. californicus* either alone or in competition with *E. stipulatus*. However, when competing with *P. persimilis*, AC was the only significant factor (Table 2S). Pollen increased the survival of *N. californicus* either alone (Fig. 2d) or when competing with *E. stipulatus* (Fig. 2e) at FAC when offered together with *T. urticae* eggs. Survival was nil when *N. californicus* was alone, and pollen was the only food available at FAC

Table 1

Significance (Wald X^2 ; *df*; *P*-value) of the different GLMM fit to survival (multinomial), and oviposition (Poisson) for each phytoseiid using the factors phytoseiid sp. combination, diet (control, *C. edulis* pollen, *T. urticae* eggs, and *T. urticae* eggs plus pollen), abiotic conditions (present and future), and their interactions as explanatory variables.

Factors	<i>Euseius stipulatus</i>		<i>Neoseiulus californicus</i>		<i>Phytoseiulus persimilis</i>	
	Survival	Oviposition	Survival	Oviposition	Survival	Oviposition
Phytoseiid sp. combination	4.36; 2; 0.014	12.24; 2; < 0.001	58.12; 2; < 0.001	7.34; 2; 0.001	0.42; 2; 0.996	25.08; 2; < 0.001
Diet × Phytoseiid sp. combination	2.02; 9; 0.021	6.28; 9; < 0.001	1.62; 9; 0.108	7.14; 9; < 0.001	0.74; 9; 0.670	22.67; 8; < 0.001
Abiotic conditions × Phytoseiid sp. combination	1.75; 3; 0.156	10.36; 3; < 0.001	11.13; 3; < 0.001	6.38; 3; < 0.001	0.85; 3; 0.467	1.85; 3; 0.137
Diet × Abiotic conditions × Phytoseiid sp. combination	2.70; 9; 0.005	1.15; 9; 0.325	4.51; 9; < 0.001	0.42; 8; 0.909	1.81; 9; 0.065	1.87; 8; 0.065
Model	2.16; 23; 0.002	5.51; 23; < 0.001	6.55; 23; < 0.001	5.82; 22; < 0.001	2.39; 23; < 0.001	18.90; 20; < 0.001

Table 2

Predation (number of eggs eaten) by *Euseius stipulatus*, *Neoseiulus californicus*, *Phytoseiulus persimilis* when offered either *T. urticae* eggs (T) or *T. urticae* eggs + Pollen (TP) at present (PAC; 25 ± 1 °C and 70 ± 5% RH) and future abiotic conditions (FAC; 30 ± 1 °C and 50 ± 5%).

Phytoseiid sp.	Diet	Abiotic conditions (AC)	Predation	Statistics (<i>F</i> ; <i>df</i> ; <i>P</i> -value)
<i>Euseius stipulatus</i>	T	PAC	7.9 ± 2.1b	Diet: 23.96; 1; <0.001
		FAC	3.7 ± 1.0c	
	TP	PAC	16.3 ± 1.9 a	AC: 17.44; 1; 0.014
		FAC	8.6 ± 1.5b	Diet*AC: 13.78; 7; <0.001
<i>Neoseiulus californicus</i>	T	PAC	19.9 ± 0.9b	Diet: 35.42; 1; 0.128
		FAC	26.1 ± 2.6 a	AC: 62.34; 1; 0.004
	TP	PAC	15.2 ± 0.6c	Diet*AC: 29.65; 7; <0.001
		FAC	26.9 ± 0.8 a	
<i>Phytoseiulus persimilis</i>	T	PAC	35.7 ± 4.1 a	Diet: 18.26; 1; 0.021
		FAC	20.3 ± 3.8b	AC: 18.37; 1; 0.034
	TP	PAC	21.5 ± 1.4b	Diet*AC: 15.42; 7; 0.013
		FAC	25.4 ± 2.7b	

For each phytoseiid species, predation values followed by the same letter are not significantly different (Bonferroni post hoc test at *P* < 0.05).

(Fig. 2d). When competing with *E. stipulatus*, *N. californicus* did mostly better at FAC, with the highest survival when offered the mixed diet at FAC and nil at PAC with pollen only (Fig. 2e). When competing with *P. persimilis*, survival of *N. californicus* was higher at FAC irrespective of the diet (Fig. 2f).

For *P. persimilis*, the interaction between AC and diet significantly affected survival irrespective of the combination (Table 3S). Although survival never increased at FAC, the mixed diet allowed survival to be the same at PAC and FAC (Fig. 3).

3.2. Oviposition

Oviposition in *E. stipulatus* alone was affected by diet only (Table 1S). It was highest when offered the mixed diet of *T. urticae* eggs and pollen and zero when no food was available (Fig. 4a). When competing with *N. californicus*, both diet and AC were significant, but their interaction was not. Oviposition was higher when pollen was available but was always lower at FAC and nil in two cases (Fig. 4b). When competing with *P. persimilis*, oviposition was always nil irrespective of diet and AC

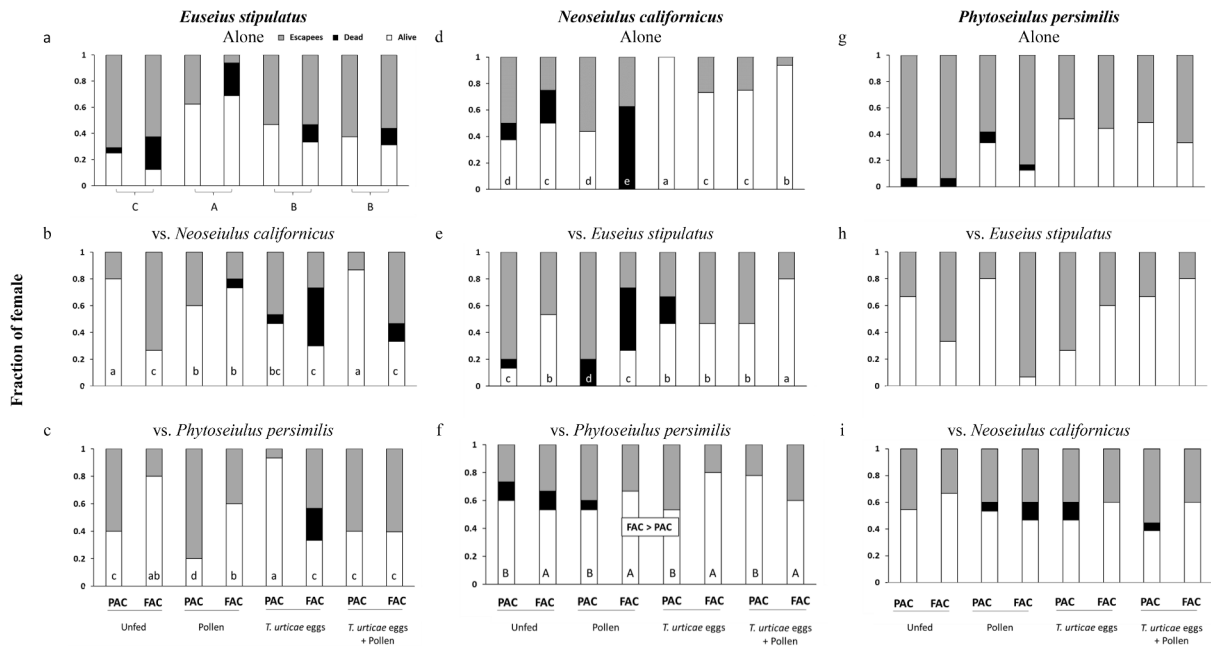


Fig. 2. Survival: escapees (grey bars), dead (black bars) and live (white bars) individuals of *Euseius stipulatus*, *Neoseiulus californicus* and *Phytoseiulus persimilis* either alone (upper figures), or in competition with heterospecifics (middle and lower figures). Phytoseiids were offered three different diets (pollen, *T. urticae* eggs, and a combination of both). An unfed control was also considered at present and future abiotic conditions (PAC: 25 ± 1 °C and 70 ± 5% RH; FAC and FAC: 30 ± 1 °C and 50 ± 5%, respectively). For each figure, survival bars with the same letters are not statistically different (GLMM; Bonferroni P < 0.05). Capital letters refer to cases where either abiotic conditions (*N. californicus* vs. *P. persimilis*) or diet (*E. stipulatus* alone) were the solely significant factor. Lowercase letters refer to cases where the interaction between diet and abiotic conditions was significant (the remaining figures; see Fig. 3 for *P. persimilis*, as differences between combinations were not significant). See Tables 2S-4S for statistical analyses.

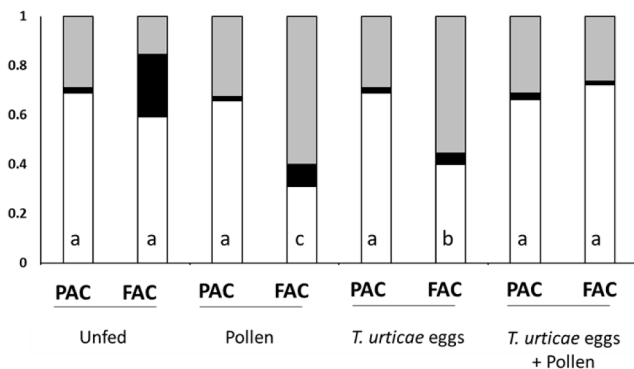


Fig. 3. Survival: escapees (grey bars), dead (black bars) and live (white bars) individuals of *Phytoseiulus persimilis* irrespective of whether alone or in combination with heterospecifics (see Fig. 2; n.s.d. between mite combinations). Phytoseiids were offered three different diets (pollen, *T. urticae* eggs, and a combination of both). An unfed control was also considered at present and future abiotic conditions (PAC: 25 ± 1 °C and 70 ± 5% RH; FAC and FAC: 30 ± 1 °C and 50 ± 5%, respectively). Survival bars with the same letters are not statistically different (GLMM; Bonferroni P < 0.05). See Table 4S for statistical analyses.

(Fig. 4c).

For *N. californicus* alone, diet and AC were significant, but their interaction was not (Table 2S). The provision of *T. urticae* eggs resulted in higher oviposition, which was highest at FAC, independently of pollen availability (Fig. 4d). When competing with *E. stipulatus*, only diet affected oviposition, with higher values observed when eggs of *T. urticae* were available independently of AC and pollen supply (Fig. 4e). When the competing pair was *P. persimilis*, the interaction between diet and AC was significant. In this case, though, oviposition only occurred when *T. urticae* eggs were available at FAC independently of pollen supply

(Fig. 4f)

Diet was the only factor affecting the oviposition of *P. persimilis* irrespective of whether alone or competing with a heterospecific phytoseiid (Table 3S). Oviposition was highest when *T. urticae* eggs were available (Fig. 4g, 4h, 4i), and only when competing with *E. stipulatus* the mixed diet resulted better than that of *T. urticae* eggs alone (Fig. 4h). No oviposition was recorded when pollen was the only food source available, but some oviposition occurred when unfed either alone (Fig. 4g) or when competing with *E. stipulatus* (Fig. 4h).

3.3. Predation

The effect of the interaction between diet and AC on predation was significant for all phytoseiids alone (Table 2) and when competing with a heterospecific, except in the case of the pair *P. persimilis* vs. *E. stipulatus*, where these two factors were not significant (Table 3).

For *E. stipulatus* alone, predation was highest at PAC when pollen was also available. Pollen supply, however, could not compensate for the harmful effects of FAC, and predation almost halved at FAC relative to PAC (Table 2). In the case of *N. californicus* alone, the highest predation occurred at FAC. Pollen supply successfully kept predation levels at FAC. For *P. persimilis* alone, the highest predation occurred at PAC when *T. urticae* eggs were the only available food. Similar to *N. californicus*, the pollen supply successfully kept predation levels at FAC.

When *N. californicus* was competing with *E. stipulatus*, the highest predation occurred at PAC when only *T. urticae* eggs were available and at FAC when a mixed diet was provided (Table 3). In all combinations, though, the observed predation values were lower than those expected. A similar situation was found for the pair *N. californicus* and *P. persimilis*. In this case, though higher predation occurred at FAC when no pollen was available. Contrarily, when the competing pair was *P. persimilis* and *E. stipulatus*, the observed predation values either matched or were even higher than those predicted except for PAC when no pollen was provided. However, this value was not significantly different from those

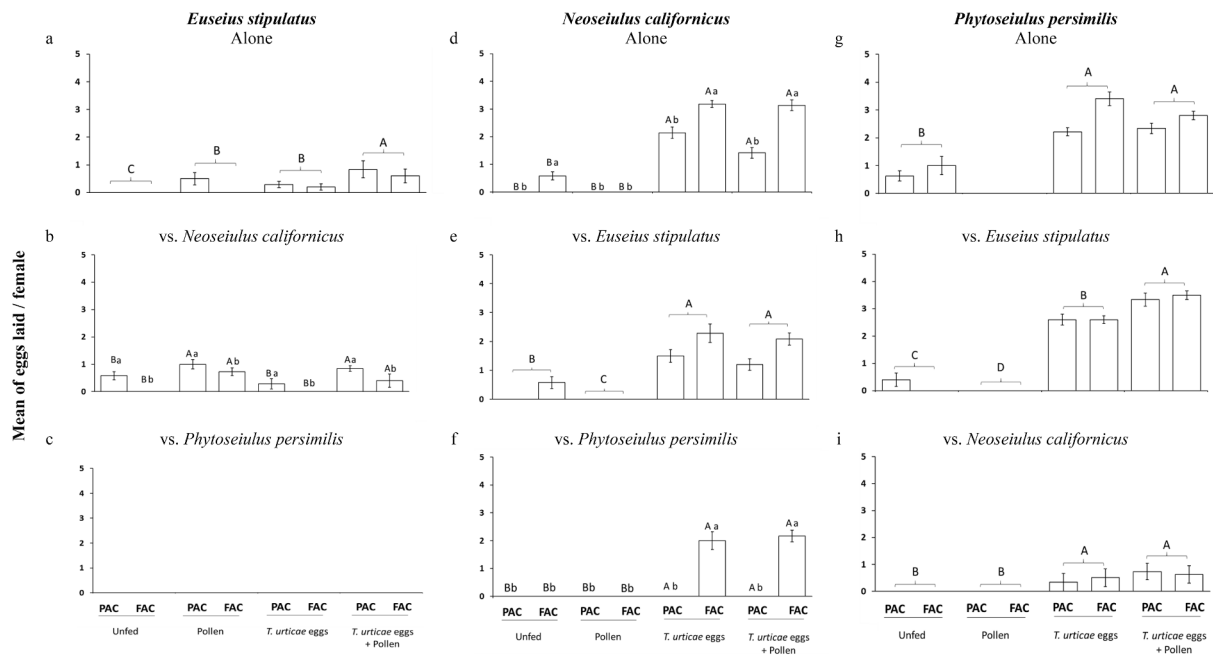


Fig. 4. Oviposition of *Euseius stipulatus*, *Neoseiulus californicus* and *Phytoseiulus persimilis* either alone or in competition with heterospecifics. Phytoseiids were offered three different diets (pollen, *T. urticae* eggs, and a combination of both). An unfed control was also considered at present and future abiotic conditions (PAC: 25 ± 1 °C and 70 ± 5% RH; FAC and FAC: 30 ± 1 °C and 50 ± 5%, respectively). Bars with the same letters are not statistically different (GLMM; Bonferroni P < 0.05). Because the interaction between diet and abiotic condition was never significant (see Tables 2S-4S for statistical analyses), capital letters refer to diet and lowercase letters to abiotic conditions.

Table 3

Observed and expected predation (number of eggs eaten) by *Euseius stipulatus*, *Neoseiulus californicus*, and *Phytoseiulus persimilis* when co-occurring in competition with heterospecifics. Phytoseiids were offered *T. urticae* eggs (T) and *T. urticae* eggs + pollen (TP) at present abiotic conditions (PAC; 25 ± 1 °C and 70 ± 5% RH), and future abiotic conditions (FAC; 30 ± 1 °C and 50 ± 5%).

Phytoseiid sp. combination	Diet	Abiotic conditions (AC)	Observed predation	Expected predation	χ^2	Statistics (F; df; P-value)
<i>Euseius stipulatus</i> vs <i>Neoseiulus californicus</i>	T	PAC	21.2 ± 2.8 a	27.7	P < 0.001	Diet: 5.31; 1; 0.123
		FAC	15.8 ± 2.7b	29.8	P < 0.001	AC: 14.1; 1; 0.078
	TP	PAC	14.6 ± 1.4b	31.5	P < 0.001	Diet*AC: 15.36; 1; 0.036
		FAC	22.8 ± 3.8 a	35.5	P < 0.001	
<i>Neoseiulus californicus</i> vs <i>Phytoseiulus persimilis</i>	T	PAC	26.5 ± 3.2b	55.5	P < 0.001	Diet: 14.35; 1; 0.003
		FAC	34.7 ± 2.5 a	46.4	P < 0.001	AC: 8.96; 1; 0.059
	TP	PAC	25.9 ± 1.8b	36.7	P < 0.001	Diet*AC: 14.21; 1; 0.002
		FAC	22.6 ± 3.6b	52.27	P < 0.001	
<i>Phytoseiulus persimilis</i> vs <i>Euseius stipulatus</i>	T	PAC	34.9 ± 1.7 a	43.6	P < 0.001	Diet: 2.32; 1; 0.712
		FAC	32.8 ± 2.5 a	24.1	P < 0.001	AC: 1.32; 1; 0.451
	TP	PAC	31.2 ± 1.8 a	37.8	P = 0.003	Diet*AC: 12.12; 1; 0.078
		FAC	31.9 ± 1.1 a	34.1	P = 0.032	

For each combination (phytoseiid-diet-abiotic conditions), chi-squared test (χ^2) was used to compare observed and expected predation.

For each phytoseiid combination, observed predation followed by the same letter is not significantly different (GLMM; Bonferroni post hoc test at P < 0.05).

observed in the other diet*AC combinations.

4. Discussion

The aim of this study was to assess (a) whether the provision of alternative food (pollen) could mitigate the negative effects of harsher conditions typical of climate change on interspecific competition between phytoseiids and (b) thus pollen supply could be an effective tactic for the conservation of these natural enemies in a rapidly approaching warmer future. Our results show that, in agreement with previous results (Urbaneja-Bernat and Jaques, 2020), access to high-quality pollen enhanced the performance under FAC of the generalist *E. stipulatus* in terms of survival and oviposition and that of *N. californicus* in terms of oviposition and predation (Table 4). When the phytoseiids considered in our study were forced to compete, pollen provision had contrasting

effects on survival and oviposition of each species depending on the competing pair (Table 5). Overall, though, predation levels were the same under PAC and FAC. However, these values were lower than those expected except in the case of the pair *P. persimilis* and *E. stipulatus*, which may be related to their extremely different lifestyles (McMurtry et al., 2013) and their shared geographical origin contrary to *N. californicus*. Therefore, pollen supply should be considered a helpful tactic to maintain the effectiveness of phytoseiids as biological control agents of *T. urticae* in a warmer future. Importantly, we observed more escapees than dead phytoseiid individuals (Figs. 2 and 3) and this result suggests that in the real world, these individuals would have been able to survive in refuges (i.e., crevices or cracks in branches). This behavior, which may impact predator fitness in terms of lost foraging time and reproduction opportunities when looking for shelter (Gillespie et al. 2012), may increase its survival under field conditions.

Table 4

Changes observed in survival, oviposition, and predation of the different phytoseiids considered in this study when comparing future and present abiotic conditions in control (=unfed) specimens and those offered *T. urticae* eggs (=eggs) with or without a supplement of pollen (=pollen). Data based Figs. 2-4 and Tables 2-3.

Phytoseiid	Parameter	Unfed vs. Pollen	Eggs vs. Eggs + pollen
<i>E. stipulatus</i>	Survival	Increase	Same
	Oviposition	Increase	Increase
	Predation	–	Same
<i>N. californicus</i>	Survival	Decrease (=0)	Decrease
	Oviposition	Decrease (=0)	Increase
	Predation	–	Increase
<i>P. persimilis</i>	Survival	Decrease	Same
	Oviposition	Decrease (=0)	Same
	Predation	–	Decrease

Table 5

Changes observed in survival, oviposition, and predation of the different phytoseiids considered in this study when competing in pairs and comparing future and present abiotic conditions in control (=unfed) specimens and those offered *T. urticae* eggs (=eggs) with or without a supplement of pollen. Data based Figs. 2-4 and Tables 2-3.

Pair (A vs. B)	Parameter	Unfed vs. Pollen		Eggs vs. Eggs + pollen	
		A	B	A	B
<i>E. stipulatus</i> vs. <i>N. californicus</i>	Survival	Decrease	Same	Decrease	Increase
	Oviposition	Increase	Same (=0)	Increase	Increase
	Predation	–	–	Same, lower than expected	
<i>E. stipulatus</i> vs. <i>P. persimilis</i>	Survival	Increase	Decrease	Decrease	Same
	Oviposition	Same (=0)	Same (=0)	Same (=0)	Same
	Predation	–	–	Same, as expected	
<i>N. californicus</i> vs. <i>P. persimilis</i>	Survival	Increase	Decrease	Increase	Same
	Oviposition	Same (=0)	Same (=0)	Increase	Same
	Predation	–	–	Same, lower than expected	

According to McMurtry et al. (2013), the three phytoseiid species considered in this study belong to different lifestyle groups with different diet specializations. *P. persimilis* belongs to the group of specialized predators of *Tetranychus* spp., which are adapted to attacking spider mites producing complicated web. *N. californicus* belongs to the group of selective predators of tetranychid mites and, unlike *P. persimilis*, *N. californicus* can feed on a broader range of tetranychid species and can feed and reproduce on mites of other families, as well as on pollen. Finally, *E. stipulatus* is a pollen feeding generalist predator, with a high reproductive capacity when feeding on high-quality pollen (Pina et al., 2012). Similar to other phytoseiids in this group, *E. stipulatus* is able to pierce leaf cells to feed (Messelink et al., 2008; Aguilar-Fenollosa et al., 2011c; Dunson and Travis, 1991; Cruz-Mirallas et al., 2021). Therefore, *P. persimilis* is the species with the narrowest host range from the three considered. This may explain why pollen showed almost no positive effects on the performance of this species (i.e., it maintained oviposition when competing with *E. stipulatus* and *T. urticae* eggs were available; Table 5) and also why this phytoseiid was the only one for which survival did not depend on the phytoseiid combination considered (Table 1). This result correlates well with results of earlier semi-field assays where the simultaneous release of the same pairs of phytoseiids included in the present study resulted in *P. persimilis* showing the same final densities irrespective of the heterospecific mite it was initially released with Urbaneja et al. (2019).

As expected from its feeding habits (McMurtry et al., 2013), *E. stipulatus* was the species most benefiting from pollen supply (Table 4). However, these benefits did not allow higher predation rates at FAC when competing with *N. californicus*, as already observed under semi-field conditions (Urbaneja-Bernat et al., 2019). Moreover, higher than expected predation rates observed when competing with *P. persimilis* at FAC coincided with lower survival and oviposition for *E. stipulatus*. This result, which also coincides with those observed in semi-field assays where this phytoseiid combination was the only one that did not lose efficacy under hotter and drier summer conditions (representative of future climate change in the Mediterranean basin conditions) compared to spring (Urbaneja-Bernat et al., 2019), could be explained by *P. persimilis* increased predation on *E. stipulatus* at FAC (Table 5). *E. stipulatus* has been considered a superior phytoseiid competitor (i.e., the intra-guild predator) as it adversely affected the establishment of *N. californicus* and *P. persimilis* (the intra-guild prey) in semi-field conditions in citrus at 25 °C and 70% RH (Abad-Moyano et al., 2010a). However, these authors did not check what could happen in harsher conditions typical of climate change. In line with González-Fernández et al. (2009) and Beltrà et al. (2017), our results show that pollen provision can boost *E. stipulatus* populations (Table 4), which in turn could be exploited by both *P. persimilis* and *N. californicus*. However, only in the case of *P. persimilis*, co-occurrence did not impair predation (Table 5). Co-occurrence of alternative food and the target pest may promote predator abundance and pest control through apparent competition (Holt, 1977), as reported in several studies (Messelink et al., 2008; González-Fernández et al., 2009; Nomikou et al., 2010; Aguilar-Fenollosa et al., 2011c; Maoz et al., 2011). Montserrat et al. (2013a) observed that although pollen supply promoted phytoseiid populations, under climate change conditions, biological control of the persea mite, *Oligonychus perseae* Tuttle (Acari: Tetranychidae), was disrupted in avocado. In that case, phytoseiid key predators were another generalist, *Euseius scutalis* (Athias-Henriot), and *N. californicus*. This highlights the importance of the co-occurring species on the result of the interaction, and eventually on the success of biological control. The disruption of the natural regulation of *T. urticae* observed by Urbaneja-Bernat et al. (2019) for combinations including *N. californicus* when comparing spring and summer semi-field conditions in citrus are consistent with the lower-than-expected values of predation found in pairs including *N. californicus*. These results could be related to the high reproductive performance of the *N. californicus* strain used in our studies (previously characterized by Toyoshima and Hinomoto (2004)), which suggests that it may have the potential to displace both native populations of the same species and different competing species. The fact that the populations of *E. stipulatus* and *P. persimilis* used in the present study were originally collected in two clementine orchards in the same area could also explain why the negative impacts of competition between these two species on predation were lower when released together than when released with *N. californicus*.

In conclusion, we have shown that the structure of the mite community occurring in Spanish citrus can be affected by abiotic conditions (present versus future climate change conditions) and food availability (pollen supply), and this is achieved through their effect on interspecific relationships such as competition among others (Dunson and Travis, 1991). Our work demonstrates that pollen provision can partially mitigate the negative effects of climate change on some of the biological parameters of the three main predators of *T. urticae* when they are competing in the system. Although pollen supply could be an effective tactic to maintain the effectiveness of these natural enemies in a rapidly approaching warmer future, contrary to what other authors have proposed (Montserrat et al., 2013b), in our case, pollen seems not to reduce the strength of intraguild predation. Indeed, our results point at all phytoseiids considered in our study preying on heterospecific eggs. Therefore, the occurrence of reciprocal intraguild predation (Montserrat et al., 2012, 2008; Schausberger and Croft, 2000) cannot be excluded and should be further considered. Only a thorough understanding of

how this system works will allow pest managers to take the most sound and sustainable decisions to maintain the efficacy of the biological control of a relevant pest as *T. urticae*.

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Ethics approval

This article does not contain any studies with human participants or animals performed by any of the authors.

Consent for publication and participate

Informed consent was obtained from all co-authors included in the study.

Code availability

Not applicable.

Authors' contributions

JAJ and PUB conceived and designed research, conducted the experiments, analyzed the results, and wrote the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocontrol.2021.104789>.

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