Effects of predation pressure and prey density on short-term indirect interactions between two prey species that share a common predator

S A R A   E .   E M E R Y[1,2] and N I C H O L A S   J .   M I L L S[1]   [1]Department of Environmental Science, Policy and Management, University of California, Berkeley, California, U.S.A. and [2]Department of Ecology, Agricultural Entomology Unit, Swedish University of Agricultural Science, Uppsala, Sweden

Abstract. 1. Generalist predators are important contributors to reliable conservation biological control. Indirect interactions between prey species that share a common generalist predator can influence both community dynamics and the efficacy of biological control.

2. Laboratory cage experiments investigated the impact of the combined consumptive and non-consumptive effects of predation by adult *Hippodamia convergens* as a shared predator on the population growth and relative abundance of *Acyrthosiphon pisum* and *Aphis gossypii* as prey species. Predation pressure and prey density were varied.

3. At low predation pressure the indirect interaction between aphid species was asymmetrical with a proportionally greater negative impact of predation on *A. gossypii* than on *A. pisum*. At intermediate predation pressure, the indirect interaction became symmetrical. At high predation pressure and higher levels of prey density, it was asymmetrical with greater negative impact on *A. pisum*, often driven to local extinction while *A. gossypii* populations persisted.

4. A linear mixed-effects model including early population growth of both aphid species and predation pressure explained 96% and 92% of the variation in the population growth of *A. pisum* and *A. gossypii*, respectively, over an 8-day period. The overall effect of shared predation on the indirect interaction between the two aphid species is best described as apparent commensalism, where *A. pisum* benefited from early population growth of *A. gossypii*, while *A. gossypii* was unaffected by early population growth of *A. pisum*. Considering these indirect interactions is important for conservation biological control efforts to be successful.

Key words. Aphididae, apparent commensalism, biological control, Coccinellidae.

Introduction

Numerous studies have addressed the importance of native predator and parasitoid assemblages in providing conservation biological control of herbivorous pests (Jonsson *et al.*, 2015, 2017; Begg *et al.*, 2017; Mace & Mills, 2017; Rusch *et al.*, 2017; Gardarin *et al.*, 2018; Shields *et al.*, 2019; Snyder, 2019), and the question of whether interactions between multiple generalist predators limit control through intraguild predation or add to it through complementarity (Gontijo *et al.*, 2015; Tscharntke

et al., 2016; Riggi *et al.*, 2017; Roubinet *et al.*, 2017, 2018; Snyder, 2019). Although effective control by generalist predators has been shown, these evaluations most often focus on the impact of either single or multiple predators on the population growth of a single focal prey species (Losey & Denno, 1998; Symondson *et al.*, 2002; Donaldson *et al.*, 2007; Gardiner & Landis, 2007; Gardarin *et al.*, 2018; Vandervoet *et al.*, 2018). The biological control potential of generalist predators on a focal prey species in the inevitable context of multiple prey species is less frequently considered (but see Koss *et al.*, 2004; Messelink *et al.*, 2010; Krey *et al.*, 2017). Whenever multiple prey species exist, however, both the direct effects of predation on multiple prey populations and the indirect effects of predators on prey community dynamics must be considered to

Correspondence: Sara E. Emery, University of California Berkeley, Department of Environmental Science, Policy and Management, 130 Mulford Hall, Berkeley, CA 94720-3114, U.S.A. E-mail: sara.emery@slu.se

accurately quantify biological control potential (Alhmedi *et al.*, 2011; Jaworski *et al.*, 2015; Ingerslew & Finke, 2018).

Populations of two prey species that do not compete directly for food resources can nevertheless interact indirectly via a shared predator when in close spatial proximity. These indirect interactions are common, can range from positive to negative and can be either symmetrical or asymmetrical between the two prey species (Abrams & Matsuda, 1996; Chaneton & Bonsall, 2000; Brassil & Abrams, 2004; Tack *et al.*, 2011). Apparent competition, the mutually negative effect of one prey species on the population of another mediated by a shared natural enemy (Holt, 1977; Holt & Bonsall, 2017), is an important indirect interaction that can structure insect communities through both time and space (Blitzer & Welter, 2011; Jaworski *et al.*, 2015; Frost *et al.*, 2016). Apparent amensalism (Chaneton & Bonsall, 2000) in which the population of one species is negatively affected, but the other is not, and apparent commensalism (Dethier & Duggins, 1984), whereby one species benefits, but not the other, have also been documented in insect communities with co-occurring prey species that do not directly interact (van Nouhuys & Kraft, 2012; Blubaugh *et al.*, 2018). Finally, apparent mutualism is a positive effect between prey species when the impact of a shared predator is limited and the two prey species buoy each other to mitigate the negative effects of predation (Abrams & Matsuda, 1996). Although often neglected, the effects of positive indirect interactions in shaping community dynamics might have been underestimated (Ims *et al.*, 2011; Tack *et al.*, 2011; van Maanen *et al.*, 2012). Theory suggests that mutually positive and mutually negative indirect effects are the extremes of a continuum and that transition between them in a single community can be mediated by frequent shifts in the transient dynamics of predator and prey populations (Brassil & Abrams, 2004).

Predator preference, satiation and prey switching are the factors thought to be responsible for changes in the strength and directionality of consumptive effects of predation on the indirect interactions between prey (Abrams & Matsuda, 1996; Holt & Bonsall, 2017). Another form of indirect interaction between predators and prey relates to non-consumptive or trait-mediated effects in which prey respond to the presence of a predator through shifts in host plant preference, within-plant distribution, predator-avoidance behaviour and/or reductions in feeding and reproduction (Preisser *et al.*, 2005; Buchanan *et al.*, 2017; Hermann & Landis, 2017). There is often a trade-off between risk of predation and prey fitness associated with the non-consumptive effects of predation, caused by prey moving to plant species or parts of a plant that have lower nutritive value. While non-consumptive effects of predation are typically negative for prey populations, they can vary from symmetrical to asymmetrical and so consequently can also influence the continuum of indirect interactions in a way that is analogous to the effects of predator preference. Figure 1 illustrates the hypothesised effects of both consumptive and non-consumptive aspects of predation on the continuum of indirect interactions between prey species. Most of the research on indirect interactions represents snapshots in time (Muller & Godfray, 1997; Blitzer & Welter, 2011; Jaworski *et al.*, 2015; Blubaugh *et al.*, 2018) and does not evaluate the possibility that such interactions within a community can range from positive to negative over short time periods and under different environmental circumstances (but see Long *et al.*, 2012). In addition, many interaction models fail to take into account the
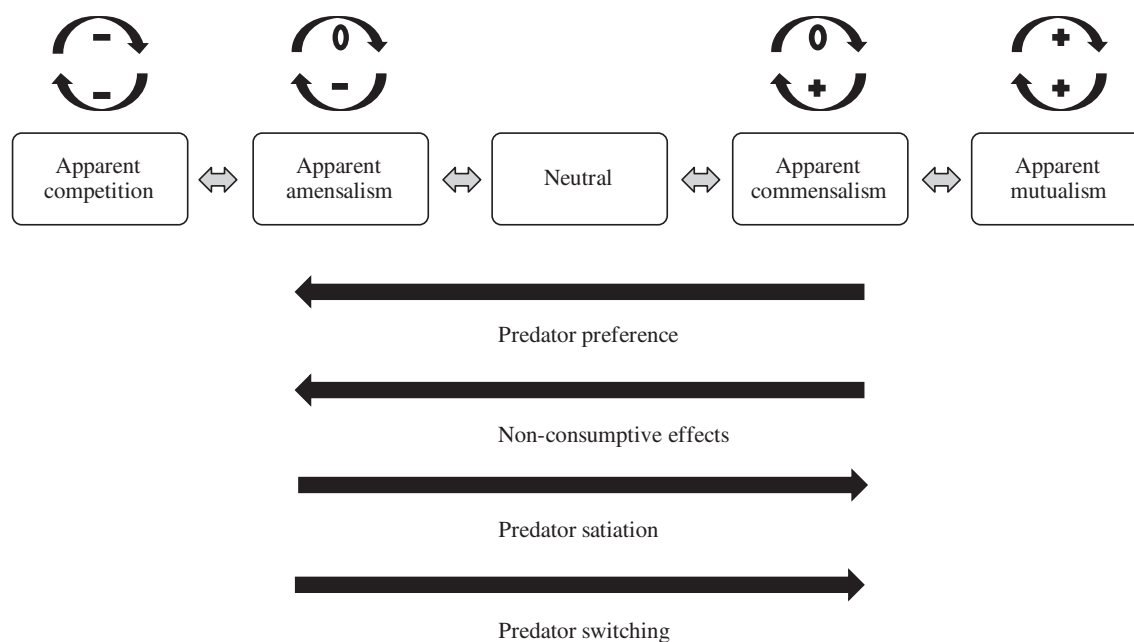
Fig. 1. A schematic illustration of the continuum of possible indirect interactions among prey species along with factors that can affect the sign, strength or symmetry of the indirect interactions. '+', '0' and '−' represent the effects of the indirect interaction on each prey species that result from the impact of predation by a shared predator.

habitat complexity and prey density that predators and prey encounter in the real world which can lead to short-term changes in the saturation of predator functional responses (Abrams & Matsuda, 1996).

At shorter timescales, less than a predator generation, indirect interactions among prey species can result from changes in either predator or prey behaviour (Holt & Lawton, 1994). While none of the behavioural drivers occur independently of each other, the resultant balance of these combined effects may still differentially affect the relative abundance of prey species and consequently the indirect interactions between them. Rather than trying to isolate the role of any specific driver of predation effects on indirect interactions between prey, the main goal of this study was to evaluate whether the combined consumptive and non-consumptive effects of predation on the population growth and relative abundance of two prey species that share a common predator can be altered under varying environmental circumstances. The two prey species used in this study were *Acyrthosiphon pisum* Harris (green pea aphid) and *Aphis gossypii* Glover (cotton aphid; Hemiptera: Aphididae), which are both important agricultural pests (Blackman & Eastop, 2017). The shared predator was *Hippodamia convergens* Guérin-Méneville (Coleoptera: Coccinellidae), a consistent component of the natural enemy assemblages of both aphid species (Frazer & Gilbert, 1976; Wells *et al.*, 2001). The interactions between these three species were manipulated either by increasing predation pressure (number of predators per cage) or by increasing prey density (reducing the number of plants per cage). By increasing either predation pressure or prey density, predator consumption of aphid prey would increase such that one or both prey species would probably be driven to local extinction. At lower rates of predator consumption, however, indirect interactions between aphid species would probably be more variable and could be driven towards apparent competition through predator preference and non-consumptive effects, or towards apparent mutualism through predator switching and satiation (Fig. 1). A second goal of the study was to determine whether the effects of predation on early population growth of one aphid species could add to the predictive power of the experimental treatment in explaining the population growth of the other aphid species over the course of the experiment.

Materials and methods

A series of laboratory cage experiments examined the effects of predation pressure and initial prey density per plant on the population growth of *A. pisum* and *A. gossypii*. The two aphid species were collected from urban gardens in the spring of 2015 in Berkeley, California. Colonies of both aphid species were kept separately in a greenhouse set at a temperature of 18 °C and reared on potted *Vicia faba* plants. *Hippodamia convergens* were obtained from Rincon-Vitova Insectaries, Inc. (Ventura, California) as overwintering batches of 500 adults that were stored in a cold room at 5 °C. Before each experiment, the adult beetles were transferred to an incubator at 18 °C in individual Petri dishes lined with moist filter paper, and after 48 h vigorously active individuals were selected for experiments.

An initial experiment was conducted to evaluate whether *H. convergens* shows any prey preference between *A. gossypii* and *A. pisum*. A single adult *H. convergens* was placed in a 22-ml translucent polystyrene cup (SOLO, Highland Park, Illinois) with wet filter paper with 20 adults of each aphid species. A set of 36 replicate cups were kept at 18 °C over a 24-h period to compare the number of *A. gossypii* and *A. pisum* that remained alive, using a *t*-test.

The environmental circumstances under which the two aphid species interacted via a shared predator were manipulated via either predation pressure or initial prey density per plant. The experiments were conducted in organdy-sided sleeve cages ($1 \times 1 \times 1$ m) in an insectary room that was held at 20 °C and LD 16:8 h. Inside the cages broad bean (*Vicia faba*) plants (30–40 cm high) in individual 10-cm plastic pots provided a food source for both aphid species and were watered every second day. Each level of the predation pressure and prey density treatments consisted of 15 replicates carried out in blocks of five cages randomly initiated on each of three separate weeks. On day 0 of each 8-day experiment, 40 individuals each of *A. pisum* and *A. gossypii* were placed onto the apical meristem of potted bean plants in each cage. Individuals of both species were a mix of fourth-instar and adults. To reduce the likelihood of direct interaction between the aphid species, plants were placed equidistant from each other in two rows on either side of the cage with one aphid species assigned randomly to plants on either side. At the beginning of each experiment, plants neither touched each other nor the sides of the cages. Aphids were subsequently counted on day 4 and day 8 of each experiment and recorded as the number of each species per cage.

Predation pressure

To evaluate the effect of predation pressure, the number of adult predators was manipulated in four treatment levels with either zero, one, five or 10 *H. convergens* per cage and an initial prey population of 40 aphids of each species. Each cage had eight potted bean plants and 10 *A. pisum* or *A. gossypii* were placed on the apical meristem of each plant on day 0.

Prey density

In a separate set of experiments, predator abundance was held constant at five adult *H. convergens*, while prey density was manipulated by altering the number of plants per cage, consequently simplifying the habitat as well. To evaluate this effect, three treatment levels consisted of either eight, four or two potted bean plants per cage such that the initial aphid densities per plant were 10, 20 or 40, respectively.

Statistical analysis

All statistical analyses were conducted using R v.3.4.2 (R Development Core Team, 2017). To address the two main goals of the study, the impact of predation on the two aphid species, from a combination of consumptive and

non-consumptive effects, was analysed using two separate approaches. For the first approach log response ratios (RR) were used separately for each aphid species as a measure of the strength (effect size) of the negative impact of predation, and mean ratios of the log abundance of the two aphid species were used as a measure of the symmetry of the impact of predation on each aphid species. In each case, the impacts of predation at each treatment level were compared with the control (no *H. convergens* for predation pressure and 10 aphids per plant for prey density).

For both the predation pressure and prey density experiments, log RR was used to estimate the log-proportional difference between the mean of a particular treatment level and that of a control (Hedges *et al.*, 1999). As log RR is biased at small sample sizes, following Lajeunesse (2015), a delta correction (RR^Δ, Eqn 1) and its variance [$var(RR^\Delta)$; Eqn 2] were used based on the standard deviation (SD), sample size (N) and mean ($\overline{X}$) of the treatment (T) and control (C):

$$RR^\Delta = \ln \frac{\overline{X}_T}{\overline{X}_C} + \frac{1}{2}\left[\frac{(SD_T)^2}{N_T \overline{X}_T^2} - \frac{(SD_C)^2}{N_C \overline{X}_C^2}\right] \quad (1)$$

$$var(RR\Delta) = \left[\frac{(SD_T)^2}{N_T \overline{X}_T^2} + \frac{(SD_C)^2}{N_C \overline{X}_C^2}\right] + \frac{1}{2}\left[\frac{(SD_T)^4}{N_T^2 \overline{X}_T^4} + \frac{(SD_C)^4}{N_C^2 \overline{X}_C^4}\right] \quad (2)$$

The mean ratio of the log abundance of *A. pisum* relative to that of *A. gossypii* was used as a measure of the symmetry of the impacts of predation on the two aphid species. A constant of 0.1 was added to aphid abundance before transformation using $\log_e$ (Gelman & Hill, 2007). As the treatment levels in each experiment were expected to alter the indirect interactions between aphid species, the relationship between the mean abundance of the two aphids across treatment levels was also examined graphically for days 4 and 8. For each experiment the mean ratios of log abundance at each treatment level were tested for significant differences from the control using a Welch two-sample *t*-test (Liermann *et al.*, 2004). A significant departure from the control mean ratio provided evidence of an asymmetrical benefit for one species over the other from the combined consumptive and non-consumptive effects of predation. Although significance tests were performed on transformed data, for ease of interpretation, back-transformations for $\log_e$ are also reported.

As a second step in the analysis, linear mixed models were used to test whether early population growth (difference in abundance between days 0 and 4) of one aphid species could add to the experimental treatment (predation pressure or prey density) to explain the net change in abundance (difference between days 0 and 8) of the other aphid species. In this case, a significant contribution of early population growth was expected to indicate the importance of the indirect interaction between the aphid species and the sign of the fitted coefficient to indicate whether the balance of these combined effects was positive (a shift towards apparent mutualism) or negative (a shift towards apparent competition). Models were developed using the function 'lmer' of the LME4 package (Bates *et al.*,

2015) to evaluate the direct effects of the experimental treatment and early population growth of the same aphid species, as well as any indirect effects of early population growth by the other aphid species on net change in abundance of each aphid species. As some of the treatment effects appeared nonlinear, models including quadratic polynomials were compared with models with linear effects only using the Akaike information criterion (AIC). Block was included as a random effect. Root mean square error (RMSE) was used to compare the observed net change in abundance with that predicted from the linear mixed-effects model for predation pressure. A simpler linear model was developed for the prey density experiment as aphid abundance in this experiment was too low by day 8 for early population growth to contribute effectively to an explanation of the outcome.

Results

There was no significant difference in the number of *A. pisum* adults (mean = 9.2, SD = 3.8) and *A. gossypii* adults (mean = 9.8, SD = 3.3) that remained alive after 24 h ($t = -0.7$, $P = 0.5$, $n = 36$), indicating that *H. convergens* had no inherent preference for either species of aphid prey.

Predation pressure

In the absence of predation, *A. gossypii* exhibited exponential growth, but the population growth of *A. pisum* was linear (Fig. 2a). The mean abundance of the aphid species in the absence of predation was used as a baseline control for the effect size (RR^Δ) of different levels of predation pressure on each aphid species. The negative impact of predation for both aphid species increased with time and predation pressure, and was proportionally greater for *A. gossypii* than for *A. pisum* except at the highest level of predation pressure (Fig. 3a; Table S1). The mean ($\pm$ SE) ratio of the log abundance of *A. pisum* to *A. gossypii* in the absence of predation on day 4 was 1.04 ± 0.01, indicating that the *A. pisum* population grew more rapidly in the first half of the experiment than did *A. gossypii*. On day 8 in the absence of predation, the mean ratio was 0.92 ± 0.01, indicating that the *A. gossypii* population was consistently more abundant than that of *A. pisum* by the end of the experiment. At low predation pressure (one adult *H. convergens*) the mean ratio on day 4 was marginally greater than that of the control (1.11 ± 0.04, $t = -1.9$, d.f. = 15.9, $P = 0.07$) and on day 8 was significantly greater than that of the control (0.99 ± 0.03, $t = -2.4$, d.f. = 17.8, $P = 0.03$; Fig. 3b; Table S2). This indicated that low predation pressure had a more significant negative impact on *A. gossypii* than on *A. pisum*. At intermediate predation pressure (five adult *H. convergens*) the mean ratio on day 8 (0.85 ± 0.04) was not statistically different from that of the control ($t = 1.5$, d.f. = 15.1, $P = 0.15$), although on day 4 the mean ratio was significantly greater than that of the control (1.12 ± 0.03, $t = -2.5$, d.f. = 16.6, $P = 0.02$). At the highest predation pressure (10 adult *H. convergens*) the mean ratio on both days 4 and 8 was significantly lower than that of the control (day 4, $t = 7.6$, d.f. = 21.9, $P < 0.001$; day 8, $t = 12.8$, d.f. = 19.7, $P < 0.001$). Populations of *A. gossypii*
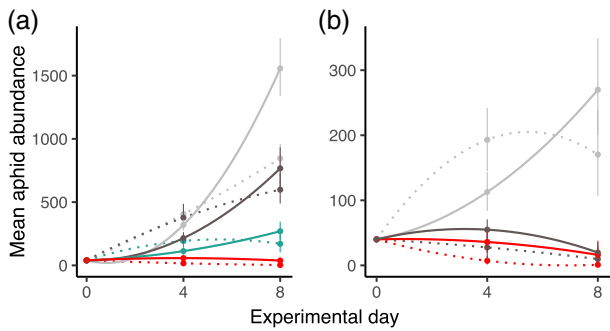
Fig. 2. Aphid population growth over the course of the experiment for *Acyrthosiphon pisum* (dotted lines) and *Aphis gossypii* (solid lines) in relation to: (a) predation pressure for the absence of predators (grey) and the presence of one (black), five (green) or 10 (red) adult *Hippodamia convergens*; (b) initial aphid density for 10 aphids per plant (grey), 20 aphids per plant (black) or 40 aphids per plant (red). The points are means per cage (± SE). [Colour figure can be viewed at wileyonlinelibrary.com].

were able to persist whereas those of *A. pisum* were driven to local extinction at high predation pressure in 11 out of 15 cages.

In the linear mixed-effects model, early population growth of both *A. pisum* and *A. gossypii* had significant positive effects on the net change in abundance of *A. pisum* over the course of the experiment (Table 1). The effect of increasing predation pressure from *H. convergens* on the abundance of *A. pisum* was better described by a quadratic polynomial [AIC = 704, $\chi^2(1, 60) = 18.7$, $P < 0.001$; Fig. 4a] than by a linear relationship (AIC = 720). These three factors contributed to a model with high predictive power (RMSE = 68.9, Table 1). For the net change in abundance of *A. gossypii*, however, only the early population growth of *A. gossypii* and predation pressure provided significant explanatory power in the linear mixed-effects model (Table 1). The effect of predation pressure on the net change in abundance of *A. gossypii* was also better described by a quadratic polynomial [AIC = 816, $\chi^2(1, 60) = 7.4$, $P = 0.007$; Fig. 4b] than by a linear relationship (AIC = 821). The two-factor model for net change in abundance of *A. gossypii* also had good predictive power (RMSE = 165.7; Table 1).

Prey density

Increasing prey density per plant caused negative growth for *A. pisum* populations throughout the experiment, while *A. gossypii* populations were more stable especially in the first 4 days of the experiment (Fig. 2b). The negative impact of predation on both aphid species increased with time and prey density as indicated by the delta-corrected log RR (Fig. 3c; Table S1). In contrast to the predation pressure experiment, however, increased prey density per plant at a constant predation pressure of five *H. convergens* per cage had a proportionally larger negative effect on *A. pisum* than on *A. gossypii*. The mean ratio of the log abundance of *A. pisum* to *A. gossypii* was lower than the control on day 4 (Fig. 3d; Table S2), but was not significantly different from the control on day 8 for either the 20 aphids per plant ($t = 1.5$, d.f. = 14.0, $P = 0.15$)

or the 40 aphids per plant treatment levels ($t = 1.8$, d.f. = 14.0, $P = 0.1$). Although the variability of the mean ratios of log abundance between replicates appeared quite high for the low levels of aphid abundance that resulted from these experiments, the back-transformation of the logs shows that they were not unreasonable (Table S2). Both the intermediate and high prey density treatment levels showed that while *A. gossypii* populations were often able to persist, those of *A. pisum* were consistently driven to local extinction (13 and 14 out of 15 cages, respectively).

Early population growth provided no useful explanatory power for the net change in abundance of the aphid populations in the mixed effects models for either aphid species as the populations of *A. pisum* were driven to local extinction by day 4 in half of the replicates at both increased aphid density treatment levels. The effect of prey density on the net change in abundance of the aphids was also nonlinear (Fig. 4b). A quadratic polynomial provided a better fit overall than a linear relationship for both *A. pisum* [AIC = 532 vs. 540, $\chi^2(1, 45) = 10.4$, $P = 0.001$] and *A. gossypii* [AIC = 540 vs. 550, $\chi^2(1, 45) = 12.14$, $P < 0.001$].

Discussion

The main goal of the study was to evaluate whether different predation pressures and prey densities can alter the impact of the combined consumptive and non-consumptive effects of predation by *H. convergens* on the population growth of *A. gossypii* and *A. pisum*. Although the indirect interactions could not be directly quantified, we were able to provide evidence for a proof of concept that indirect interactions between prey species that share a common predator can be shifted in the short term and can change to favour one or other prey species with varying predation pressure and prey density.

A number of factors are known to influence the indirect interactions between two prey species that share a common predator (Holt & Hochberg, 1997). As predator preference leads to apparent competition, a critical first step was to establish if there was any evidence for preference between the two aphid species by *H. convergens*. In the absence of predator preference, even if non-consumptive effects of predation are present, there is a greater opportunity for a shift in the sign of the indirect interactions between prey species from negative to positive through predator satiation or switching (Abrams & Matsuda, 1996).

In our analysis of the two experimental treatments, predation pressure and prey density, we compared the relationships between the relative abundance of the two aphid species over the duration of each experiment. The delta-corrected response ratio quantified the effect size of predation on *A. pisum* and *A. gossypii* individually in proportion to their abundance in the controls. This was useful as a measure of the strength of the impact of predation and also served as an initial indicator of potential asymmetrical effects between the two aphid species. The *t*-test of the mean ratios of the log abundance of *A. pisum* to *A. gossypii* was then used to test for asymmetry in comparison to the mean ratios of the control treatments. While asymmetry provided evidence that one aphid species benefited relative to the other in the
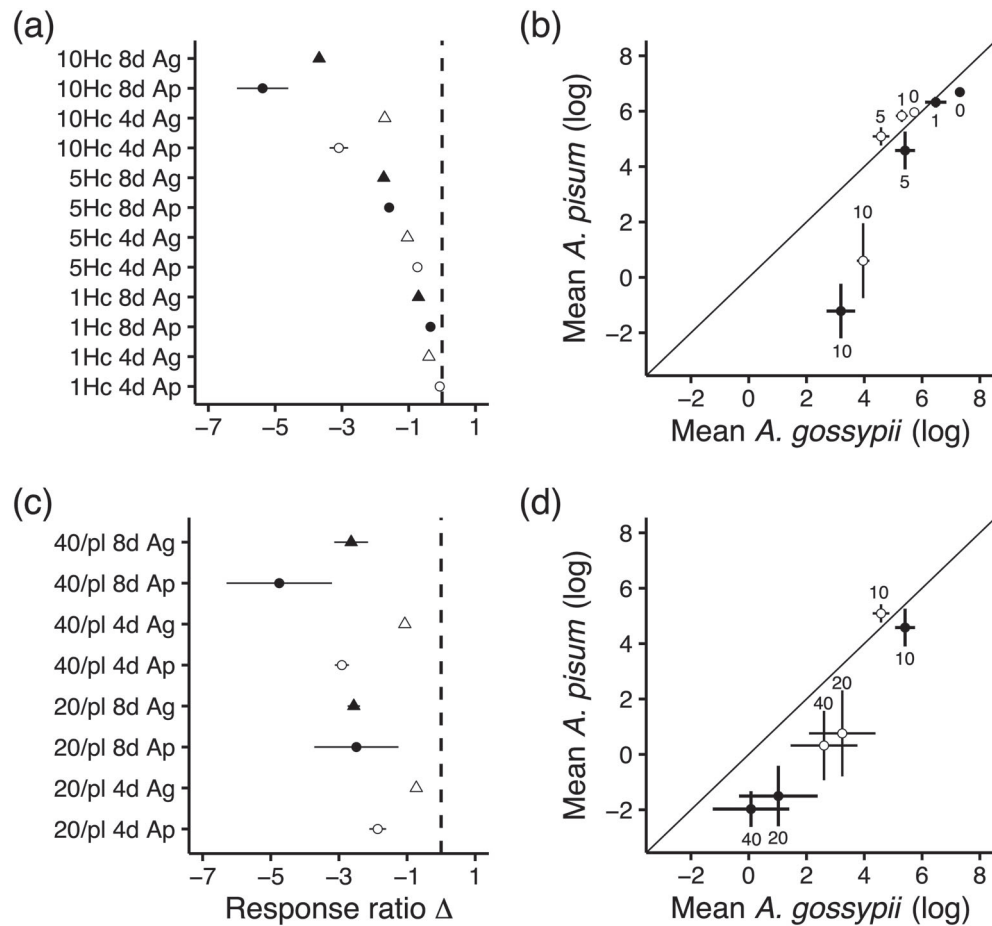
Fig. 3. Relationships between the relative abundance of *Acyrthosiphon pisum* (Ap) and *Aphis gossypii* (Ag) for different levels of predation pressure from *Hippodamia convergens* (Hc) adults (a, b) and prey density per plant ('/pl') (c, d). For (a, c) the dashed vertical line at a log response ratio of zero indicates no change in mean abundance from the control (0Hc or 10 aphids per plant) and each data point shows the delta-corrected log response ratio on days 4 (open) and 8 (filled) for each treatment level $\pm$ var(RR$^\Delta$). Circles are data for *A. pisum*, triangles for *A. gossypii*. Data points with error bars that do not cross the vertical dashed line were significantly different from the mean abundance of the control treatment. For (b, d) the mean log abundance of *A. pisum* and *A. gossypii* ($\pm$ 2SE) are compared for day 4 (open, treatment values above) and day 8 (filled, treatment values below) in relation to a 45° solid line showing equal mean abundance of the two aphids.

Table 1. Effects of predation pressure from *Hippodamia convergens* and early aphid population growth on the net change in aphid abundance between day 0 and day 8 for *Acyrthosiphon pisum* and *Aphis gossypii* from the fitted linear mixed-effects models.

| Component model	R_m^2	R_c^2	Intercept	# *H. convergens*	# *H. convergens*^{2}	Early growth *A. pisum*	Early growth *A. gossypii*
A. pisum net change (days 0–8)	0.95	0.96	160.0	−90.9	7.3	1.2	0.7
A. gossypii net change (days 0–8)	0.89	0.92	466.0	−164.2	11.3	NS	3.3

All factors with estimated coefficients have a $P < 0.05$.
NS, not significant; R_m^2, marginal R^2 value for fixed effects only; R_c^2, conditional R^2 value that also includes random effects; # *H. convergens*^{2} refers to the second-order polynomial term in the model.

presence of a shared predator, it did not allow us to distinguish positive from negative indirect interactions between the aphids or consumptive from non-consumptive effects of the predator. Consequently, we used linear mixed-effects models in which early population growth of one aphid was tested as an additional explanatory factor for the net change in abundance of the other

aphid to evaluate the sign and strength of the indirect interaction between aphid species.

From the predation pressure experiment, we found that low predation pressure had a strong negative asymmetrical impact on *A. gossypii* population growth (Fig. 3a), despite high predator satiation. This asymmetric indirect interaction between aphid
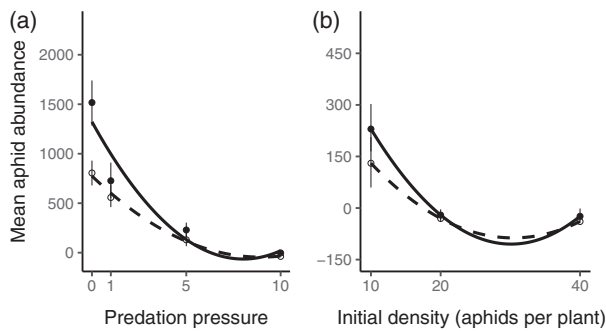
Fig. 4. The impact of predation on the net change in abundance (days 0–8) of *Acyrthosiphon pisum* (dashed line, open circles) and *Aphis gossypii* (solid line, filled circles) in relation to: (a) predation pressure (*A. pisum*, $y = 774.4 - 183.1x + 10.2x^2$, $R^2 = 0.77$, $P < 0.001$; *A. gossypii*, $y = 1322.3 - 345.7x + 21.5x^2$, $R^2 = 0.73$, $P < 0.001$); and (b) initial prey density (*A. pisum*, $y = 20.4 - 410.4x + 323.5x^2$, $R^2 = 0.49$, $P < 0.001$; *A. gossypii*, $y = 62.0 - 609.0x + 514.4x^2$, $R^2 = 0.64$, $P < 0.001$). The data points are means per cage ($\pm$ SE).

species may have resulted either from differential foraging success of the predator or from asymmetric non-consumptive effects on the prey. While we were able to rule out an inherent preference of the predator for one or other aphid species, we failed to consider differential predator foraging success for the two aphid species on living plants as a component of prey preference, although it is known to affect the predation efficacy of *H. convergens* (Grevstad & Klepetka, 1992; Eigenbrode *et al.*, 1998). As *A. gossypii* disproportionately colonised the apical meristem of the bean plants while *A. pisum* colonies more evenly colonised the plant, it remains possible that differential foraging success by *H. convergens* could have contributed to the asymmetrical effect. However, the extent of the difference in abundance of *A. gossypii* between control and low predation pressure treatments (Fig. 2a) was too large to be attributable to direct consumption by a single adult *H. convergens*. As a result, we suspect that this effect was primarily due to asymmetric non-consumptive effects of predation on *A. gossypii*. In addition, by day 8 at low predation pressure, the relative abundance of *A. pisum* and *A. gossypii* was statistically equal (with a mean ratio very close to 1), perhaps indicating circumstances in which low levels of predation can have a stabilising effect on the dynamics and persistence of two-prey systems (Oaten & Murdoch, 1975). The asymmetric impact of predation on the two aphids may, in fact, have created a situation in which *A. pisum* populations could have persisted over time through linear growth without being outcompeted by the exponential population growth of *A. gossypii* (Sanders & van Veen, 2012). By contrast, at intermediate predation pressure (five adult *H. convergens*), the mean ratio of abundance was statistically equivalent to that of the control treatment, indicating a symmetric indirect interaction between the two aphids (Fig. 3b). With multiple predators present in each cage, the change from asymmetry at low predation pressure to symmetry at intermediate predation pressure may have been due to interactions among predator individuals. For example, predator interference may have promoted increased movement and facilitated predator

switching or reduced levels of predator satiation. In addition, at low and intermediate levels of predation pressure, both aphid species were able to persist throughout the experiment as the impact of direct consumption by *H. convergens* was not excessive.

At the highest level of predation pressure and the two higher prey densities, the impact of predation was also asymmetrical, but under these conditions the strongest negative impact was on *A. pisum* rather than *A. gossypii*, and a few *A. gossypii* individuals seemed to consistently survive while *A. pisum* was frequently driven to local extinction. We had expected that higher prey densities would have resulted in saturation of the predator functional response and a greater incidence of predator satiation. However, direct consumption by the multiple *H. convergens* in these treatments proved to be too intense. In addition, *A. pisum* may have suffered from greater non-consumptive effects of predation under these treatment conditions, as the characteristic dropping behaviour of this species in response to predation may have reduced rates of aphid reproduction (Nelson, 2007). The fact that populations of *A. gossypii* were able to persist under these treatment conditions also suggests that the apical meristems of the bean plants provided some protection from predation for younger aphids.

The second goal of this study was to determine whether early population growth of one aphid species could add to the causal prediction of the net change in abundance of the other aphid species over the duration of the experiment. Although the impact of predation was too high in the prey density experiment, linear mixed-effects models provided a useful approach to evaluating the contribution of both direct and indirect effects of predation on aphid population growth in the predation pressure experiment. Using a quadratic polynomial to explain the nonlinearity of predation pressure, the linear mixed-effects models for each aphid species performed well. It was surprising that the early population growth of *A. pisum* did not contribute any explanatory power to the net change in abundance of *A. gossypii*, considering that the *A. pisum* populations grew more quickly in the first half of the experiment than did the *A. gossypii* populations in all but the highest treatment level. Early population growth of *A. gossypii*, however, did make a significant positive contribution to the net change in abundance of *A. pisum*. The overall effect of shared predation on the indirect interaction between the two aphid species may be thought of as apparent commensalism where *A. pisum* generally benefited from early population growth of *A. gossypii*, while *A. gossypii* was unaffected by early population growth of *A. pisum*. Though short-term apparent commensalism has been less of a focus in the literature on indirect interactions, it can have significant negative impacts on the potential for effective biological control (Bompard *et al.*, 2013; Chailleux *et al.*, 2014; Blubaugh *et al.*, 2018).

This study would have benefited from a greater range of low to intermediate levels of predation pressure and prey density as aphid populations were driven to very low abundance or local extinction at the higher treatment levels. Furthermore, in order to better quantify the indirect interactions between *A. pisum* and *A. gossypii*, an additional set of control treatments

in which each aphid species was present alone, both with and without predation pressure, would have allowed a more rigorous assessment of whether the indirect interactions were positive or negative. Under such conditions, the experiments could also have been run for a slightly longer period of time with frequent sampling to better capture the environmental circumstances that led to a change in the strength and sign of the indirect interactions between aphid species (Holt & Lawton, 1994). Negative indirect interactions, in particular, are hypothesised to occur over longer time periods as many predator species show aggregative responses to patches with high prey abundance (Muller & Godfray, 1997; Chailleux *et al.*, 2014). Finally, path analysis could also have been a helpful approach for disentangling the complex interactions along the continuum of negative to positive indirect interactions among multiple prey species with shared predation (Wootton, 1994).

The value of mesocosm experiments conducted under controlled environmental conditions, as used in this study, is that the dynamics of the interactions between two prey species and a shared predator can be monitored over time and add further detail to the snapshot interactions that have been observed in larger field studies. It is especially important to determine experimentally how and when these indirect interactions can shift in order to relate such changes to the context of how and when conservation biological control programmes that depend on generalist predators succeed or fail (Van Veen *et al.*, 2006; Chailleux *et al.*, 2014).

Acknowledgements

Author contributions

SEE and NJM designed the study. SEE collected and analysed the data. Both authors discussed the theoretical background and study hypotheses. SEE wrote the first version of the manuscript and NJM contributed substantially to subsequent editing.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. The delta-corrected log response ratio (RR^Δ) and variance ($\text{var}\, RR^\Delta$) relative to the controls (zero *H. convergens* for predation pressure and 10 aphids per plant for aphid density) for *A. pisum* (Ap) and *A. gossypii* (Ag) on days 4 and 8 for the different treatment levels of both experiments.

Table S2. The mean ratio of the log abundance of *A. pisum* (Ap) to *A. gossypii* (Ag) and standard error, and the back-transformed equivalents on days 4 and 8 for the different treatment levels of both experiments.

References

Abrams, P.A. & Matsuda, H. (1996) Positive indirect effects between prey species that share predators. *Ecology*, **77**, 610–616.

Alhmedi, A., Haubruge, E., D'Hoedt, S. & Francis, F. (2011) Quantitative food webs of herbivore and related beneficial community in non-crop and crop habitats. *Biological Control*, **58**, 103–112.

Bates, D.M., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**, 1–48.

Begg, G.S., Cook, S.M., Dye, R., Ferrante, M., Franck, P., Lavigne, C. et al. (2017) A functional overview of conservation biological control. *Crop Protection*, **97**, 145–158.

Blackman, R.L. & Eastop, V.F. (2017) Taxonomic issues. *Aphids as Crop Pests* (ed. by H. F. van Emden and R. Harrington), pp. 1–36. CAB International, Oxfordshire, U.K.

Blitzer, E.J. & Welter, S.C. (2011) Emergence asynchrony between herbivores leads to apparent competition in the field. *Ecology*, **92**, 2020–2026.

Blubaugh, C.K., Asplund, J.S., Eigenbrode, S.D., Morra, M.J., Philips, C.R., Popova, I.E. et al. (2018) Dual-guild herbivory disrupts predator-prey interactions in the field. *Ecology*, **99**, 1089–1098.

Bompard, A., Jaworski, C.C., Bearez, P. & Desneux, N. (2013) Sharing a predator: can an invasive alien pest affect the predation on a local pest? *Population Ecology*, **55**, 433–440.

Brassil, C.E. & Abrams, P.A. (2004) The prevalence of asymmetrical indirect effects in two-host-one-parasitoid systems. *Theoretical Population Biology*, **66**, 71–82.

Buchanan, A.L., Hermann, S.L., Lund, M. & Szendrei, Z. (2017) A meta-analysis of non-consumptive predator effects in arthropods: the influence of organismal and environmental characteristics. *Oikos*, **126**, 1233–1240.

Chailleux, A., Mohl, E.K., Alves, M.T., Messelink, G.J. & Desneux, N. (2014) Natural enemy-mediated indirect interactions among prey species: potential for enhancing biocontrol services in agroecosystems. *Pest Management Science*, **70**, 1769–1779.

Chaneton, E.J. & Bonsall, M.B. (2000) Enemy-mediated apparent competition: empirical patterns. *Oikos*, **88**, 380–394.

Dethier, M.N. & Duggins, D.O. (1984) An "indirect commensalism" between marine herbivores and the importance of competitive hierarchies. *American Naturalist*, **124**, 205–219.

Donaldson, J.R., Myers, S.W. & Gratton, C. (2007) Density-dependent responses of soybean aphid (*Aphis glycines* Matsumura) populations to generalist predators in mid to late season soybean fields. *Biological Control*, **43**, 111–118.

Eigenbrode, S., White, C., Rohde, M. & Simon, C. (1998) Behavior and effectiveness of adult *Hippodamia convergens* (Coleoptera: Coccinellidae) as a predator of *Acyrthosiphon pisum* (Homoptera: Aphididae) on a wax mutant of *Pisum sativum*. *Environmental Entomology*, **27**, 902–909.

Frazer, B.D. & Gilbert, N. (1976) Coccinellids and aphids: a quantitative study of the impact of adults ladybirds (Coleoptera: Coccinellidae) preying on field populations of pea aphids (Homoptera: Aphididae). *Journal of the Entomological Society of British Columbia*, **73**, 33–56.

Frost, C.M., Peralta, G., Rand, T.A., Didham, R.K., Varsani, A. & Tylianakis, J.M. (2016) Apparent competition drives community-wide parasitism rates and changes in host abundance across ecosystem boundaries. *Nature Communications*, **7**, 1–12.

Gardarin, A., Plantegenest, M., Bischoff, A. & Valantin-Morison, M. (2018) Understanding plant–arthropod interactions in multitrophic communities to improve conservation biological control: useful traits and metrics. *Journal of Pest Science*, **91**, 943–955.

Gardiner, M.M. & Landis, D.A. (2007) Impact of intraguild predation by adult *Harmonia axyridis* (Coleoptera: Coccinellidae) on *Aphis*

glycines (Hemiptera: Aphididae) biological control in cage studies. *Biological Control*, **40**, 386–395.

Gelman, A. & Hill, J. (2007) *Data Analysis Using Regression and Multilevel/hierarchical Models*. Cambridge University Press, Cambridge, U.K.

Gontijo, L.M., Beers, E.H. & Snyder, W.E. (2015) Complementary suppression of aphids by predators and parasitoids. *Biological Control*, **90**, 83–91.

Grevstad, F.S. & Klepetka, B.W. (1992) The influence of plant architecture on the foraging efficiencies of a suite of ladybird beetles feeding on aphids. *Oecologia*, **92**, 399–404.

Hedges, L.V., Gurevitch, J. & Curtis, P.S. (1999) The meta-analysis of response ratios in experimental ecology. *Ecology*, **80**, 1150–1156.

Hermann, S.L. & Landis, D.A. (2017) Scaling our understanding of non-consumptive effects in insect systems. *Current Opinion in Insect Science*, **20**, 54–60.

Holt, R.D. (1977) Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology*, **229**, 197–229.

Holt, R.D. & Bonsall, M.B. (2017) Apparent competition. *Annual Review of Ecology, Evolution, and Systematics*, **48**, 447–471.

Holt, R. & Hochberg, M. (1997) When is biological control evolutionary stable (or is it)? *Ecology*, **78**, 1673–1683.

Holt, R.D. & Lawton, J.H. (1994) The ecological consequences of shared natural enemies. *Annual Review of Ecology and Systematics*, **25**, 495–520.

Ims, R.A., Yoccoz, N.G. & Killengreen, S.T. (2011) Determinants of lemming outbreaks. *Proceedings of the National Academy of Sciences*, **108**, 1970–1974.

Ingerslew, K.S. & Finke, D.L. (2018) Multi-species suppression of herbivores through consumptive and non-consumptive effects. *PLoS One*, **13**, e0197230.

Jaworski, C.C., Chailleux, A., Bearez, P. & Desneux, N. (2015) Apparent competition between major pests reduces pest population densities on tomato crop, but not yield loss. *Journal of Pest Science*, **88**, 793–803.

Jonsson, M., Straub, C.S., Didham, R.K., Buckley, H.L., Case, S., Hale, R.J. *et al.* (2015) Experimental evidence that the effectiveness of conservation biological control depends on landscape complexity. *Journal of Applied Ecology*, **52**, 1274–1282.

Jonsson, M., Kaartinen, R. & Straub, C.S. (2017) Relationships between natural enemy diversity and biological control. *Current Opinion in Insect Science*, **20**, 1–6.

Koss, A.M., Chang, G.C. & Snyder, W.E. (2004) Predation of green peach aphids by generalist predators in the presence of alternative, Colorado potato beetle egg prey. *Biological Control*, **31**, 237–244.

Krey, K.L., Blubaugh, C.K., Chapman, E.G., Lynch, C.A., Snyder, G.B., Jensen, A.S. *et al.* (2017) Generalist predators consume spider mites despite the presence of alternative prey. *Biological Control*, **115**, 157–164.

Lajeunesse, M.J. (2015) Bias and correction for the log response ratio in ecological meta-analysis. *Ecology*, **96**, 2056–2063.

Liermann, M., Steel, A., Rosing, M. & Guttorp, P. (2004) Random denominators and the analysis of ratio data. *Environmental and Ecological Statistics*, **11**, 55–71.

Long, W.C., Gamelin, E.F., Johnson, E.G. & Hines, A.H. (2012) Density-dependent indirect effects: apparent mutualism and apparent competition coexist in a two-prey system. *Marine Ecology Progress Series*, **456**, 139–148.

Losey, J.E. & Denno, R.F. (1998) Positive predator-predator interactions: enhanced predation rates and synergistic suppression of aphid populations. *Ecology*, **79**, 2143–2152.

van Maanen, R., Messelink, G.J., van Holstein-Saj, R., Sabelis, M.W. & Janssen, A. (2012) Prey temporarily escape from predation in the presence of a second prey species. *Ecological Entomology*, **37**, 529–535.

Mace, K.C. & Mills, N.J. (2017) Connecting natural enemy metrics to biological control activity for aphids in California walnuts. *Biological Control*, **106**, 16–26.

Messelink, G.J., van Maanen, R., van Holstein-Saj, R., Sabelis, M.W. & Janssen, A. (2010) Pest species diversity enhances control of spider mites and whiteflies by a generalist phytoseiid predator. *BioControl*, **55**, 387–398.

Muller, A.C.B. & Godfray, H.C.J. (1997) Apparent competition between two aphid species. *Journal of Animal Ecology*, **66**, 57–64.

Nelson, E.H. (2007) Predator avoidance behavior in the pea aphid: costs, frequency, and population consequences. *Oecologia*, **151**, 22–32.

van Nouhuys, S. & Kraft, T.S. (2012) Indirect interaction between butterfly species mediated by a shared pupal parasitoid. *Population Ecology*, **54**, 251–260.

Oaten, A. & Murdoch, W.W. (1975) Functional response and stability in predator-prey systems. *The American Naturalist*, **109**, 289–298.

Preisser, E.L., Bolnick, D.I. & Benard, M.E. (2005) Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology*, **86**, 501–509.

R Development Core Team. (2017) *R: A Language and Environment for Statistical Computing. Version 3.4.2*. R Foundation for Statistical Computing, Vienna, Austria.

Riggi, L.G., Gagic, V., Rusch, A., Malsher, G., Ekbom, B. & Bommarco, R. (2017) Pollen beetle mortality is increased by ground-dwelling generalist predators but not landscape complexity. *Agriculture, Ecosystems and Environment*, **250**, 133–142.

Roubinet, E., Birkhofer, K., Malsher, G., Staudacher, K., Ekbom, B., Traugott, M. *et al.* (2017) Diet of generalist predators reflects effects of cropping period and farming system on extra- and intraguild prey. *Ecological Applications*, **27**, 1167–1177.

Roubinet, E., Jonsson, T., Malsher, G., Staudacher, K., Traugott, M., Ekbom, B. *et al.* (2018) High redundancy as well as complementary prey choice characterize generalist predator food webs in agroecosystems. *Scientific Reports*, **8**, 8054.

Rusch, A., Bommarco, R. & Ekbom, B. (2017) Conservation biological control in agricultural landscapes. *Insect-plant Interactions in a Crop Protection Perspective* (ed. by N. Sauvion, D. Thiéry and P.-A. Calatayud), pp. 333–360. Elsevier Ltd, Amsterdam, The Netherlands.

Sanders, D. & van Veen, F.J.F. (2012) Indirect commensalism promotes persistence of secondary consumer species. *Biology Letters*, **8**, 960–963.

Shields, M.W., Johnson, A.C., Pandey, S., Cullen, R., Gonzalez-Chang, M., Wratten, S.D. *et al.* (2019) History, current situation and challenges for conservation biological control. *Biological Control*, **131**, 25–35.

Snyder, W.E. (2019) Give predators a complement: conserving natural enemy biodiversity to improve biocontrol. *Biological Control*, **135**, 73–82.

Symondson, W.O.C., Glen, D.M., Ives, A.R., Christopher, J., Symondson, W.C., Glen, D.M. *et al.* (2002) Dynamics of the relationship between a generalist predator and slugs over five years. *Ecology*, **83**, 137–147.

Tack, A.J.M., Gripenberg, S. & Roslin, T. (2011) Can we predict indirect interactions from quantitative food webs? – an experimental approach. *Journal of Animal Ecology*, **80**, 108–118.

Tscharntke, T., Karp, D.S., Chaplin-Kramer, R., Batary, P., DeClerck, F., Gratton, C. *et al.* (2016) When natural habitat fails to enhance

biological pest control – five hypotheses. *Biological Conservation*, **204**, 449–458.

Van Veen, F.J.F., Morris, R.J. & Godfray, H.C.J. (2006) Apparent competition, quantitative food webs, and the structure of phytophagous insect communities. *Annual Review of Entomology*, **51**, 187–208.

Vandervoet, T.F., Ellsworth, P.C., Carrière, Y. & Naranjo, S.E. (2018) Quantifying conservation biological control for management of *Bemisia tabaci* (Hemiptera: Aleyrodidae) in cotton. *Journal of Economic Entomology*, **111**, 1056–1068.

Wells, M.L., McPherson, R.M., Ruberson, J.R. & Herzog, G.A. (2001) Coccinellids in cotton: population response to pesticide application and feeding response to cotton aphids (Homoptera: Aphididae). *Environmental Entomology*, **30**, 785–793.

Wootton, T.J. (1994) Predicting direct and indirect effects: an integrated approach using experiments and path analysis. *Ecology*, **75**, 151–165.