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Temporal synchrony mediates the outcome of indirect effects between prey via a shared predator

Nicolas Desneux^{1,*}, Ian Kaplan², Ho Jung S. Yoo³, Su Wang^{4,*} and Robert J. O'Neil^{2†}

¹ Université Côte d'Azur, INRA, CNRS, UMR-ISA, 06000, Nice, France

- ² Department of Entomology, Purdue University, Smith Hall, 901 W. State St., West Lafayette, IN 47907, USA
- ³ Division of Biological Sciences, University of California San Diego, La Jolla, CA 92093, USA
- ⁴ Institute of Plant and Environment Protection, Beijing Academy of Agriculture and Forestry Sciences (BAAFS), Beijing 100097, PR China
- * Corresponding authors: nicolas.desneux@inra.fr, wangsu@ipepbaafs.cn

With 5 figures and 1 table and 3 appendices

Abstract: The role of generalist predators in suppressing herbivores in complex food webs is controversial because alternative prey can modulate predation on focal prey through various indirect interactions, e.g. by distracting or enhancing predation (i.e. apparent mutualism and apparent competition, respectively). We predict that temporal synchrony (i.e., whether the two prey items co-occur at the same time) mechanistically shifts the indirect predator-mediated effect from mutualism in the short-term to competition in the long-term. The impact of alternative prey on population growth of soybean aphid (Aphis glycines), a key invasive pest in Northern American sovbean fields, was tested over two years in 520 replicated open field plots. Specifically, we tested short- and long-term predator-mediated indirect interactions, respectively, by quantifying these relationships instantaneously vs. implementing a time lag with alternative prey preceding aphid trials by two weeks. This allowed us to statistically disentangle behavioral effects of prey preferences from population-level effects mediated by numerical responses of natural enemies. The predator, Orius insidiosus, constituted >90% of the aphidophagous predator community and was thus considered the driver of indirect interactions between pests. Of the alternative prey, soybean thrips, Neohydatothrips variabilis, was the dominant species and predicted variation in aphid population growth rates in three of four analyses. Notably, thrips increased aphid growth when co-occurring in the short-term, presumably by satiating O. insidiosus, but negatively affected aphids when tested with a time lag (i.e., asynchronous dynamics). Mites also weakened aphid suppression in the short-term during one of two years. These data suggest that indirect effects in food webs are not static, but fluctuate between positive and negative depending on the time scale over which interactions are tracked. Consequently, alternative foods can be simultaneously beneficial and detrimental to prey suppression with the net effect likely driven by the degree of phenological synchrony exhibited by the co-occurring herbivores.

Keywords: indirect interactions, food web, alternative prey, generalist predator, prey preference

1 Introduction

The impact of generalist predators is difficult to predict in multi-prey communities (Rosenheim et al. 1993, Polis & Strong 1996). A major benefit of broad diet is that consumers are loosely tied to any one resource and thereby buffered against spatiotemporal fluctuations in food availability i.e., if one prey crashes, generalists can switch to alternative prey and thus remain in the system, unlike specialists that are driven to local extinction. Alternatively, the effects of polyphagous consumers may attenuate in complex food webs because their consumptive power is diluted across many weak trophic links (Halaj & Wise 2001, Denno & Finke 2006).

A powerful tool for disentangling these contradicting outcomes is to view the impact of predators in simplified community modules consisting of a single predator and two herbivorous prey. In this context, indirect interactions between the prey can be driven by the actions of their shared predator (Holt & Lawton 1994, Wootton 1994). Apparent competition occurs when the presence of herbivore 'A' elevates predation on herbivore 'B' (Holt 1977, Chaneton & Bonsall 2000, van Veen et al. 2006). This type of indirect effect between cooccurring species has received strong empirical support when experimentally tested (e.g., Bonsall & Hassell 1997, Müller & Godfray 1997, Morris et al. 2004, Blitzer & Welter 2011; Munoz-Cardenas et al. 2017). While not as widely described, the opposite outcome – termed 'apparent mutualism' – occurs when herbivore 'A' satiates or otherwise distracts the predator, thus reducing consumption of herbivore 'B' (Holt & Lawton 1994, Abrams & Matsuda 1996; Desneux & O'Neil 2008).

Apparent competition and apparent mutualism are not mutually exclusive processes, depending on the time scale considered. Ecological context can shift outcomes between the same species pair from positive to negative, but few studies have uncovered the mediating factors (Abrams et al. 1998, Harmon & Andow 2004, Blitzer & Welter 2011, Bompard et al. 2013; Jaworski et al. 2013, 2015, and see Chailleux et al. 2014 for a thorough review). Holt & Lawton (1994) suggested that time scale may play a key role: "Theoretical studies suggest that when predators are largely limited by prey availability...alternative prey should experience longterm, negative-negative interactions via shared predation (apparent competition), regardless of short-term...apparent mutualism due to predator satiation". In other words, adding an alternative food item is likely to distract predators in the short-term, leading to relaxed consumption of the focal prey. But over a longer time interval that allows for aggregative and/or reproductive responses by the natural enemy, the interaction should gradually shift from apparent mutualism to apparent competition.

Understanding the outcome of indirect interactions in multi-prey systems is central in agriculture where generalist predators are conserved and managed to suppress one or more pest species. Their contribution to pest management, however, remains a hotly debated topic (Symondson et al. 2002). Alternative prey can reduce focal pest consumption (Musser & Shelton 2003, Koss & Snyder 2005, Prasad & Snyder 2006, Desneux & O'Neil 2008, Jaworski et al. 2013), but in other cases have no impact (Halaj & Wise 2002) or enhance predation and parasitism rates (Doutt & Nakata 1973, Settle & Wilson 1990, Karban et al. 1994, Evans & England 1996, Settle et al. 1996, Messelink et al. 2008). Resolving these discrepancies is a first step towards manipulating alternative foods as a reliable management tactic (Harmon & Andow 2004, van Veen et al. 2006). For example, the entire concept of the banker plant system is to exploit apparent competition by introducing an innocuous non-pest herbivore to retain beneficial arthropods, and ultimately improve biocontrol of the focal pest (Langer & Hance 2004, Frank 2010, Parolin et al. 2012). Doing so, however, necessitates a deeper and more mechanistic understanding of when and where alternative foods contribute to prey suppression versus detract from it (Desneux & O'Neil 2008).

Our *central hypothesis* is that the presence of alternative prey relaxes predation pressure on focal herbivores in the short-term (apparent mutualism), but this effect reverses over a longer time period, i.e., enhanced suppression in association with alternative food (apparent competition). Thus, the outcome of predator-mediated indirect interactions between co-occurring herbivores is predicted to be time scale dependent. To test the aforementioned hypothesis, we used the well-studied interaction between the minute pirate bug, *Orius insidiosus* (Hemiptera: Anthocoridae), and two of its primary prey items in soybean fields, the soybean aphid, *Aphis glycines* (Hemiptera: Aphididae), and soybean thrips, *Neohydatothrips variabilis* (Thysanoptera: Thripidae). This is an ideal system because of its trophic simplicity and established feeding relationships; *O. insidiosus* dominates the foliar predator community in soybean in Indiana (Desneux et al. 2006, Yoo & O'Neil 2009), and this occurs independently of the sampling method considered (Yoo & O'Neil 2009). In this community, aphids are the focal pest because of their known impact on soybean yield, whereas thrips rarely cause substantial crop damage and are thus considered a minor pest or, for our purposes, the 'alternative prey'.

Soybean aphid was introduced from China in 2000 and has since spread throughout the Midwestern U.S. (Ragsdale et al. 2011). This species is also a specialist whose host-plant in the invasive range is cultivated soybean during the field season (with buckthorn being used as overwintering host). Although classical biocontrol programs have been underway for some time (e.g. *Binodoxys communis*, Desneux et al. 2009, 2012, and *Aphelinus glycinis*, Hopper et al. 2017), the role of generalist predators has been the main focus during the initial 10 years of its spread. Below, we highlight several of the more salient points from this predator-pest-crop system:

- (i) A multi-species complex of generalist predators suppresses soybean aphid in the U.S., but the magnitude of this effect is inconsistent across sites and years (Rutledge et al. 2004, Costamagna et al. 2007, Costamagna et al. 2008; Ragsdale et al. 2011; Maisonhaute et al. 2017; Bannerman et al. 2018). Within this predator complex, the anthocorid *O. insidiosus* was identified as a key natural enemy, particularly during the initial phase of aphid colonization (Rutledge et al. 2004, Brosius et al. 2007). In multi-year field experiments in Indiana, it was demonstrated to be the only predator whose abundance negatively correlated with soybean aphid population growth (Desneux et al. 2006); no other predators (coccinellids, spiders, lacewings, etc.) showed significant effect on soybean aphid population growth in this specific area.
- (ii) Thrips colonize soybean fields well in advance of aphids, providing an early-season resource that promotes *O. insidiosus* establishment prior to aphid arrival (Harwood et al. 2007, 2009). Interestingly, *O. insidiosus* mounts a strong numerical response to soybean thrips, as is the case for anthocorids and thrips in other systems (Coll & Ridgway 1995), but does not respond numerically to the later-colonizing soybean aphid (Yoo & O'Neil 2009). Thus, the sequence of arrival and population-level response of predators to these two herbivores sets-up a scenario whereby thrips attract *O. insidiosus* into fields, resulting in asymmetrical apparent competition for aphids. In fields where *O. insidiosus* colonizes early and is well-

established before *A. glycines*, aphids remain at low densities; the opposite is true (i.e., large outbreaks occur) when *O. insidiosus* arrives late relative to aphid colonization (see Fig. 4 in Rutledge et al. 2004). Consequently, the existing data strongly implicate early-season thrips infestation as critical to soybean aphid biocontrol.

(iii) While molecular gut content analyses demonstrate that *O. insidiosus* routinely feeds on both pests in the field (Harwood et al. 2007, 2009), laboratory preference assays show that thrips are strongly preferred over aphids (Desneux & O'Neil 2008) and predators perform better (e.g., development time, fecundity) when reared on a thrips-only diet compared with aphids (Butler & O'Neil 2007). As a result, *O. insidiosus* consumed far fewer aphids when tested on soybean plants with thrips compared with thrips-free plants, resulting in short-term apparent mutualism between the pests in laboratory microcosms (Desneux & O'Neil 2008).

2 Material and methods

We conducted a two-year field experiment to quantify the short- and long-term relationships between alternative prey and soybean aphid population growth, and evaluate the potential role of *O. insidiosus* in these interactions. During the 2004 and 2005 field seasons, we established experimental soybean fields (7.5 and 11.9 ha, respectively) at the Purdue University Agronomy Center for Research & Education (ACRE) in Tippecanoe County, Indiana. Fields were managed using standard agronomic techniques for soybean cultivation, including herbicide regimes but not foliar insecticides.

2.1 Aphid population growth

To evaluate aphid population growth, we used open field plots consisting of five consecutive soybean plants within the same row. Plots were randomly placed within the field and delineated with flagging on each end (plots were separated by at least 5 meters each other). In addition, there was a 30m-buffer from the edge of the field). We visually searched and manually removed naturally-occurring aphids from plots and all soybeans in a two-plant buffer surrounding each plot to minimize re-colonization from neighboring plants. To begin a trial, ten adult aphids were taken from a greenhouse colony and transferred to the highest leaflet of the central plant within the plot (i.e., plant #3 in the five plant row). After 7 days, we returned and counted all aphids on each of the five plants. This plot-level final aphid count was used as our estimate of population growth. Plants and aphids were discarded from the field at the end of each trial.

Open field plots were established over a six-week period in 2004 (July–August) and a four week period in 2005 (June– July). In each year, we ended trials when ambient aphid densities exceeded the threshold beyond which manual removal was no longer practical. Two trials were conducted within each week of the experiment with trials spaced 3–4 days apart (2004: 6 weeks \times 2 trials/week = 12 trials; 2005: 4.5 weeks \times 2 trials/week = 9 trials). In 2004 and 2005, 28–30 and 17–20 replicated plots, respectively, were established per trial (~360 total plots in 2004 and ~160 total plots in 2005).

2.2 Alternative prey and natural enemy survey

Potential alternative prey and generalist predators were sampled twice per week (end of June–August in 2004, June–July in 2005) in the soybean field. In 2004, the surveyed area consisted of five 0.12-ha sections of the soybean field randomly distributed throughout the field and in 2005 we used four 0.2-ha sections of the field. On each sample date, 12 to 20 plants per plot were visually surveyed at 10 m intervals and all arthropods identified and counted. The survey sections encompassed the field area in which aphid manipulation plots were established every week. In addition, predator and prey densities were highly correlated when comparing surveyed soybean field sections (Desneux, Yoo & O'Neil, unpublished data).

2.3 Statistical analyses

To test for indirect thrips-aphid interactions, we conducted a regression analysis with thrips abundance as the predictor variable and plot-level aphid population growth as the response variable (for seasonal population trends for each of the three species, see Supplementary material Appendix A). This analysis was conducted in two ways. First, we tested for short-term apparent mutualism by using thrips counts on the same day that aphid trials were established. Next, we tested for long-term apparent competition by using thrips abundance with a two-week time lag, i.e., counts two weeks prior to establishing aphid test plots. Our prior work in this system suggested that two weeks were sufficient for O. insidiosus to mount a numerical response to thrips and for predator eggs to turn to active predator against aphids (Desneux et al. 2005, Yoo & O'Neil 2009). However, we also explored additional time lags to prevent missing potential unexpected relationship(s) (Supplementary material Appendix B). Furthermore, we evaluated these short- and long-term relationships with other potential prey that were common in soybean fields (e.g., potato leafhopper nymphs, mites, whiteflies) and may have served an analogous role as thrips.

3 Results

The numerically dominant aphidophagous predator in soybean fields at our study site was clearly *Orius insidiosus*, which constituted >90% of individuals across both years and was thus >9-times more abundant than all other predators combined (Fig. 1). In addition to their sheer abundance, a companion study conducted in the same fields in



Fig. 1. Pie charts displaying the relative abundance of aphidophagous predators in soybean fields during the 2004 and 2005 field experiment periods. Data were collected by visually searching plants and summed over the entire June–August (2004) and June–July (2005) sampling periods.

2004 and 2005, but at a longer time scale, demonstrated a significant negative relationship between *O. insidiosus* density and aphid population growth (Desneux et al. 2006); all other predators showed no relationship. Thus, *O. insidiosus* is likely the main driver of population change for aphids in soybean fields at our study site. Syrphid fly larvae were the second most abundant group (but represented only 3–6% of individuals), followed by spiders and coccinellid beetles. Because *A. glycines* is a recently introduced species to the U.S. and classical biocontrol agents have not yet established in the invasive range, parasitism rates were negligible (only two total mummies found).

Of the potential alternative prey to aphids, thrips were the numerically dominant group (Fig. 2). This was particularly true in 2004 when they constituted 96% of the prey assemblage. In 2005, the community was more even with spider mites (*Tetranychus urticae*) and potato leafhopper nymphs (*Empoasca fabae*) occurring at higher densities than the previous year, but thrips remained the most abundant group (63% of individuals). Across both years, the majority of all thrips (83.4%) were nymphs, which cannot be identified to species in the field. Of the remainder, 10.4% were soybean thrips (*N. variabilis*) and 5.8% eastern flower thrips (*Frankliniella tritici*), followed by other minor species (0.4%), e.g., *Frankliniella fusca, Aeolothrips fasciatus*.

Thrips were also the best predictor of aphid population growth with significant relationships in three of our four regression models (Table 1). The directionality of these relationships, however, varied with time scale. During both years of the study, thrips positively affected aphid population growth when tested in the short-term with no time lag (Figs. 3A and 4A). In 2004, thrips abundance negatively affected aphid population growth over the long-term (Fig. 3B), although this relationship was non-significant in 2005 (Fig. 4B). Aside from thrips, the only other alternative prey item affecting aphids was mites, whose total density was positively related to aphid growth rate over the shortterm in 2005 (Fig. 5).

4 Discussion

The ecological patterns emerging from our two-year field study strongly support the view that, embedded within the broader soybean food web, thrips indirectly affect aphid population dynamics via shared predation by O. insidiosus. This perspective is partly driven by the sheer abundance of O. insidiosus in the area where the study was conducted, but it is also the only predator capable of suppressing (or slowing down) aphid population growth (Desneux et al. 2006). Our hypothesized trophic interaction web is also largely shaped by prior work in this system, namely three pieces of evidence. First, molecular gut content analyses of field-collected predators demonstrate that thrips and aphids are routinely consumed by O. insidiosus in soybean fields (Harwood et al. 2007, 2009). Oftentimes, these are even the same individuals. For example, 59% of those predators testing positive for thrips consumption also contained A. glycines DNA, highlighting the frequency of shared predation. These data are crucial since predation is inferred rather than



Fig. 2. Pie charts displaying the relative abundance of potential alternative prey to aphids in soybean fields during the 2004 and 2005 field experiment periods. Data were collected by visually searching plants and summed over the entire June–August (2004) and June–July (2005) sampling periods. Prey developmental stages sampled: Lepidoptera = larvae; lacewings = eggs; leafhoppers and whiteflies = nymphs; thrips and mites = nymphs + adults.



Fig. 3. Relationship between thrips density and soybean aphid (= SBA) population growth over a one week period in open field plots during the 2004 field season. Data were analyzed to quantify the: **(A)** *short-term* relationship by regressing thrips density vs. aphid population growth with no time lag (i.e., instantaneous dynamics); and **(B)** *long-term* relationship by regressing thrips density vs. aphid population growth with a two-week time lag (i.e., thrips abundance measured two weeks prior to aphid growth estimates). Dashed lines represent the starting aphid density per plot. Thus, values above the line indicate populations that are growing, whereas values below the line denote populations that are declining. Aphid y-axis data points are the average (±SEM) of 28–30 replicated plots for each of 12 trials over the summer. Thrips x-axis



Fig. 4. Relationship between thrips density and soybean aphid (=SBA) population growth over a one week period in open field plots during the 2005 field season. Data were analyzed to quantify the: **(A)** *short-term* relationship by regressing thrips density vs. aphid population growth with no time lag (i.e., instantaneous dynamics); and **(B)** *long-term* relationship by regressing thrips density vs. aphid population growth with a two-week time lag (i.e., thrips abundance measured two weeks prior to aphid growth estimates). Dashed lines represent the starting aphid density per plot. Thus, values above the line indicate populations that are growing, whereas values below the line denote populations that are declining. Aphid y-axis data points are the average (±SEM) of 17–20 replicated plots for each of 9 trials over the summer. Thrips x-axis data points are per plant averages (±SEM) calculated from sampling in four replicated sections of the field.

directly measured in our study. Second, an earlier laboratory experiment demonstrated that thrips presence relaxes O. insidiosus consumption of co-occurring soybean aphids (Desneux & O'Neil 2008), and thus our short-term field relationships are well-supported by smaller-scale mechanistic studies in this three-species food web. Third, the indirect interactions observed between aphids and thrips could not result from plant-mediated interactions; absence of such interaction was demonstrated in the lab (Supplementary material Appendix C), as well as reported for another aphidthrips-plant model (Mouttet et al. 2011). In overall, the work reported here is the first realistic field-scale test linking alternative prey with soybean aphid biocontrol, which is notable because the importance of early-season prey resources has long been speculated in this food web but never directly tested (Rutledge et al. 2004, Desneux et al. 2006, Harwood et al. 2007, 2009, Yoo & O'Neil 2009).

Interestingly, in 2004, thrips abundance was the determining factor that predicted whether aphid populations were growing or declining in both instantaneous and lagged regressions (i.e., Fig. 3 – values over the dashed line are plots where populations are higher than the starting density, whereas values below the dashed line are populations shrinking). In 2005, populations in all plots increased, albeit at differing rates depending on thrips density. The higher aphid abundance in 2005 corresponds with the two-year oscillation cycle for A. glycines, which consistently peaks in odd numbered years since its invasion of North America (Rhainds et al. 2010). This inter-annual cycle may also explain why we did not detect a time lagged response to thrips in 2005 (Fig. 4B). If soybean aphids were abundant on surrounding plants, it may have constrained the likelihood for O. insidiosus to track low density populations established in our open plots (10 aphids per 5 plants). An alternative explanation is that thrips densities were simply lower in 2005 (compare scaling of x-axes in Figs 3B vs. 4B). Ultimately, we suspect that indirect interactions are progressively more challenging to accurately predict with increasing temporal separation between species due to stochastic factors. Thus, it is not particularly surprising that short-term dynamics were more consistent than long-term ones in this system.

A second interesting outcome from our analyses, and another difference across years, was the unanticipated miteaphid link. In 2005, soybean fields experienced a large spider mite outbreak, which drove short-term relaxation of aphid biocontrol. Anthocorids are polyphagous consumers that readily feed on mites (Venzon et al. 2002, Rosenheim 2005), and therefore this link is not surprising. Ultimately,

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Fig. 5. Relationship between total mite density and soybean aphid (=SBA) population growth over a one week period in open field plots during the 2005 field season. Data were analyzed to quantify the: **(A)** *short-term* relationship by regressing total mite density vs. aphid population growth with no time lag (i.e., instantaneous dynamics); and **(B)** *long-term* relationship by regressing total mite density vs. aphid population growth with a two-week time lag (i.e., total mite abundance measured two weeks prior to aphid growth estimates). The dashed line represents starting aphid density per plot. Thus, values above the line indicate populations that are growing, whereas values below the line denote populations that are declining. Aphid y-axis data points are the average (±SEM) of 17–20 replicated plots for each of 9 trials over the summer. Mite x-axis data points are per plant averages (±SEM) calculated from sampling in four replicated sections of the field.

Table 1. Relationship between abundance of alternative prey (predictor variable) and soybean aphid population growth (response variable) in the field. Regressions were calculated over two summers based on long-term (i.e., time lag with alternative prey preceding soybean aphid trials by two weeks) and short-term (i.e., instantaneous relationship) dynamics. Significant effects are bolded (at P < 0.05 level).

	2004				2005				
	Short-term		Long-term		Short-term		Long-term		
	R ²	Р	R ²	Р	R ²	Р	R ²	P	
Lepidoptera larvae	0.046	0.502	0.062	0.433	0.099	0.409	0.267	0.154	
Lacewing eggs	0.047	0.500	0.316	0.057	0.116	0.370	0.170	0.271	
Potato leafhopper	0.001	0.909	0.014	0.713	0.357	0.089	0.109	0.386	
Spider mites	0.149	0.215	0.002	0.903	0.447	0.049	0.010	0.796	
Thrips	0.605	0.003	0.552	0.006	0.709	0.004	0.049	0.565	
Whitefly nymphs*	0.022	0.644	0.167	0.188	0.002	0.916	-	-	

"-" Densities were too low to analyze the long-term relationship in 2005

any acceptable and shared prey item is capable of driving indirect interactions with aphids, and thrips are not unique in this respect. That being said, thrips are a far more consistent, abundant, and preferred early-season resource at our study site (Butler & O'Neil 2007, Desneux & O'Neil 2008). Across both years, thrips drove three of four potential relationships, all of which were highly significant (P < 0.01), compared with mites that displayed a marginally significant relationship (P = 0.049) in one of four assessments. Given that thrips are the numerically dominant alternative prey, it is unclear whether abundance and/or prey preferences are responsible for their role in these interactions.

Because the documented relationships are correlative rather than experimentally manipulated (i.e., removing thrips and observing subsequent aphid population dynamics), our ability to conclusively link thrips with aphid-predator interactions is somewhat limited. In a companion study, we suppressed early-season soybean thrips with insecticide and quantified the response in *O. insidiosus* and later-colonizing *A. glycines* (Yoo & O'Neil 2009). Unfortunately, the insecticide used (Spinosad) also affected *O. insidiosus* populations (through sublethal effects, Desneux et al. 2007, Biondi et al. 2012), thereby confounding the interpretation of those data. This outcome underscores the challenges of experimentally testing for apparent competition and mutualism over large spatial scales in the field.

At a broader level, our work is a novel contribution to the food web literature because it identifies an explanatory mechanism - prey synchrony - that predicts when indirect effects will generate positive vs. negative effects. Although this mechanism is not new at a conceptual-level (Holt & Lawton 1994, Abrams et al. 1998, Ostman & Ives 2003, Harmon & Andow 2004), to our knowledge it has never been explicitly demonstrated in empirical field studies. Recently, Blitzer & Welter (2011) documented that asynchronous emergence drove apparent competition between two leafminer species mediated by a shared parasitoid. In this system, however, leafminers undergo distinct generations, resulting in nonoverlapping temporal dynamics. In contrast, thrips precede aphid colonization, but still remain in the soybean system throughout aphid population development (Harwood et al. 2007, Yoo & O'Neil 2009). Consequently, apparent competition and mutualism can be methodologically dissected in this food web, but are not mutually exclusive outcomes. It is likely that both processes occur simultaneously, resulting in a 'double-edged sword' for biocontrol purposes. The net outcome is likely beneficial nonetheless because O. insidosus is ineffective at suppressing moderate to high density aphid populations, and therefore thrips are essential as an earlyseason bridge to attract predators while they are still ecologically capable of preventing an outbreak.

This work adds to the previous literature on indirect food web interactions and the potential benefits of a higher biodiversity of herbivores in crops (Settle & Wilson 1990, Karban et al. 1994, Evans & England 1996, Lynch et al. 2006, Settle et al. 2006, Kaplan et al. 2007, Messelink et al. 2008, Bompard et al. 2013, Jaworski et al. 2013, 2015, Mouttet et al. 2013; Chailleux et al. 2014). Additional tests of the role of phenological synchrony in other systems will be valuable to establish the ubiquity of this mechanism and the strength of its predictive power for ecosystem management.

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Appendices: Appendix A, B, C

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