Spring Forward: Molecular detection of early season predation in agroecosystems

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Abstract

Agroecosystems undergo disturbance early in the season and host simple food webs that are often comprised of pests, generalist predators, and alternative prey. This is a critical time because predator: pest ratios are highest, in favor of predators, and most likely to affect the trajectory of pest populations, a concept we describe as early season predation. Conservation biological control of these pests utilizes on-farm management schemes to increase predator populations, in part, by providing or enhancing alternative resources. These resources may include beneficial alternative prey that sustains predators prior to pest arrival, but if predator affinity for these alternative prey is strong, pest suppression may be disrupted. Early in the season, when the abundance of pests is low compared to alternative prey, predators do not typically consume prey in direct proportion to their relative abundance, often feeding at disproportionately high rates on “rare” prey items. Therefore, molecular tools, such as gut content analysis, have been used to reveal trophic linkages and decouple the relationship between prey abundance and consumption. Using molecular techniques, numerous studies across different agroecosystems have determined that early season predation occurs regularly and may contribute to pest control and is probably most effective for pests with the potential for exponential population growth, where suppression early in the season may be essential to prevent these outbreaks. Studies incorporating molecular tools and field studies can provide insight for growers to create successful conservation biological control programs utilizing generalist predators in early season predation.

38 **Keywords**

39 predators, pests, conservation biological control, alternative prey, prey abundance, molecular gut

40 content analysis

Introduction

Upper trophic levels sometimes regulate lower ones, and in agroecosystems, predators have the capacity to maintain pest populations below economic thresholds (Chiverton, 1986). However, predators often feed on other predators (Gagnon et al., 2011; Polis et al., 1989; Rosenheim et al., 1995) or non-target prey (Kuusk and Ekbom, 2010), possibly reducing their ability for pest suppression. Molecular tools, in combination with prey abundance data, natural enemy-pest population dynamics, and/or behavioral experiments have been used to characterize these complicated feeding relationships in a variety of agroecosystems including vegetables (Balmer et al., 2013; Schmidt et al., 2014), row crops (Agustí et al., 2003; Hagler and Blackmer, 2013; Lundgren and Fergen, 2014), forage crops (Welch et al., 2014), and fruit (Boreau de Roince et al., 2013; Mollot et al., 2014) (see also King, 2008; Sheppard and Harwood, 2005; Symondson, 2002 for reviews). Molecular information on trophic pathways, often delineating the strength of unique predator-pest interactions, could be used to modify agricultural practices, such as adding beetle banks or nectar providing flowering plants, making these agroecosystems more hospitable for predators through conservation biological control (Landis et al., 2000). The greatest likelihood for success in control of a pest species may be early in the season, when the predator: pest ratio is highest and most favorable for the predators (Landis and Van Der Werf, 1997; Settle et al., 1996). Molecular techniques can aid in the identification of major predators that can be exploited through early season immigration and thereby exert maximal pressure on pest species. Ultimately, such a phenomenon of early season control aims to facilitate predation on pests when regulation is most likely to occur and pest populations can be maintained at a low level. Here, we describe the concept of early season predation on pest populations in agroecosystems and propose that this interaction between generalist predators (hereafter referred

to as predators) and pests, in conjunction with on-farm management techniques, may be critically important for maintaining pest populations below outbreak levels.

2. Agricultural Systems

2.1. Seasonal Dynamics

In most simple, high-impact agricultural schemes (e.g., large scale monoculture or those characterized by significant chemical inputs, heavy tillage regimes, and/or required irrigation), humans significantly disturb the soil to channelize primary production towards one or a few rapidly growing valuable plant species. These systems are predictably ephemeral habitats, where disturbance both at the beginning and end of the season breaks down the existing habitat structure through cultivation or harvest, respectively (Wissinger, 1997). Early season in agricultural fields is characterized by rapid emergence, dispersal, and growth. Interactions between predators and pests at this point in the season could have impacts on the populations of these taxa later in the season by reducing pest establishment in agroecosystems (Fox et al., 2005; Landis and Van Der Werf, 1997; Landis et al., 2000).

The role of predators in agroecosystems precludes simple predictions of their impacts on the surrounding environment. Importantly, predators can indirectly affect lower trophic levels by participating in emergent food web phenomena such as trophic cascades and apparent prey-prey interactions. The trophic cascade (Carpenter et al., 1985) is a cornerstone of community ecology wherein predators consume prey (e.g., herbivores), thus indirectly benefiting the resource base of their prey (e.g., primary producers). These cascades are ubiquitous (Estes et al., 2011; Halaj and Wise, 2001; Pace et al., 1999; Schmitz et al., 2000; Shurin et al., 2002) and modified by many factors such as habitat type, food quality, and predator-prey body size ratios (Borer et al., 2005; Preisser et al., 2005; Shurin et al., 2002; 2006). One important consideration for predators is the

existence of alternative prey (i.e., prey species not directly involved in the trophic cascade), as these species have the potential to modify cascade strength via direct and indirect interactions with both predators and focal prey. Alternative prey in this paper is any non-pest species present in the agroecosystem on which predators can feed. In agricultural systems where the focal prey are typically crop pests, understanding the impacts of alternative prey is critical to maintaining plant productivity and effective biological control (Landis et al., 2000). This is especially true as alternative prey can sustain predators in highly disturbed habitats, possibly facilitating early season predation (henceforth referred to as ESP) (Landis et al., 2000; Symondson, 2002).

2.2. Integrated Pest Management

Conservation biological control can enable predator populations to be enhanced through management of the local flora and fauna and may be accomplished most effectively early in the season when the ratios of predator to pest are the highest (Settle et al., 1996). Habitat manipulation enables the enhancement of natural enemy populations through provisioning of resources typically lacking in agricultural fields (Landis et al., 2000), and can strengthen top-down control of insect pests (Costamagna et al., 2007; Holland et al., 2012). These provisions include extra-floral nectaries (Baggen and Gurr, 1998; Edwards et al., 1979; Heil, 2015), refugia for predators (Halaj et al., 2000; Knapp and Rezac, 2015), and alternative prey (Gurr et al., 2004; Landis et al., 2005). For example, field margins provide alternative prey for natural enemies (Bickerton and Hamilton, 2012; Frank et al., 2009; Thomas and Marshall, 1999), act as a trap crop for pests (Deol and Rataul, 1978; Fereres, 2000; Hooks and Fereres, 2006; Mitchell et al., 2000), and may ultimately reduce damage to the crop (Balzan and Moonen, 2013). In addition, providing refugia increases spider abundance, spider species richness in soybeans increased by 60% with a concomitant 33% reduction in damage to seedlings in manipulated plots (Halaj et al.,

2000). Moreover, in cropping systems with aphid pests, strip-planting with ryegrass may replace at least one insecticide application per season, which has long-term economic and environmental benefits (Dong et al., 2012). While there is a good deal of information on the effect of conservation biological control on pests, considerations of both spatial and temporal scales need to be taken into account when making pest management recommendations.

The terrestrial ecology literature suggests that many natural enemies in agricultural systems migrate cyclically between fields and surrounding permanent environments (Wissinger, 1997), seeking food in several habitats within a single growing season (Gardiner et al., 2009a). Consequently, the landscape composition and prey availability in crop and non-crop habitats influence the abundance and diversity of natural enemies (Elliott et al., 1999; Gardiner et al., 2009b; Tscharntke et al., 2005). Complex landscapes have higher natural enemy populations and lower pest pressure (Bianchi et al., 2006), which should equate to higher pest control, but evaluating biological control success is sometimes challenging due to cryptic feeding events. Early in the season is a key time to manipulate predators through conservation biological control to maintain pests at low levels and delay, or prevent, pest populations from exceeding economic thresholds (Welch and Harwood, 2014).

3. Early season predation

ESP may be of central importance when utilizing predators for biological control purposes. Although these predators feed on a diverse array of food items and are likely incapable of regulating prey populations to reduce crop damage once pest populations have peaked late in the growing season, temporal predator-prey population dynamics suggest that, when pest numbers are low, the community of predators can be effective agents of biological control. These predators are most likely to provide effective pest control service when predator:pest ratios are

large early in the season, thus preventing or delaying the small population of early colonizing pests from reaching an exponential growth phase (Chiverton, 1987; Welch and Harwood, 2014). In contrast, if predator:pest ratios are small, in favor of the pests, early in the season, then there may be insufficient control over colonizing pests, thus resulting in exponential pest population trajectories. Evidence for ESP is apparent, as predators have been repeatedly shown to consume pests early in the growing season, despite the overall paucity of pests in the community (Chapman et al., 2013; Harwood et al., 2004; 2007; 2009).

In a variety of crops, predators have been documented to reduce pest numbers when utilized early in the season. Studies have often focused on aphids and spider mites, which have unique adaptations to maximize population growth, such as parthenogenesis (Beccaloni, 2009; Blackman and Eastop, 2007) and short development times (Beccaloni, 2009; Kindlmann and Dixon, 1989). Additionally, aphids have telescoping generations that contribute to exponential population growth (Blackman and Eastop, 2007; Kindlmann and Dixon, 1989). Initial studies of ESP investigated the impact of lady beetle, *Coleomegilla maculata* De Geer (Coleoptera: Coccinellidae), predation on green peach aphid, *Myzus persicae* Sulzer (Hemiptera: Aphididae), revealing that *C. maculata* is only effective early in the season (Mack and Smilowitz, 1981). There have been a number of subsequent studies documenting the role of ESP, illustrating that predators can significantly reduce aphid establishment in sugar beets (Landis and Van Der Werf, 1997), winter wheat (Edwards et al., 1979), grain sorghum (Kring and Gilstrap, 1986), and spring barley (Chiverton, 1986; Holopainen and Helenius, 1992). Importantly, research conducted in the latter crop demonstrated that aphid populations were maintained below economic thresholds through ESP (Chiverton, 1986). Soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), and its predators, especially the insidious flower bug, *Orius*

insidiosus (Say) (Anthocoridae: Hemiptera), have been widely studied in the context of ESP, with evidence that the establishment of these predators early in the season greatly reduced soybean aphid numbers later in the year (Brosius et al., 2007; Rutledge et al., 2004; Yoo and O'Neil, 2009). Similarly, delayed outbreaks of spider mites in cotton occur when predators are present early in the season (Wilson et al., 1996). We propose that pest characteristics shared in the examples above, such as short generation times, parthenogenesis, and exponential population growth, may be predictive of instances where ESP may be particularly effective.

4. Alternative prey

Predators frequently rely on alternative prey (or non-prey foods) to establish and subsequently persist in agroecosystems, as pests typically have strong seasonal dynamics (Symondson, 2002) that lack synchrony with predator populations. The presence of alternative prey prior to pest occurrence allows predators to increase their numbers, by reproduction or aggregation, and thus provide enhanced control over pests (Michels and Matis, 2008; Rutledge et al., 2004). Given that predators generally enter the field early in the season, the presence of alternative prey at this time can be crucial for sustaining predators until the arrival of the pests (Agustí et al., 2003; Settle et al., 1996).

Beyond the direct interactions between predators and alternative prey, a variety of indirect interactions between pests and alternative prey occur when they both share a common predator (Holt, 1977). These interactions range from beneficial (i.e., contributing to pest suppression) to disruptive (i.e., reducing predator effectiveness at controlling pests), and the outcome is dependent on numerous factors such as spatial and temporal overlap, prey growth rate, predator attack rates, and prey quality (Chailleux et al., 2014; Holt and Lawton, 1994).

4.1 Beneficial effects

When predators consume prey from distinct food webs (e.g., consumption of detritivores and herbivores), this form of multichannel feeding (Wolkovich et al., 2014) can promote herbivore suppression (Figure 1a). Predators may respond positively to these alternative prey through short-term (e.g., immigration) and/or long-term (e.g., increased reproductive output) processes (Abrams and Matsuda, 1996). Settle et al. (1996) demonstrated how utilization of detritivores as prey allowed predator populations to increase prior to pest outbreaks, facilitating ESP and allowing effective crop damage control. Predators have also been shown to consume detritivore prey until herbivore numbers increased and became the more abundant prey (von Berg et al., 2009; Wimp et al., 2013), reflecting temporal dynamics typical of an agricultural community that develops as new crop biomass is produced (Welch et al., 2014). Cascading benefits from multichannel feeding are apparent when alternative prey from decompositional food webs enhances the impact of predators on pests, ultimately reducing damage to primary producers (Oelbermann and Scheu, 2009; Rypstra and Marshall, 2005). These beneficial effects have been documented repeatedly in agricultural systems by demonstrating that the presence of alternative prey increases consumption of target pests (Langer and Hance, 2004; Liu et al., 2006; Madsen et al., 2004).

4.2 Disruptive effects

In contrast to beneficial forces, disruptive effects occur when alternative prey reduce predation pressure on a target pest (Desneux and O'Neil, 2008; Östman and Ives, 2003; Xu et al., 2006), and may be attributable to changes in predator foraging behavior (Koss and Snyder, 2005; Madsen et al., 2004; Symondson et al., 2006; Tack et al., 2011). These interactions are similarly common in agricultural food webs, and it is essential to consider both effects when assessing the biological control impact of non-pest food resources. The consumption of alternative prey by

predators may reduce the effectiveness of these biological control agents when preference is given towards detritivores over herbivores if the former represent larger (Hines and Gessner, 2012) or higher quality prey (Toft, 1995; Toft and Wise, 1999). Ultimately, the effect of this interaction is increasing predator abundance but weakening or failing to initiate a trophic cascade benefiting plant production (Birkhofer et al., 2008a; Halaj and Wise, 2002; Miyashita et al., 2003) (Figure 1b). Alternative prey may also serve to enhance overall predator numbers, diversity, or encounter rate, creating the potential for strong predator-predator interactions.

These predator-predator interactions can include intraguild predation (IGP), the killing and subsequent consumption of an organism that competes for the same resources. IGP is capable of significantly altering the distribution and abundance of the species involved (Polis et al., 1989) and is widespread in many systems (Arim and Marquet, 2004; Gagnon et al., 2011). This common interaction between predators can destabilize a system, resulting in temporarily low populations of predators (Holt and Polis, 1997), thus reducing pest control potential. In fact, high predator diversity and abundance have been demonstrated to increase IGP frequency and interfere with pest suppression (Finke and Denno, 2005; Rosenheim et al., 1993; 1995).

Whether alternative prey generates beneficial or disruptive effects in biological control, the relative strength of these effects ultimately depend on the identities of the predators and prey involved. As an illustration of this point, a single study utilizing multiple predators documented beneficial, disruptive, and neutral (i.e., neither beneficial nor disruptive) effects of alternative prey, depending on the predator (Madsen et al., 2004). A practical challenge in implementing predators to manage pests in agroecosystems is determining the degree to which predators utilize target pests and alternative prey as resources. Traditional methods based on recording relative abundances of available prey species may fail to fully characterize trophic connections between

predators and their prey, whereas modern molecular techniques can enhance abundance-based methods to provide greater resolution of food web structure.

5. Molecular gut content analysis

One of the major advances in food web ecology and biological control is the use of molecular tools to empirically verify feeding relationships within hypothesized interaction webs. The detection of prey-associated molecules such as proteins (enzyme-linked immunosorbent assay (ELISA)) or DNA (polymerase chain reaction (PCR)) in the guts of predators provides insight into trophic connections structuring food webs (Furlong, 2015; Hagler, 2011; Hagler et al., 2013; Hagler et al., 2015; Juen and Traugott, 2007; King, 2008; Sheppard and Harwood, 2005; Weber and Lundgren, 2009). Molecular gut content analysis employing PCR is a popular tool for characterizing trophic linkages across a variety of habitats, including agroecosystems (Hagler and Blackmer, 2013; Schmidt et al., 2014), forest systems (Heidemann et al., 2014; Jelaska et al., 2014; Schoeller et al., 2012), and soil (Lundgren and Fergen, 2014; Wallinger et al., 2014).

As with any technique, there are known limitations to estimating consumption patterns with molecular gut content analysis. For example, if decay rates of gut contents are high, predation can be under-estimated as there is a very short detection window (Greenstone et al., 2014). Variables which may be unknown at the time of testing such as predator identity, prey identity, sex, and temperature influence the rates of decay and the detection window size (Hagler and Naranjo 1997; Greenstone et al 2014), making it difficult to determine the predation rates. In addition, scavenging and secondary predation (consumption of another predator that had consumed the target prey itself) cannot be separated from primary predation and may inflate trophic linkage estimates. For instance, von Berg et al.(2012) found that 26-41% of predator

species tested consumed dead aphids when offered both live and dead aphids. Similarly, cannibalism cannot be detected using PCR as this method cannot distinguish between individuals (Gagnon et al., 2011). Additionally, molecular gut content analysis is only a qualitative measure of predation unless controlled feeding trials and statistical analyses using Bayesian or other non-parametric methods are used in tandem to determine relative predation levels (Greenstone et al., 2010; Welch et al., 2014).

Non-consumptive effects would not be detectable using molecular gut content analysis though these effects have been well documented to alter pest behavior, survival, and reproduction. For instance, superfluous killing (Maupin and Riechert, 2001), could result in mortality for a prey item without consumption by the predator. Predator-induced behavioral changes (decreased feeding rates and reproduction) can also negatively affect prey populations without consumption by the predator (Brown et al., 1999; Preisser and Bolnick, 2008; Preisser et al., 2005; Schmitz et al., 1997; Sitvarin et al., 2016). Despite these limitations, molecular gut content analysis is a useful tool for visualizing food web linkages especially when coupled with abundance data (Furlong, 2015).

Within agricultural systems, predictions of predation rates are typically based on the population densities of both predators and target pest species. Assessing the validity of this assumption requires more than abundance data, as predators have the ability to selectively forage (Bilde and Toft, 1994; Greenstone, 1979; Mayntz et al., 2005; Toft, 1995; Welch et al., 2013) and make choices based on characteristics of prey (e.g., mobility (Eubanks and Denno, 2000) and nutritional quality (Schmidt et al., 2012)). Therefore, techniques other than estimating predator and prey abundance are needed to evaluate food web structure. Using molecular assessment of predator guts and/or feces provides greater insight into foraging choices made by

predators than can be gained from relying solely on counts of prey availability. These molecular methods, often used under open field conditions, reveal predator preferences and can be integrated into the agricultural setting to determine trophic pathways most likely to contribute to effective pest suppression. This is especially important when considering early season predation and the tendency of predators to locate and consume pests at a greater frequency than would be identified by researchers relying on abundance data (Agustí et al., 2003; Chapman et al., 2013; Gomez-Polo et al., 2014; Harwood et al., 2007; 2009).

6. Molecular ecology for ESP

Dissimilarities between trophic linkage strength and prey abundance may be an indicator of ESP; hence, solely relying on prey population density to predict consumption could provide an incomplete understanding of the roles played by predators early in the growing season (Chapman et al., 2013). Decoupling prey abundance and detection frequency of a predation event can easily be examined via molecular gut content analyses, and this decoupling has been revealed in many agricultural systems. One early example of this was a study of *Rhopalosiphum padi* L. (Hemiptera: Aphididae) consumption by various carabids and linyphiids. Utilizing ELISA, Chiverton (1987) showed that these predators were consuming *R. padi* during its sensitive establishment phase. The same result was found when many predator groups were tested for multiple aphid species, with up to 20% of predators testing positive for aphid consumption when zero aphids had been collected from the field (Sunderland et al., 1987). Using ELISA, this trend was also observed for several groups preying upon aphids (Sunderland and Vickerman, 1980).

Boreau de Roince et al. (2013) examined predation by spiders from ten families on six species of aphids within apple orchards. After measuring aphid abundance and consumption by

spiders over the year, they found significant levels of spider predation occurred on initial aphid colonizers, supporting results reported in a soybean agroecosystem (Harwood et al., 2007). Aphid availability was not a reliable metric for predation frequency, as spiders readily consumed colony founders before exponential aphid population growth. These examples indicate how molecular gut content analysis can be utilized to determine if predators are engaging in ESP.

Molecular gut content analysis has been used in many other agricultural systems to delineate trophic linkages and indicate general trends in biological control and ESP. Predators and their interactions with soybean aphids have been extensively studied using gut content analysis to understand underlying mechanisms of biological control. The ground beetle, *Pterostichus melanarius* (Illiger) (Coleoptera: Carabidae), was found to have a high incidence of predation on soybean aphids early in the season when pest population levels were very low, with a loss of control over the aphids when populations peaked later in the season (Firlej et al., 2013). Similarly, the insidious flower bug, *O. insidiosus*, was shown to exert ESP on soybean aphids before pest numbers could increase exponentially (Harwood et al., 2007; 2009). Loss of control over cereal aphids by *Poecilus cupreus* (L.) (Coleoptera: Carabidae) was also shown later in the season once aphid populations were established in winter wheat (Griffiths et al., 2008).

In citrus orchards, the earwig, *Forficula auricularia* L. (Dermaptera: Forficulidae), consumed aphids in accordance with their prey availability, except in the early season, when aphid abundance was very low but 30% of earwigs tested positive for aphid predation (Romeu-Dalmau et al., 2012). Other combinations of predators and pests support the phenomenon of consumption of pests early in the growing season (Birkhofer et al., 2008b; Chapman et al., 2013; Jaramillo et al., 2010; Moser et al., 2011). These studies indicate that effective ESP, which maintains pests below economic thresholds, may require a decoupling of abundance data and

direct levels of consumption. Additionally, predators may rely on alternative prey to establish and persist in the system before pests arrive. It is therefore important to understand the trophic interactions of predators, pest species, and alternative prey by using molecular gut content analysis in conjunction with abundance data to provide a clearer picture of predator-prey interactions in agroecosystems.

7. Conclusions

Molecular gut-content analysis of predators is valuable for elucidating consumptive relationships and determining whether a given predator will be able to exert ESP upon an agricultural pest before yield loss is induced. Using molecular techniques, numerous studies have examined arthropod communities and determined that ESP occurs and may contribute to effective pest control. Other pest management strategies, such as classical biological control using specialist natural enemies, cultural control, and selective chemical control options, can be used in conjunction with ESP in an integrated pest management (IPM) regime (Kogan, 1998; Lewis et al., 1997). Furthermore, molecular tools can contribute to an effective application of IPM by elucidating trophic connections between predators and their prey (Bureau de Roince et al., 2013; Chapman et al., 2013; Firlej et al., 2013; Harwood et al., 2007; 2009).

ESP is most likely to be effective for pests with the potential for exponential population growth, where suppression early in the season may be essential to prevent costly outbreaks. Many of these pests have evolved resistance to insecticides (Bass et al., 2014; Van Leeuwen et al., 2010), highlighting the need to use alternative control measures such as ESP in on farm management practices.

ESP should be considered when implementing conservation biological control, as predators can contribute to a pest management scheme by exerting pressure when pests are at

low levels in agricultural fields. Prey availability, although important, does not necessarily predict trophic links, so the additional use of molecular tools allow enhanced understanding of trophic connections and consumption patterns. In addition, understanding the consequences of alternative prey, including intraguild predators, for ESP is crucial to creating successful conservation biological control programs. By combining molecular tools and large-scale field studies, researchers can begin to understand the spatial and temporal interactions among predators and prey in open field conditions. Studies incorporating these techniques can ultimately lead to recommendations for farmers and land managers pertaining to the implementation of successful conservation biological control programs.

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References

- Abrams, P. A., and Matsuda, H. 1996. Positive indirect effects between prey species that share predators. *Ecology* 77, 610-616.
- Agustí, N., Shayler, S. P., Harwood, J. D., Vaughan, I. P., Sunderland, K. D., and Symondson, W. O. C. 2003. Collembola as alternative prey sustaining spiders in arable ecosystems: prey detection within predators using molecular markers. *Mol. Ecol.* 12, 3467-3475.
- Baggen, L. R., and Gurr, G. M. 1998. The influence of food on *Copidosoma koehleri* (Hymenoptera : Encyrtidae), and the use of flowering plants as a habitat management tool to enhance biological control of potato moth, *Phthorimaea operculella* (Lepidoptera : Gelechiidae). *Biol. Control* 11, 9-17.
- Balmer, O., Pfiffner, L., Schied, J., Willareth, M., Leimgruber, A., Luka, H., and Traugott, M. 2013. Noncrop flowering plants restore top-down herbivore control in agricultural fields. *Ecology and Evolution* 3, 2634-2646.
- Balzan, M. V., and Moonen, A. C. 2013. Field margin vegetation enhances biological control and crop damage suppression from multiple pests in organic tomato fields. *Entomol. Exp. Appl.* 150, 45-65.
- Bass, C., Puinean, A. M., Zimmer, C. T., Denholm, I., Field, L. M., Foster, S. P., Gutbrod, O., Nauen, R., Slater, R., and Williamson, M. S. 2014. The evolution of insecticide resistance in the peach potato aphid, *Myzus persicae*. *Insect Biochem. Mol. Biol.* 51, 41-51.
- Beccaloni, J. 2009. *Arachnids*. University of California Press, Berkeley and Los Angeles, California.
- Bianchi, F., Booij, C. J. H., and Tscharntke, T. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control.

379 Proc. R. Soc. Biol. Sci. Ser. B 273, 1715-1727.

380 Bickerton, M. W., and Hamilton, G. C. 2012. Effects of intercropping with flowering plants on
 381 predation of *Ostrinia nubilalis* (Lepidoptera: Crambidae) eggs by generalist predators in
 382 bell peppers. Environ. Entomol. 41, 612-620.

383 Bilde, T., and Toft, S. 1994. Prey preference and egg production of the carabid beetle, *Agonum*
 384 *dorsale*. Entomol. Exp. Appl. 73, 151-156.

385 Birkhofer, K., Bezemer, T. M., Bloem, J., Bonkowski, M., Christensen, S., Dubois, D., Ekelund,
 386 F., Fliessbach, A., Gunst, L., Hedlund, K., Mader, P., Mikola, J., Robin, C., Setälä, H.,
 387 Tatin-Froux, F., Van der Putten, W. H., and Scheu, S. 2008a. Long-term organic farming
 388 fosters below and aboveground biota: Implications for soil quality, biological control and
 389 productivity. Soil Biol. Biochem. 40, 2297-2308.

390 Birkhofer, K., Gavish-Regev, E., Endlweber, K., Lubin, Y. D., von Berg, K., Wise, D. H., and
 391 Scheu, S. 2008b. Cursorial spiders retard initial aphid population growth at low densities
 392 in winter wheat. Bull. Entomol. Res. 98, 249-255.

393 Blackman, R. L., and Eastop, V. F. 2007. Aphids on the world's crops. Wiley, New York.

394 Boreau de Roince, C., Lavigne, C., Mandrin, J. F., Rollard, C., and Symondson, W. O. C. 2013.
 395 Early-season predation on aphids by winter-active spiders in apple orchards revealed by
 396 diagnostic PCR Bull. Entomol. Res. 103, 495-495.

397 Borer, E. T., Seabloom, E. W., Shurin, J. B., Anderson, K. E., Blanchette, C. A., Broitman, B.,
 398 Cooper, S. D., and Halpern, B. S. 2005. What determines the strength of a trophic
 399 cascade? Ecology 86, 528-537.

400 Brosius, T. R., Higley, L. G., and Hunt, T. E. 2007. Population dynamics of soybean aphid and
 401 biotic mortality at the edge of its range. J. Econ. Entomol. 100, 1268-1275.

402 Brown, J. S., Laundre, J. W., and Gurung, M. 1999. The ecology of fear: Optimal foraging, game
403 theory, and trophic interactions. *Journal of Mammalogy* 80, 385-399.

404 Carpenter, S. R., Kitchell, J. F., and Hodgson, J. R. 1985. Cascading trophic interactions and lake
405 productivity. *Bioscience* 35, 634-639.

406 Chailleux, A., Mohl, E. K., Teixeira Alves, M., Messelink, G. J., and Desneux, N. 2014. Natural
407 enemy-mediated indirect interactions among prey species: potential for enhancing
408 biocontrol services in agroecosystems: NE-mediated indirect interactions among prey
409 species for biocontrol in agroecosystems. *Pest Manag. Sci.* 70, 1769-1779.

410 Chapman, E. G., Schmidt, J. M., Welch, K. D., and Harwood, J. D. 2013. Molecular evidence for
411 dietary selectivity and pest suppression potential in an epigeal spider community in
412 winter wheat. *Biol. Control* 65, 72-86.

413 Chiverton, P. A. 1986. Predator density manipulation and its effects on populations of
414 *Rhopalosiphum padi* (Hom, Aphididae) in spring barley. *Ann. Appl. Biol.* 109, 49-60.

415 Chiverton, P. A. 1987. Predation of *Rhopalosiphum padi* (Homoptera: Aphididae) by
416 polyphagous predatory arthropods during the aphids prepeak period in spring barley.
417 *Ann. Appl. Biol.* 111, 257-269.

418 Costamagna, A. C., Landis, D. A., and Difonzo, C. D. 2007. Suppression of soybean aphid by
419 generalist predators results in a trophic cascade in soybeans. *Ecol. Appl.* 17, 441-451.

420 Deol, G. S., and Rataul, H. S. 1978. Role of various barrier crops in reducing the incidence of
421 cucumber mosaic virus in chili *Capsicum annuum*. *Indian J. Entomol.* 40, 261-264.

422 Desneux, N., and O'Neil, R. J. 2008. Potential of an alternative prey to disrupt predation of the
423 generalist predator, *Orius insidiosus*, on the pest aphid, *Aphis glycines*, via short-term
424 indirect interactions. *Bull. Entomol. Res.* 98.

425 Dong, Z. K., Gao, F. J., and Zhang, R. Z. 2012. Use of ryegrass strips to enhance biological
 426 control of aphids by ladybirds in wheat fields. *Insect Sci.* 19, 529-534.

427 Edwards, C. A., Sunderland, K. D., and George, K. S. 1979. Studies on polyphagous predators of
 428 cereal aphids. *J. Anim. Ecol.* 16, 811-823.

429 Elliott, N. C., Kieckhefer, R. W., Lee, J. H., and French, B. W. 1999. Influence of within-field
 430 and landscape factors on aphid predator populations in wheat. *Landsc. Ecol.* 14, 239-252.

431 Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S.
 432 R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen,
 433 T., Paine, R. T., Pickett, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T.
 434 W., Shurin, J. B., Sinclair, A. R. E., Soule, M. E., Virtanen, R., and Wardle, D. A. 2011.
 435 Trophic downgrading of planet earth. *Science* 333, 301-306.

436 Eubanks, M. D., and Denno, R. F. 2000. Health food versus fast food: the effects of prey quality
 437 and mobility on prey selection by a generalist predator and indirect interactions among
 438 prey species. *Ecol. Entomol.* 25, 140-146.

439 Fereres, A. 2000. Barrier crops as a cultural control measure of non-persistently transmitted
 440 aphid-borne viruses. *Virus Res.* 71, 221-231.

441 Finke, D. L., and Denno, R. F. 2005. Predator diversity and the functioning of ecosystems: the
 442 role of intraguild predation in dampening trophic cascades. *Ecol. Lett.* 8, 1299-1306.

443 Firlej, A., Doyon, J., Harwood, J. D., and Brodeur, J. 2013. A multi-approach study to delineate
 444 interactions between carabid beetles and soybean aphids. *Environ. Entomol.* 42, 89-96.

445 Fox, T. B., Landis, D. A., Cardoso, F. F., and Difonzo, C. D. 2005. Impact of predation on
 446 establishment of the soybean aphid, *Aphis glycines* in soybean, *Glycine max*. *Biocontrol*
 447 50, 545-563.

448 Frank, T., Aeschbacher, S., Barone, M., Kuenzle, I., Lethmayer, C., and Mosimann, C. 2009.
 449 Beneficial arthropods respond differentially to wildflower areas of different age. *Ann.*
 450 *Zool. Fenn.* 46, 465-480.

451 Furlong, M. J. 2015. Knowing your enemies: Integrating molecular and ecological methods to
 452 assess the impact of arthropod predators on crop pests. *Insect Sci.* 22, 6-19.

453 Gagnon, A. E., Heimpel, G. E., and Brodeur, J. 2011. The ubiquity of intraguild predation among
 454 predatory arthropods. *PLoS One* 6.

455 Gardiner, M. M., Landis, D. A., Gratton, C., DiFonzo, C., D., O'Neal, M., Chacon, J. M., Wayo,
 456 M. T., Schmidt, N. P., Mueller, E. E., and E., H. G. 2009a. Landscape diversity enhances
 457 biological control of an introduced crop pest in the north-central USA. *Ecol. Appl.* 19,
 458 143-154.

459 Gardiner, M. M., Landis, D. A., Gratton, C., Schmidt, N., O'Neal, M., Mueller, E., Chacon, J.,
 460 Heimpel, G. E., and DiFonzo, C. D. 2009b. Landscape composition influences patterns of
 461 native and exotic lady beetle abundance. *Divers. Distrib.* 15, 554-564.

462 Gomez-Polo, P., Traugott, M., Alomar, O., Castane, C., Rojo, S., and Agusti, N. 2014.
 463 Identification of the most common predatory hoverflies of Mediterranean vegetable crops
 464 and their parasitism using multiplex PCR. *J. Pest. Sci.* 87, 371-378.

465 Greenstone, M. H. 1979. Spider feeding-behavior optimizes dietary essential amino acid
 466 composition. *Nature* 282, 501-503.

467 Greenstone, M. H., Szendrei, Z., Payton, M. E., Rowley, D. L., Coudron, T. C., and Weber, D.
 468 C. 2010. Choosing natural enemies for conservation biological control: use of the prey
 469 detectability half-life to rank key predators of Colorado potato beetle. *Entomol. Exp.*
 470 *Appl.* 136, 97-107.

471 Greenstone, M. H., Payton, M. E., Weber, D. C., and Simmons, A. M. 2014. The detectability
 472 half-life in arthropod predator-prey research: what it is, why we need it, how to measure
 473 it, and how to use it. *Mol. Ecol.* 23, 3799-3813.

474 Griffiths, G. J. K., Alexander, C. J., Holland, J. M., Kennedy, P. J., Perry, J. N., Symondson, W.
 475 O. C., and Winder, L. 2008. Monoclonal antibodies reveal changes in predator efficiency
 476 with prey spatial pattern. *Mol. Ecol.* 17, 1828-1839.

477 Gurr, G. M., Scarratt, S. L., Wratten, S. D., Berndt, L., and Irvin, N. 2004. Ecological
 478 engineering, habitat manipulation and pest management. Pages 1-12 *in* G. M. Gurr,
 479 Wratten, S.D., Altieri, M.A., editor. *Ecological Engineering for Pest Management: Advances in Habitat Manipulation for Arthropods*. Comstock Publishing Associates,
 480 Ithaca, New York.

482 Hagler, J. R., and Naranjo, S. E. 1997. Measuring the sensitivity of an indirect predator gut
 483 content ELISA: Detectability of prey remains in relation to predator species, temperature,
 484 time, and meal size. *Biol. Control* 9, 112-119.

485 Hagler, J. R. 2011. An immunological approach to quantify consumption of protein-tagged
 486 *Lygus hesperus* by the entire cotton predator assemblage. *Biol. Control* 58, 337-345.

487 Hagler, J. R., and Blackmer, F. 2013. Identifying inter- and intra-guild feeding activity of an
 488 arthropod predator assemblage. *Ecol. Entomol.* 38, 258-271.

489 Hagler, J. R., Blackmer, F., Krugner, R., Groves, R. L., Morse, J. G., and Johnson, M. W. 2013.
 490 Gut content examination of the citrus predator assemblage for the presence of
 491 *Homalodisca vitripennis* remains. *Biocontrol* 58, 341-349.

492 Hagler, J. R., Blackmer, F., and Spurgeon, D. W. 2015. Accuracy of a prey-specific DNA assay
 493 and a generic prey-immunomarking assay for detecting predation. *Methods in Ecology*

494 and Evolution 6, 1426-1434.

495 Halaj, J., Cady, A. B., and Uetz, G. W. 2000. Modular habitat refugia enhance generalist
 496 predators and lower plant damage in soybeans. Environ. Entomol. 29, 383-393.

497 Halaj, J., and Wise, D. H. 2001. Terrestrial trophic cascades: How much do they trickle? Am.
 498 Nat. 157, 262-281.

499 Halaj, J., and Wise, D. H. 2002. Impact of a detrital subsidy on trophic cascades in a terrestrial
 500 grazing food web. Ecology 83, 3141-3151.

501 Harwood, J. D., Sunderland, K. D., and Symondson, W. O. C. 2004. Prey selection by linyphiid
 502 spiders: molecular tracking of the effects of alternative prey on rates of aphid
 503 consumption in the field. Mol. Ecol. 13, 3549-3560.

504 Harwood, J. D., Desneux, N., Yoo, H. J. S., Rowley, D. L., Greenstone, M. H., Obrycki, J. J.,
 505 and O'Neil, R. J. 2007. Tracking the role of alternative prey in soybean aphid predation
 506 by *Orius insidiosus*: a molecular approach. Mol. Ecol. 16, 4390-4400.

507 Harwood, J. D., Yoo, H. J. S., Greenstone, M. H., Rowley, D. L., and O'Neil, R. J. 2009.
 508 Differential impact of adults and nymphs of a generalist predator on an exotic invasive
 509 pest demonstrated by molecular gut-content analysis. Biol. Invasions 11, 895-903.

510 Heidemann, K., Hennies, A., Schakowske, J., Blumenberg, L., Ruess, L., Scheu, S., and Maraun,
 511 M. 2014. Free-living nematodes as prey for higher trophic levels of forest soil food webs.
 512 Oikos 123, 1199-1211.

513 Heil, M. 2015. Extrafloral nectar at the plant-insect interface: A spotlight on chemical ecology,
 514 phenotypic plasticity, and food webs. Annu. Rev. Entomol. 60, 213-232.

515 Hines, J., and Gessner, M. O. 2012. Consumer trophic diversity as a fundamental mechanism
 516 linking predation and ecosystem functioning: Trophic diversity and ecosystem

517 functioning. J. Anim. Ecol. 81, 1146-1153.

518 Holland, J. M., Oaten, H., Moreby, S., Birkett, T., Simper, J., Southway, S., and Smith, B. M.

519 2012. Agri-environment scheme enhancing ecosystem services: A demonstration of

520 improved biological control in cereal crops. Agric. Ecosyst. Environ. 155, 147-152.

521 Holopainen, J. K., and Helenius, J. 1992. Gut contents of ground beetles (Coleoptera:

522 Carabidae), and activity of these and other epigeal predators during an outbreak of

523 *Rhopalosiphum padi* (Homoptera: Aphididae). Acta Agric. Scand. Sect. B Soil Plant Sci.

524 42, 57-61.

525 Holt, R. D. 1977. Predation, apparent competition, and structure of prey communities. Theor.

526 Popul. Biol. 12, 197-229.

527 Holt, R. D., and Lawton, J. H. 1994. The ecological consequences of shared natural enemies.

528 Annu. Rev. Ecol. Syst. 25, 495-520.

529 Holt, R. D., and Polis, G. A. 1997. A theoretical framework for intraguild predation. Am. Nat.

530 149, 745-764.

531 Hooks, C. R. R., and Fereres, A. 2006. Protecting crops from non-persistently aphid-transmitted

532 viruses: A review on the use of barrier plants as a management tool. Virus Res. 120, 1-16.

533 Jaramillo, J., Chapman, E. G., Vega, F. E., and Harwood, J. D. 2010. Molecular diagnosis of a

534 previously unreported predator-prey association in coffee: *Karnyothrips flavipes* Jones

535 (Thysanoptera: Phlaeothripidae) predation on the coffee berry borer. Naturwissenschaften

536 97, 291-298.

537 Jelaska, L. Š., Jurasovic, J., Brown, D. S., Vaughan, I. P., and Symondson, W. O. C. 2014.

538 Molecular field analysis of trophic relationships in soil-dwelling invertebrates to identify

539 mercury, lead and cadmium transmission through forest ecosystems. Mol. Ecol. 23, 3755-

540 3766.

541 Juen, A., and Traugott, M. 2007. Revealing species-specific trophic links in soil food webs:
542 molecular identification of scarab predators. *Mol. Ecol.* 16, 1545-1557.

543 Kindlmann, P., and Dixon, A. F. G. 1989. Developmental constraints in the evolution of
544 reproductive strategies – telescoping of generations in parthenogenetic aphids. *Funct.*
545 *Ecol.* 3, 531-537.

546 King, R. A., Read, D.S., Traugott, M., Symondson, W.O.C. 2008. Molecular analysis of
547 predation: a review of best practice for DNA-based approaches. *Mol. Ecol.* 17, 947-963.

548 Knapp, M., and Rezac, M. 2015. Even the smallest non-crop habitat islands could be beneficial:
549 Distribution of carabid beetles and spiders in agricultural landscape. *PLoS One* 10.

550 Kogan, M. 1998. Integrated pest management: Historical perspectives and contemporary
551 developments. *Annu. Rev. Entomol.* 43, 243-270.

552 Koss, A. M., and Snyder, W. E. 2005. Alternative prey disrupt biocontrol by a guild of generalist
553 predators. *Biol. Control* 32, 243-251.

554 Kring, T. J., and Gilstrap, F. E. 1986. Beneficial role of corn leaf aphid, *Rhopalosiphum maidis*
555 (Fitch) (Homoptera, Aphididae), in maintaining *Hippodamia spp.* (Coleoptera,
556 Coccinellidae) in grain sorghum. *Crop Prot.* 5, 125-128.

557 Kuusk, A. K., and Ekbom, B. 2010. Lycosid spiders and alternative food: Feeding behavior and
558 implications for biological control. *Biol. Control* 55, 20-26.

559 Landis, D. A., and Van Der Werf, W. 1997. Early-season predation impacts the establishment of
560 aphids and spread of beet yellows virus in sugar beet. *Entomophaga* 42, 499-516.

561 Landis, D. A., Wratten, S. D., and Gurr, G. M. 2000. Habitat management to conserve natural
562 enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* 45, 175-201.

563 Landis, D. A., Menalled, F. D., Costamagna, A. C., and Wilkinson, T. K. 2005. Manipulating
 564 plant resources to enhance beneficial arthropods in agricultural landscapes. *Weed Sci.* 53,
 565 902-908.

566 Langer, A., and Hance, T. 2004. Enhancing parasitism of wheat aphids through apparent
 567 competition: a tool for biological control. *Agric. Ecosyst. Environ.* 102, 205-212.

568 Lewis, W. J., vanLenteren, J. C., Phatak, S. C., and Tumlinson, J. H. 1997. A total system
 569 approach to sustainable pest management. *Proc. Natl. Acad. Sci. U. S. A.* 94, 12243-
 570 12248.

571 Liu, C. z., Yan, L., Li, H. r., and Wang, G. 2006. Effects of predator-mediated apparent
 572 competition on the population dynamics of *Tetranychus urticae* on apples. *Biocontrol* 51,
 573 453-463.

574 Lundgren, J. G., and Fergen, J. K. 2014. Predator community structure and trophic linkage
 575 strength to a focal prey. *Mol. Ecol.* 23, 3790-3798.

576 Mack, T. P., and Smilowitz, Z. 1981. The vertical distribution of green peach aphids and its
 577 effect on a model quantifying the relationship between green peach aphids and a predator.
 578 *Am. Potato J.* 58, 345-353.

579 Madsen, M., Terkildsen, S., and Toft, S. 2004. Microcosm studies on control of aphids by
 580 generalist arthropod predators: effects of alternative prey. *Biocontrol* 49, 483-504.

581 Maupin, J. L., and Riechert, S. E. 2001. Superfluous killing in spiders: a consequence of
 582 adaptation to food-limited environments? *Behav. Ecol.* 12, 569-576.

583 Mayntz, D., Raubenheimer, D., Salomon, M., Toft, S., and Simpson, S. J. 2005. Nutrient-specific
 584 foraging in invertebrate predators. *Science* 307, 111-113.

585 Michels, G. J., and Matis, J. H. 2008. Corn leaf aphid, *Rhopalosiphum maidis* (Hemiptera:

586 Aphididae), is a key to greenbug, *Schizaphis graminum* (Hemiptera: Aphididae),
 587 biological control in grain sorghum, *Sorghum bicolor*. Eur. J. Entomol. 105, 513-520.
 588 Mitchell, E. R., Hu, G., and Johanowicz, D. 2000. Management of diamondback moth
 589 (Lepidoptera: Plutellidae) in cabbage using collard as a trap crop. Hortscience 35, 875-
 590 879.
 591 Miyashita, T., Takada, M., and Shimazaki, A. 2003. Experimental evidence that aboveground
 592 predators are sustained by underground detritivores. Oikos 103, 31-36.
 593 Mollot, G., Duyck, P.-F., Lefeuvre, P., Lescourret, F., Martin, J.-F., Piry, S., Canard, E., and
 594 Tixier, P. 2014. Cover Cropping Alters the Diet of Arthropods in a Banana Plantation: A
 595 Metabarcoding Approach. PLoS One 9.
 596 Moser, S. E., Kajita, Y., Harwood, J. D., and Obrycki, J. J. 2011. Evidence for utilization of
 597 Diptera in the diet of field-collected coccinellid larvae from an antibody-based detection
 598 system. Biol. Control 58, 248-254.
 599 Oelbermann, K., and Scheu, S. 2009. Control of aphids on wheat by generalist predators: effects
 600 of predator density and the presence of alternative prey. Entomol. Exp. Appl. 132, 225-
 601 231.
 602 Östman, O., and Ives, A. R. 2003. Scale-dependent indirect interactions between two prey
 603 species through a shared predator. Oikos 102, 505-514.
 604 Pace, M. L., Cole, J. J., Carpenter, S. R., and Kitchell, J. F. 1999. Trophic cascades revealed in
 605 diverse ecosystems. Trends Ecol. Evol. 14, 483-488.
 606 Polis, G. A., Myers, C. A., and Holt, R. D. 1989. The ecology and evolution of intraguild
 607 predation - potential competitors that eat each other. Annu. Rev. Ecol. Syst. 20, 297-330.
 608 Preisser, E. L., Bolnick, D. I., and Benard, M. F. 2005. Scared to death? The effects of

609 intimidation and consumption in predator-prey interactions. *Ecology* 86, 501-509.

610 Preisser, E. L., and Bolnick, D. I. 2008. The Many Faces of Fear: Comparing the Pathways and
611 Impacts of Nonconsumptive Predator Effects on Prey Populations. *PLoS One* 3.

612 Romeu-Dalmau, C., Pinol, J., and Agusti, N. 2012. Detecting aphid predation by earwigs in
613 organic citrus orchards using molecular markers. *Bull. Entomol. Res.* 102, 566-572.

614 Rosenheim, J. A., Wilhoit, L. R., and Armer, C. A. 1993. Influence of intraguild predation
615 among generalist insect predators on the suppression of an herbivore population.
616 *Oecologia* 96, 439-449.

617 Rosenheim, J. A., Kaya, H. K., Ehler, L. E., Marois, J. J., and Jaffee, B. A. 1995. Intraguild
618 predation among biological control agents - theory and evidence. *Biol. Control* 5, 303-
619 335.

620 Rutledge, C. E., O'Neil, R. J., Fox, T. B., and Landis, D. A. 2004. Soybean aphid predators and
621 their use in integrated pest management. *Ann. Entomol. Soc. Am.* 97, 240-248.

622 Rypstra, A. L., and Marshall, S. D. 2005. Augmentation of soil detritus affects the spider
623 community and herbivory in a soybean agroecosystem. *Entomol. Exp. Appl.* 116, 149-
624 157.

625 Schmidt, J. M., Sebastian, P., Wilder, S. M., and Rypstra, A. L. 2012. The Nutritional Content of
626 Prey Affects the Foraging of a Generalist Arthropod Predator. *PLoS One* 7.

627 Schmidt, J. M., Barney, S. K., Williams, M. A., Bessin, R. T., Coolong, T. W., and Harwood, J.
628 D. 2014. Predator-prey trophic relationships in response to organic management
629 practices. *Mol. Ecol.* 23, 3777-3789.

630 Schmitz, O. J., Beckerman, A. P., and Obrien, K. M. 1997. Behaviorally mediated trophic
631 cascades: Effects of predation risk on food web interactions. *Ecology* 78, 1388-1399.

632 Schmitz, O. J., Hamback, P. A., and Beckerman, A. P. 2000. Trophic cascades in terrestrial
 633 systems: A review of the effects of carnivore removals on plants. *Am. Nat.* 155, 141-153.
 634 Schoeller, E. N., Husseneder, C., and Allison, J. D. 2012. Molecular evidence of facultative
 635 intraguild predation by *Monochamus titillator* larvae (Coleoptera: Cerambycidae) on
 636 members of the southern pine beetle guild. *Naturwissenschaften* 99, 913-924.
 637 Settle, W. H., Ariawan, H., Astuti, E. T., Cahyana, W., Hakim, A. L., Hindayana, D., and
 638 Lestari, A. S. 1996. Managing tropical rice pests through conservation of generalist
 639 natural enemies and alternative prey. *Ecology* 1975-1988.
 640 Sheppard, S. K., and Harwood, J. D. 2005. Advances in molecular ecology: tracking trophic
 641 links through predator-prey food-webs. *Funct. Ecol.* 19, 751-762.
 642 Shurin, J. B., Borer, E. T., Seabloom, E. W., Anderson, K., Blanchette, C. A., Broitman, B.,
 643 Cooper, S. D., and Halpern, B. S. 2002. A cross-ecosystem comparison of the strength of
 644 trophic cascades. *Ecol. Lett.* 5, 785-791.
 645 Shurin, J. B., Gruner, D. S., and Hillebrand, H. 2006. All wet or dried up? Real differences
 646 between aquatic and terrestrial food webs. *Proc. R. Soc. Biol. Sci. Ser. B* 273, 1-9.
 647 Sitvarin, M. I., Rypstra, A. L., and Harwood, J. D. 2016. Linking the green and brown worlds
 648 through nonconsumptive predator effects. *Oikos* 000, 001-012.
 649 Sunderland, K. D., and Vickerman, G. P. 1980. Aphid feeding by some polyphagous predators in
 650 relation to aphid density in cereal fields. *J. Anim. Ecol.* 17, 389-396.
 651 Sunderland, K. D., Crook, N. E., Stacey, D. L., and Fuller, B. J. 1987. A study of feeding by
 652 polyphagous predators on cereal aphids using elisa and gut dissection. *J. Anim. Ecol.* 24,
 653 907-933.
 654 Symondson, W. O. C. 2002. Molecular identification of prey in predator diets. *Mol. Ecol.* 11,

655 627-641.

656 Symondson, W. O. C., Cesarini, S., Dodd, P. W., Harper, G. L., Bruford, M. W., Glen, D. M.,
657 Wiltshire, C. W., and Harwood, J. D. 2006. Biodiversity vs. biocontrol: positive and
658 negative effects of alternative prey on control of slugs by carabid beetles. Bull. Entomol.
659 Res. 96, 637-645.

660 Tack, A. J. M., Gripenberg, S., and Roslin, T. 2011. Can we predict indirect interactions from
661 quantitative food webs? - an experimental approach: Food webs and indirect interactions.
662 J. Anim. Ecol. 80, 108-118.

663 Thomas, C. F. G., and Marshall, E. J. P. 1999. Arthropod abundance and diversity in differently
664 vegetated margins of arable fields. Agric. Ecosyst. Environ. 72, 131-144.

665 Toft, S. 1995. Value of the aphid *Rhopalosiphum padi* as food for cereal spiders. J. Anim. Ecol.
666 32, 552-560.

667 Toft, S., and Wise, D. H. 1999. Growth, development, and survival of a generalist predator fed
668 single- and mixed-species diets of different quality. Oecologia 119, 191-197.

669 Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., and Thies, C. 2005. Landscape
670 perspectives on agricultural intensification and biodiversity - ecosystem service
671 management. Ecol. Lett. 8, 857-874.

672 Van Leeuwen, T., Vontas, J., Tsagkarakou, A., Dermauw, W., and Tirry, L. 2010. Acaricide
673 resistance mechanisms in the two-spotted spider mite *Tetranychus urticae* and other
674 important Acari: A review. Insect Biochem. Mol. Biol. 40, 563-572.

675 von Berg, K., Thies, C., Tscharntke, T., and Scheu, S. 2009. Cereal aphid control by generalist
676 predators in presence of belowground alternative prey: Complementary predation as
677 affected by prey density. Pedobiologia 53, 41-48.

678 von Berg, K., Traugott, M., and Scheu, S. 2012. Scavenging and active predation in generalist
679 predators: A mesocosm study employing DNA-based gut content analysis. *Pedobiologia*
680 55, 1-5.

681 Wallinger, C., Staudacher, K., Schallhart, N., Mitterrutzner, E., Steiner, E.-M., Juen, A., and
682 Traugott, M. 2014. How generalist herbivores exploit belowground plant diversity in
683 temperate grasslands. *Mol. Ecol.* 23, 3826-3837.

684 Weber, D. C., and Lundgren, J. G. 2009. Detection of predation using qPCR: Effect of prey
685 quantity, elapsed time, chaser diet, and sample preservation on detectable quantity of
686 prey DNA. *J. Insect Sci.* 9.

687 Welch, K. D., Haynes, K. F., and Harwood, J. D. 2013. Prey-specific foraging tactics in a web-
688 building spider. *Agric. For. Entomol.* 15, 375-381.

689 Welch, K. D., and Harwood, J. D. 2014. Temporal dynamics of natural enemy-pest interactions
690 in a changing environment. *Biol. Control* 75, 18-27.

691 Welch, K. D., Schofield, M. R., Chapman, E. G., and Harwood, J. D. 2014. Comparing rates of
692 springtail predation by web-building spiders using Bayesian inference. *Mol. Ecol.* 23,
693 3814-3825.

694 Wilson, L. J., Bauer, L. R., and Walter, G. H. 1996. 'Phytophagous' thrips are facultative
695 predators of twospotted spider mites (Acari: Tetranychidae) on cotton in Australia. *Bull.*
696 *Entomol. Res.* 86, 297-305.

697 Wimp, G. M., Murphy, S. M., Lewis, D., Douglas, M. R., Ambikapathi, R., Van-Tull, L. A.,
698 Gratton, C., and Denno, R. F. 2013. Predator hunting mode influences patterns of prey
699 use from grazing and epigeic food webs. *Oecologia* 171, 505-515.

700 Wissinger, S. A. 1997. Cyclic colonization in predictably ephemeral habitats: A template for

701 biological control in annual crop systems. Biol. Control 10, 4-15.

702 Wolkovich, E. M., Allesina, S., Cottingham, K. L., Moore, J. C., Sandin, S. A., and de

703 Mazancourt, C. 2014. Linking the green and brown worlds: the prevalence and effect of

704 multichannel feeding in food webs. Ecology 95, 3376-3386.

705 Xu, X., Borgemeister, C., and Poehling, H.-M. 2006. Interactions in the biological control of

706 western flower thrips *Frankliniella occidentalis* (Pergande) and two-spotted spider mite

707 *Tetranychus urticae* Koch by the predatory bug *Orius insidiosus* Say on beans. Biol.

708 Control 36, 57-64.

709 Yoo, H. J. S., and O'Neil, R. J. 2009. Temporal relationships between the generalist predator,

710 *Orius insidiosus*, and its two major prey in soybean. Biol. Control 48, 168-180.

711

712 **Figure Captions**

713 Figure 1: Impacts of beneficial and disruptive alternative prey on early season predation. A)
714 Beneficial alternative prey (e.g., collembolans) present early in the season allow predators (e.g.,
715 spiders) to increase numerically so that pests (e.g., aphids) are better suppressed later in the
716 growing season. B) Disruptive alternative prey (e.g., flies) are preferentially fed upon by
717 predators, thus reducing predator control of pest populations. The dotted line represents an
718 economic threshold, above which pests will significantly compromise crop condition (i.e.,
719 quality, biomass, or yield).

A **B**