

A REVIEW OF TROPHIC INTERACTIONS AND THEIR IMPLICATIONS FOR BIOLOGICAL CONTROL OF ARTHROPOD PESTS IN AGROECOSYSTEMS

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(A review of trophic interactions and their implications for biological control of arthropod pests in agroecosystems)

– In the last four decades there has been considerable interest in understanding the role of food web dynamics in the maintenance of plant productivity in ecosystems. This topic is particularly important in agroecosystems where the attack of herbivores can reduce plant productivity and cause severe economic damage to crops. The hypothesis that natural enemies indirectly regulate plant productivity through the suppression of herbivore populations (top-down control or trophic cascade hypothesis) has been the classical framework for biological control practitioners and ecologists interested in this topic. This hypothesis has proven to be controversial because empirical evidence shows that interspecific interactions among natural enemies in the third trophic level disrupt the top-down effects responsible for the suppression of herbivores and for the indirect benefits to plant productivity. Intraguild predation (IGP) is an important ecological process that can potentially dampen top-down control and contribute to reduce plant productivity due to the attack of unsuppressed herbivores. Thus, when aiming at the development of biological control programs with multiple species of natural enemies in the third or upper trophic levels, researchers must screen for some desirable traits of competing natural enemies. When both predators and parasitoids are present, predators are desirable in the system only if they do not eat parasitized hosts, which would disrupt parasitoid populations. When only predators are present, biological traits like mobility, body size, foraging strategy, level of diet specialization and species assemblage composition should be carefully investigated. These biological traits are related to the prevalence and intensity of IGP, to the choice and number of species to use in the program and to the choice of developmental stages to be introduced into crop fields. Observating these parameters and decision criteria may be crucial for the success of biological control programs.

Key words: Biological control, intra-guild predation, tritrophic interactions.

(Uma revisão sobre interações tróficas e suas implicações para o controle biológico de artrópodes pragas em agroecossistemas)

– Nas últimas quatro décadas, tem havido um considerável interesse em compreender o papel da dinâmica de cadeias tróficas na manutenção da produtividade primária de plantas. Este tópico é particularmente importante em agroecossistemas, onde o ataque de herbívoros pode reduzir a produtividade e causar severas perdas econômicas. A hipótese de que inimigos naturais regulam indiretamente a produtividade das plantas através da supressão das populações de herbívoros (controle *top-down* ou hipótese das cascatas tróficas) tem sido a abordagem clássica utilizada por usuários do controle biológico e ecólogos interessados neste tema. Esta hipótese tem se mostrado controversa, pois evidências empíricas demonstram que interações interespecíficas entre inimigos naturais no terceiro nível trófico podem romper o efeito *top-down* responsável pela supressão de herbívoros e pelos benefícios indiretos para a produtividade das plantas. A predação intraguilda é um processo ecológico importante que pode reduzir potencialmente o controle *top-down* e contribuem para reduzir a produtividade das plantas devido ao ataque dos herbívoros que escapam do controle dos inimigos naturais. Assim, quando se objetiva o desenvolvimento de programas de controle biológico com várias espécies de inimigos naturais no terceiro nível trófico, é importante escrutinar alguns atributos desejáveis de inimigos naturais que competem pelo mesmo recurso (uma praga alvo). Quando tanto predadores como parasitóides estão presentes, os predadores são desejáveis apenas se eles forem capazes de evitar alimentar-se de hospedeiros parasitados, a fim de que as populações de parasitóides não sejam reduzidas. Quando apenas predadores estão presentes, atributos como mobilidade, tamanho do corpo, estratégia de forrageamento, nível de especialização alimentar e composição das assembléias de espécies devem ser cuidadosamente investigados. Esses atributos biológicos estão relacionados à prevalência e intensidade da predação intraguilda, à escolha e número de espécies a serem usadas no programa e à escolha dos estágios de desenvolvimento dos inimigos naturais a serem liberados no campo. A observação desses parâmetros e dos critérios de decisão deve ser considerada crucial para o sucesso de programas de controle biológico.

Palavras-chave: controle biológico, predação intraguilda, interações tritróficas.

INTRODUCTION

In the early 1960's, HAIRSTON *et al.* (1960) proposed the hypothesis that green biomass accumulates in terrestrial communities because predators in the third trophic level regulate herbivore populations in the second trophic level which in turn release plants in the first trophic level from

being intensively attacked and consumed. In this case, they propose a tritrophic community structure in which plants are resource limited (e.g., by nutrient availability or competition), herbivores are predator limited (assuming they do not deplete plants completely causing self extinction) and predators are food limited (respond to prey density). This hypothesis became known as the Green World Hypothesis

(GWH) and further generated a “top-down” control framework in the study of trophic interactions (recently also referred to as trophic cascade hypothesis).

Some years later, MURDOCH (1966) offered a critique that pointed out several inconsistencies in the GWH hypothesis. First, he argued that it would not be possible to conclude that herbivores are not food limited just because plants are not depleted. Plants may not be depleted because they (or parts of them) may be edible only to a few species in the community or because they develop defenses against herbivores. Second, that the logic structure “if plants are not depleted by herbivores or weather catastrophes, predation is responsible for biomass accumulation” does not exhaust other modes of limitation. Third, he raised doubt about the feasibility of applying the hypothesis to “whole trophic levels” or communities, arguing that trophic levels do not have empirically measurable parameters and that measuring a subset of a trophic level does not provide an extrapolation to the whole trophic level. Finally, he called for the need to reformulate the hypothesis in a way that could be experimentally tested. Murdoch’s critique became the basis to future enquiries about trophic interactions and community structure with much more theoretical and methodological consistency.

An alternative hypothesis to explain trophic interactions is based on thermodynamics principles and states that energy transfer progressively attenuates while moving up from plants, to herbivores, to primary carnivores and sometimes secondary or tertiary carnivores (POLIS & STRONG, 1996). Another approach is that secondary compounds of plants are defense mechanisms and they can affect the biology of herbivores and predators in the upper trophic levels (GILBERT, 1979; ORR & BOETHEL, 1986) allowing plants to escape massive herbivory. In both cases, organisms in each trophic level are food limited (POWER, 1992), directly or indirectly. These hypotheses generated a bottom-up control framework to study trophic interactions in communities.

The term trophic cascade was first used by PAINE (1980), but the concept is the same as the Green World Hypothesis proposed by HAIRSTON *et al.* (1960), predicting that, in multi-trophic systems, when predators control herbivores, indirect effects are triggered and cascade down to a lower trophic level (producers). Thus, according to POWER (1992), communities that exhibit trophic cascades have at least one species or a guild of species in the upper trophic level(s) with sufficiently strong potential effects on their resources to produce linear chain-like, rather than diffuse web-like responses.

Since diverse ecosystems have a complex, multi-directional network of interactions, some authors argue that a multitude of factors like omnivory, intraguild predation, detritivory, mutualism, competition, abiotic heterogeneity, ontogenetic diet shift, plant edibility, plant cover, disturbance, etc., make highly unlikely that top-down, unidirectional chain-like trophic cascades occur in a widespread set of entire communities (HUNTER & PRICE, 1992; POWER, 1992; POLIS & STRONG, 1996). According to this point of view,

bottom-up forces have primacy in food web dynamics and trophic cascades must be an exception rather than a rule (POWER, 1992; STRONG, 1992; POLIS & STRONG, 1996).

In spite of the above compelling arguments against the trophic cascade hypothesis, studies focusing on top-down forces have found that:

- 1 - In aquatic ecosystems with highly interconnected food webs, trophic cascades are triggered by top-down forces. A classical example was the study reported by CARPENTER *et al.* (1985) in which the removal of piscivorous fish from lakes allowed planktivorous fish to increase, overgraze on zooplankton and release phytoplankton to produce algal blooms. Other studies have shown that changes in top predators produced trophic cascades in ponds (SPENCER & KING, 1984), lakes (CARPENTER, 1988; CARPENTER *et al.*, 1987), rivers (POWER, 1987, 1990) and intertidal and offshore marine communities (PAINE & VADAS, 1969; PAINE, 1980; WOOTON, 1992).
- 2 - Trophic cascades involving arthropods and plants are also manifested in terrestrial ecosystems, even in the presence of dissipative forces that potentially disrupt chain-like effects, the same forces used as counter-arguments against trophic cascades. ROSENHEIM *et al.* (1993) found trophic cascades in cotton, even though their system showed high levels of intraguild predation. FAGAN (1997) detected that omnivory increased the community stability after disturbance. SNYDER & WISE (2001) found trophic cascade effects in vegetable gardens in the presence of very evident intraguild predation, and the effects were responsible for three- and four-level chains early and late in the cropping season respectively. DYER & LETOURNEAU (1999) detected a trophic cascade in a tritrophic system even in the presence of bottom-up forces. SCHMITZ *et al.* (2000) reviewed 60 independent trials to analyze the effects of predator removal on arthropod herbivores. Trophic cascade effects were reported in 45 out of 60 trials, suggesting that top-down control of arthropod herbivores is relatively common in a variety of systems. However, these studies were done in a short term and generally for one season, which makes it difficult to do any inference about stability of such systems in time.

IMPLICATIONS FOR RESEARCH ON BIOLOGICAL CONTROL IN AGROECOSYSTEMS

Most of the studies reporting top-down control or trophic cascades were conducted in poor-diversity ecosystems such as agroecosystems and subsets of communities (species-level cascade). These findings in simplified food webs might not be very attractive (actually they are vulnerable to a large set of counter-arguments) for ecologists interested in extrapolations applicable to complex communities in natural ecosystems. However, as highlighted by BOGRAN *et al.* (2002), simplified agroecosystems offer unique opportunities for population and community ecologists

to build a solid background for biological control practices based on ecological theory.

Furthermore, the economic importance of the crops, pests, and natural enemies, as well as the environmental concerns associated with present pest management practices point out the need for ecologists to apply ecological theory to pest management in agroecosystems. Only by looking at biological control in the context of population and community ecology can we advance our understanding of agroecosystem functioning to allow natural enemies to be released and conserved in successful pest management programs.

In this review, I analyze some aspects of ecological processes in the third and upper trophic levels that deserve research attention due to their potential role in strengthening or dissipating top-down forces responsible for biological control of insect pests in agroecosystems.

Generation time ratios

Most of the herbivore-plant interactions occur in a scenario where the part of the plant in which the herbivore feeds upon loses quality very fast (e.g., leaf or fruit maturation). Natural enemies of such herbivores must respond very fast to prey or host presence in order to synchronize their life cycle with the lifespan of the plant part in which herbivores are present. In this context, KINDLMANN & DIXON (2001) have hypothesized that the synchrony between the life cycle of herbivores and natural enemies is an important requirement for successful suppression of herbivores. This synchrony is defined as generation time ratio (GTR = natural enemy life time/herbivore life time). The closer to one the GTR, the higher the regulation of herbivores.

Given a prey species and two predators with different developmental times, the predator with the longer generation developmental time will have less effect on prey suppression (KINDLMANN & DIXON, 1999). That is why long lived predators like ladybird beetles and syrphids in general are successful in controlling coccids which also have long developmental times (DEBACH, 1964) but not aphids which have short developmental time (FRAZER & GILBERT, 1976; MILNE, 1988; CAMPBELL & CONE, 1994).

The GTR in predator-prey systems is also important for the achievement of successful top-down control based on long-term density-dependence equilibrium because the persistence and abundance of natural enemies over time depend on the survival rate of the offspring in resource patches. According to KINDLMANN & DIXON (2001) predators should reproduce only in prey patches that are likely to last long enough to sustain the development and high survival of their offspring. Recently established prey patches should be preferred to for oviposition than older ones, even if they have lower prey abundance. This assumption has been supported by empirical evidence in studies reporting that ladybird beetles, chrysopids and hoverflies had an inverse numerical response, laying more eggs in patches with less prey but short age (HEMPINNE *et al.*, 1993; RUZICKA, 1994).

In spite of theoretical and empirical support for

these hypotheses I call for caution on assuming them as prevalent processes in tritrophic interactions, especially in biological control programs. The hypotheses take into account a limited set of biological traits of predators related to developmental time and optimal foraging in oviposition behavior, failing to evaluate other ecological processes that occur in the predator-prey interaction per se. For instance, consider a system with a prey that has an exponential growth curve with a long latent increase phase (due to low intrinsic rate of increase or low initial number of colonizers). In this case, a predator that is able to cause high mortality upon adults before they contribute with offspring to the ascendant phase of the growth curve, would be more effective.

Predator voracity and predation upon reproductive adults might have a strong top-down impact on prey populations with low intrinsic rates of increase, and should be better studied in predator-prey models. This point of view has been supported by one of my recent field studies in which a guild of predators (mainly syrphids) had a strong top-down effect on populations of the aphid *Toxoptera aurantii* (Boyer de Fonscolombe) in several cocoa plantations. The predators were effective because they were able to kill reproductive females (colony founders) as well as their offspring, bringing the growth curve down before it started the ascendant phase (E. N. Silva, unpublished data).

Intraguild predation

Intraguild predation (IGP) occurs when one predatory species in a guild of natural enemies feeds on another species of predator or parasitoid present in the same trophic level. IGP is assumed to occur mainly with generalist predators that attack preys of smaller size (POLIS, 1981; POLIS *et al.* 1989) and when predators broaden their diet to include new entomophagous organisms due to scarcity or unavailability of their regular herbivore prey (BAILEY & POLIS, 1987). In other cases, intraguild predators eat other entomophagous insects even in the presence of high herbivore abundance. Intraguild predation is an important issue in classical (introduction of exotic natural enemies), augmentative (frequent release of mass reared natural enemies) or conservation (habitat management for diversity maintenance) biological control. In classical biological control programs, imported natural enemies can face antagonistic interactions with native ones. In augmentative programs released natural enemies interact with less abundant species already present in the agroecosystem. In conservation programs, with diverse assemblage of natural enemies, complex food webs are prone to have high numbers of antagonistic interactions.

In agricultural systems the goal of biological control is to enhance ecosystem function, such as primary productivity, based on trophic cascade frameworks, through the manipulation of natural enemies which are expected to indirectly enhance crop yield by releasing crops from herbivore consumption. This fate, according to FINKE & DENNO (2004), is more likely to occur when predator diversity is

low or antagonistic interactions among natural enemies are minimal. Studies on this topic (from both natural and managed ecosystems) have brought conflicting conclusions. Some of them show that enhancing predator diversity some times increases (SCHMITZ *et al.*, 2000; SCHMITZ & SOKOL-RESSNER, 2002; MATSUMOTO *et al.*, 2003) and other times decreases (FINKE & DENNO, 2004) plant productivity by respectively strengthening or dampening trophic cascade effects. Thus, there is a clear need to study each trophic system as deeply as possible in order to reach a better knowledge of interspecific interactions and to find plausible guidelines for successful implementation of biological control practices.

Predator-parasitoid interactions

Four experiments in which a predator was added to a host-parasitoid system are analyzed here. In all cases, the predator consumed both unparasitized and parasitized hosts. In the first one, PRESS *et al.* (1974) examined biological control of *Plodia interpunctella* (Hübner) by the parasitoid *Bracon hebetor* Say and the predator *Xylocoris flavipes* (Reuter) in the laboratory. *X. flavipes* fed directly on the ectoparasitic larvae of *B. hebetor*, but relative preferences for parasitoid vs moth prey were not measured. Each natural enemy acting alone suppressed *P. interpunctella* populations, but the parasitoid was much more effective than the predator. Adding both parasitoid and predator in the third trophic level disrupted biological control, and *P. interpunctella* densities almost doubled.

FERGUSON & STILING (1996) used field cages to assess suppression of the aphid *Dactynotus* sp. by the parasitoid *Aphidius floridaensis* Smith and the coccinellid predator *Cycloneda sanguinea* (L.). *C. sanguinea* preyed upon mummified aphids, but preferences for parasitized vs unparasitized prey were not quantified. When tested alone, both natural enemies suppressed aphids, but the parasitoid was again more effective than the predator. Adding the predator to the third trophic level caused aphid densities to increase slightly, but the main test for interaction was nonsignificant.

HEINZ & NELSON (1996) used large cages in greenhouses to test all combinations of the parasitoids *Encarsia formosa* Gahan and *Encarsia pergandiella* (Howard) and the predator *Delphastus pusillus* (LeConte) to control the whitefly *Bemisia tabaci* (Gennadius) biotype B (= *Bemisia argentifolii*). Previous laboratory studies (HEINZ *et al.*, 1994; HOELMER *et al.*, 1993) showed that *D. pusillus* feeds indiscriminately on unparasitized and parasitized whiteflies harboring parasitoid eggs or young larvae. However, this predator strongly avoids feeding on hosts harboring mature parasitoid larvae or pupae. The predator was a more effective biological control agent than either of the parasitoids, and experimental trials comprised of the whole guild of natural enemies (predator included) consistently improved whitefly suppression.

COLFER & ROSENHEIM (2001) evaluated the impact of introducing a predator, the convergent ladybird beetle,

Hippodamia convergens Guérin-Mnéville, on the biological control of the cotton aphid, *Aphis gossypii* Glover, by the parasitoid *Lysiphlebus testaceipes* (Cresson), under field conditions. Predation on immature parasitoids by *H. convergens* was intense: 98–100% of aphid mummies were consumed by the end of the experiment, and *H. convergens* substantially reduced immature parasitoid populations. Despite the negative impact of *H. convergens* on aphid parasitoids, aphid population suppression was greatest in treatments containing both *H. convergens* and parasitoids. The parasitoid alone or in combination with *H. convergens* suppressed cotton aphids in a density-dependent manner and increased total plant leaf area and biomass; *H. convergens* did not substantially alter the percentage of aphids mummified by parasitoids and showed a partial feeding preference for unparasitized aphids over aphid mummies.

These four studies demonstrate that the addition of predators to host-parasitoid systems can either enhance or disrupt top-down forces promoting biological control. They allow us to conclude that predator preferences for parasitized vs. unparasitized hosts is an important biological trait in food webs with several predator and parasitoid species. This is for sure a vital research topic when biological control programs are pursued in this scenario.

Predator-predator interactions

Five studies in which intraguild predators were added resulting in enhancement or disruption of biological control are reported here. In the first one, CISNEROS & ROSENHEIM (1997) evaluated ontogenetic diet shift, intraguild predation and aphid suppression by an intraguild predator, *Zelus renardii* Kolenati, feeding on another predator, the lacewing *Chrysoperla carnea* (Stephens), and the cotton aphid *A. gossypii*. Older nymphs of *Z. renardii* caused greater mortality of lacewings and fed on larger lacewing larvae than did the younger nymphs. Lacewings were effective in suppressing *A. gossypii*, while none of the nymphal stages of *Z. renardii* was an effective control agent of *A. gossypii*. The addition of *Z. renardii* nymphs of different developmental stages in the trophic system frequently disrupted biological control due to substantial lacewing mortality and consequently released aphid populations from regulation.

LUCAS *et al.* (1998) studied how predator mobility, body size and interaction symmetry, as well as intraguild prey density, influence the magnitude of intraguild predation. The system was comprised of the potato aphid, *Macrosiphum euphorbiae* (Thomas), a specialist predator, the gall midge *Aphidoletes aphidimyza* (Rondani), and two generalist predators, *Chrysoperla rufilabris* (Burmeister) and *Coleomegilla maculata* De Geer. Results showed that sessile or low mobility stages of all species were extremely vulnerable to intraguild predation. Larger sized individuals were generally the intraguild predators while the smaller ones were the victims in most of the predator-predator encounters. For similar sizes, lacewing larvae were superior to Coccinellidae larvae winning most of the confrontations with the latter. The *C. maculata*–*C. rufilabris* interaction

was symmetrical (predators eat one another), whereas the interactions with *A. aphidimyza* and generalist predators were asymmetric (predators do not eat one another) and always favored the generalist predators. The addition of aphids to the system decreased intraguild predation level exponentially when interacting predators were early instars generalist predators (response 1), kept it constant when older lacewing larvae were paired with early instars coccinellids (response 2) and kept it constant at low aphid densities decreasing at high densities when older lacewing larvae were paired with gall midge larvae (response 3).

HINDAYANA *et al.* (2001) studied the occurrence of IGP among the predators *C. carnea*, *Coccinella septempunctata* (L.), *Episyrphus balteatus* (De Geer) (the focal species) and *A. aphidimyza*. They also found that relatively large individuals across the different species acted as intraguild predators, while relatively smaller individuals became intraguild prey. Eggs and first- as well as second-instar larvae of *E. balteatus* were highly susceptible to predation by all other predators, whereas pupae of *E. balteatus* were preyed only by the larvae of *C. carnea*. Interactions between *A. aphidimyza* and *E. balteatus* were asymmetric and always favored the latter. Eggs and first- as well as second-instar larvae of *E. balteatus* sustained intraguild predation irrespective of the presence of extraguild prey (the pea aphid). However, the frequency of predation on third-instar larvae of *E. balteatus* was significantly reduced. In general, the presence of aphids reduced IGP. A remarkable result was the fact that the same species can be both intraguild predator and intraguild prey.

SNYDER & WISE (2001) studied the impact of lycosid spiders and carabid beetles alone or in combination on yield of cucumber in spring and squash in summer. Lycosid spiders and carabid beetles alone as well as the entire guild lycosid-carabid reduced herbivore densities and enhanced cucumber yield in spring. In summer squash gardens only carabids alone reduced herbivore densities and enhanced fruit production, whereas lycosid spiders alone reduced fruit production, possibly due to IGP on hemipteran predators that regulate the squash bug, and the entire lycosid-carabid guild had no impact on squash yield (the beneficial effects of one taxon were nullified by the negative effects of the other).

Finally, an interesting study by ROSENHEIM *et al.* (2004) show again that the more we investigate this topic the more we find contrasting results, rising more dilemmas and challenges to the work of ecologists and biological control practitioners. As seen in the results obtained by LUCAS *et al.* (1998) and HINDAYANA *et al.* (2001), empirical data may indicate that trophic interactions under the influence of IGP are size-structured (smaller predators being more prone to suffer intensive IGP). Nevertheless, ROSENHEIM *et al.* (2004) found that smaller body size in the predatory mite *Phytoseiulus macropilis* (Banks) allowed individuals to escape predation, to forage less across papaya leaf surface, and therefore to reduce its probability of encountering the web spider *Nesticodes rufipes* (Lucas), an intraguild

predator. Low predation of predatory mites by web spiders (sit and wait strategists) did not disrupt top-down control, allowing *P. macropilis* to suppress the population of the herbivore mite *Tetranychus cinnabarinus* (Boisduval). In this same system, another predator of *T. cinnabarinus*, *Stethorus siphonulus* Kapur, has a greater body size and was found to have its efficiency in suppressing its prey disrupted when intensively attacked by web spiders. So, it seems that there are no absolute rules for the construction of a theoretical consensus on the mechanisms underlying intensity of IGP in biological control systems.

FINAL CONSIDERATIONS

The empirical results reviewed above in the light of ecological theory have important implications for biological control. They show that when herbivore pests feed upon ephemeral resources natural enemies must respond very fast to prey or host presence in order to synchronize their life cycle with the lifespan of the plant part in which herbivores are present. Generation time ratios must be looked at as an important trait in selecting biological control agents in this context. But other factors, such as voracity and ability to eliminate reproductive adults of pest species might be of great importance too. This is one of the ways we can reach fast and effective top-down effects capable of reducing pest populations.

Furthermore, when looking at biological control programs with diverse assemblages of natural enemies comprised of predators and parasitoids, predator preferences for parasitized vs unparasitized hosts must be looked at as an important biological trait. Predators that cannot discriminate parasitized hosts may potentially disrupt the top-down component of pest control exerted by parasitoids. If the predator is able to avoid attacking parasitized hosts, its addition to the guild of natural enemies increases the beneficial effects of biological control.

In trophic systems where herbivore pest control is based exclusively on predators, factors like mobility, body size, foraging strategy, level of diet specialization and species assemblage composition should determine (1) the prevalence and symmetry of IGP, (2) the choice and number of species to use and (3) the choice of developmental stages to introduce. The observation of these parameters and decision criteria might be crucial for the success of biological control programs.

Finally, it is important to remark that biological control has been practiced on the last four decades based on simplified, linear chain-like food webs. However, theory in trophic interactions has become more mature, incorporating more complex conceptual frameworks.

Nowadays, understanding food web diffuse dynamics rather than simplified linear chain-like flows has been advocated as the more appropriate (and more scientifically challenging) approach to understand structure and function of ecosystems. This point of view is certainly of great scientific importance. Indeed, it is a very coherent argument in

the light of scientific rigor. Nevertheless, if simplified agroecosystems require the practice of biological control through the manipulation of more simplified subsets of food webs, ecologists and biological control practitioners have a unique opportunity to achieve successful suppression of insect pests applying ecological theory. This goal cannot be achieved for a particular agroecosystem without planned and good experiments that take into account interspecific interactions in the assemblages of natural enemies and their influence over crop productivity. It is of great advantage to us to have a simple “real world” to test ecological theo-

ries, looking at both linear chain-like as well as diffuse web effects. As seen in this review, agroecosystems, as simplified food webs, have enough complexity to be explored, unveiled and understood.

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