



Antagonism between two natural enemies improves biological control of a coffee pest: The importance of dominance hierarchies



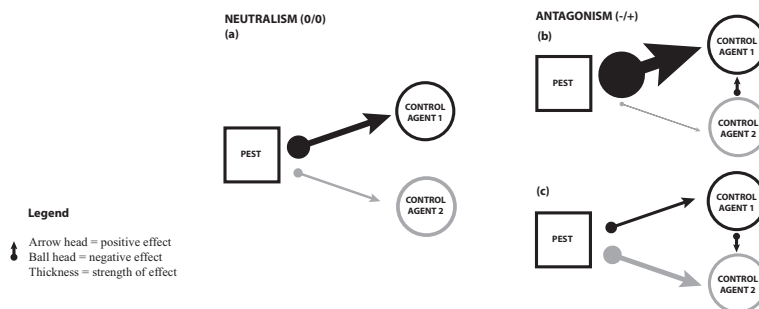
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HIGHLIGHTS

- Infection of *Coccus viridis* by *Lecanicillium lecanii* is reduced in the presence of *Azya orbigera*.
- Predation has a negative effect on pathogenesis.
- Predator was dominant control agent in field survey.
- Pathogen was dominant control agent in experiment.
- Presence of both enemies improves biological control only when predator is dominant.

GRAPHICAL ABSTRACT



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ABSTRACT

The relationship between two natural enemies of *Coccus viridis* (green coffee scale), an important hemipteran coffee pest was determined using a combination of experimental and observational approaches. Adult and larval forms of *Azya orbigera*, a coccinellid beetle predator were included on leaves of coffee plants with healthy scale populations resulting in lower proportions of scales infected with the second natural enemy, an entomopathogenic fungus (*Lecanicillium lecanii*). *C. viridis* populations on leaves where *A. orbigera* were excluded exhibited twice as much fungal infection by *L. lecanii*. In addition, field surveys of *C. viridis* populations on whole coffee plants corroborated experimental findings with eight times less fungal infection for coffee plants where *A. orbigera* was present than for plants where the predator was absent a month prior to surveys of *L. lecanii*. Despite a reduction in fungal infection in both the experiment and survey, the presence of the beetle reduced overall biological control of the pest only in the experiment where the receiver of the antagonism (*L. lecanii*) was more dominant in controlling *C. viridis* than the instigator of the antagonism (*A. orbigera*). In the survey, *A. orbigera* was dominant over *L. lecanii*, resulting in equal to greater levels of biological control depending on the degree to which *A. orbigera* was dominant over *L. lecanii*. Our results indicate that a negative relationship exists between *A. orbigera* and *L. lecanii*, but that contrary to expectations, this antagonism may in some cases improve overall biological control of the shared pest target.

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1. Introduction

In the field of biological control, managers often focus on the successful implementation of a single control agent. Although a

single agent may be introduced, the receiving environment is likely to contain a diversity of natural enemies that share the same target pest host. The effects of natural enemy diversity on the success of biological control programs are various, with no clear consensus reached to date. Recent reviews examining the relationship between natural enemy diversity and biological control conclude that although natural enemy diversity often decreased the density

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of herbivorous pests (Denoth et al., 2002), intraguild predation, where natural enemies consume one another in addition to their shared target pest (Letourneau et al., 2009), often reduce the efficacy of biological control (Cardinale et al., 2012). For this reason, (Cardinale et al., 2012) caution against broad sweeping statements that biodiversity is always beneficial for ecosystem services. Positive relationships between enemy diversity and biological control found in the reviews are theorized to work through species/niche complementarity (Straub and Snyder, 2006). By this mechanism, a variety of enemies with different host preferences are better able to exploit all life stages of a pest together than alone. However, evidence for complementarity is weak, with most studies contributing incidences of effective biological control to a single dominant species, or in systems with particularly variable environments, other species having redundant functions are thought to provide ecosystem resilience through the insurance hypothesis (Naeem and Li, 1997; Naeem, 1998; Yachi and Loreau, 1999). Still many other cases report a net zero response on biological control, explained by the reviewers as the confluence of positive and negative effects of natural enemy diversity (Straub et al., 2008). Clearly, the effects of multiple enemies on biological control are context dependent. One emerging topic of interest is the specific combination of predators and pathogens as biological control agents. Recent studies have found that functional differences (size, mode of attack, foraging strategy, etc.) may decrease the potential for predator-pathogen pairs to overlap in niche space, thereby increasing facilitation between enemies and overall effectiveness of biological control (Crowder et al., 2010; Ramirez and Snyder, 2009; Snyder and Ives, 2003). However, antagonistic relationships between predator-pathogen pairs are also possible. Intraguild predation can occur through predators consuming pathogen-infected prey, or from pathogens co-infecting prey and predator alike (Rosenheim et al., 1995). In fact, concerns over non-target effects on natural enemies often involve the implementation of generalist pathogens as control agents (Roy and Pell, 2000). However, few studies look for impacts of predation on the pathogen, even though pathogens are very effective control agents as well (Shah and Pell, 2003). In this study, we combine a small-scale field experiment with a larger scale field survey to test how the presence of a natural enemy predator influences the effectiveness of a second, pathogenic natural enemy.

Coccus viridis (the green coffee scale) is a hemipteran coffee pest that is attacked simultaneously by a coccinellid predator, *Azya orbiger* and the fungal pathogen, *Lecanicillium lecanii*. *C. viridis* feeds on the phloem of coffee plants and is capable of reducing coffee yields if densities are sufficiently high (Waller et al., 2007). However, this pest is usually controlled below damaging levels by a variety of natural enemies, the most evident of which are *A. orbiger* and *L. lecanii*. Immobility makes *C. viridis* an easy target for predation by *A. orbiger*, a voracious consumer of *C. viridis* in both its adult and larval stages (Liere and Perfecto, 2008; Uno, 2007). In addition, regular epizootics of the fungal disease, *L. lecanii* (Easwaramoorthy and Jayaraj, 1978; Jackson et al., 2009) can completely decimate large *C. viridis* populations. In our system, we envision two possible scenarios: predation could facilitate the spread of the fungus as adult beetles travel from large clusters of infected scales unwittingly carrying conidia to new, uninfected patches, or alternatively, consumption of infected scales by the predator can inhibit growth and spread of the fungus.

2. Materials and methods

2.1. Study sites

We conducted research in an organically managed coffee farm in the Soconusco region of Chiapas, Mexico, named Finca Irlanda

(15°11' N, 92°20' W). Finca Irlanda is approximately 300 ha in size with elevations ranging between 900 and 1150 m. The farm receives about 4500 mm rain/yr and consists of approximately 1200–2500 coffee plants/ha. Experiments were set up in three spatially distinct sites within Finca Irlanda.

2.2. Experimental enclosures and exclusions

At each site, all plants having at least three leaves infected with ≥ 20 scale insects each and no visible signs of *L. lecanii* infection were included, thirteen plants in total. On 28 May 2010, three suitable plants were chosen at the first site, and three leaves of each plant covered with 3.5 × 7 inch clear plastic sealable bags and randomly selected to include either (1) an adult *A. orbiger*, (2) a larval stage *A. orbiger* or (3) nothing as a control. The number of scales was surveyed at the beginning and end of the experiment. Bags were sealed at the base of the leaves and organisms left inside for approximately 24 h and then removed. The bagged leaves were the unit of replication. After seven days, bags were removed from leaves and all scales inspected for white halos of mycelia characteristic of *L. lecanii* infection. On the 10–14 June 2010, 10 additional plants (set of three leaves for each plant) were added to increase sample size; four additional plants at the first site, five at a second site, and one at a third site. For these 10 replicates, plastic bags were replaced with 3.5 × 7 inch mesh bags in order to increase airflow and decrease microclimatic effects. Five of these replicates ran for one additional day because of time constraints; we account for this statistically in Section 2.4. We combined data from the smaller previous run, and accounted for bag, initial number of scales, and site effects in our statistical model.

2.3. Field survey of *L. lecanii* and *A. orbiger*

To compliment the small scale experiments, data from larger scale field surveys conducted in June and July of 2009 were analyzed to look for associations between *L. lecanii*, *A. orbiger* and *C. viridis* populations. Each coffee bush ($n = 428$) in a plot measuring 12 × 7 ha in size was surveyed for the number of scale insects, average percentage of *L. lecanii* infection, and the number of *A. orbiger* adults and larvae. A first census of *C. viridis* and *L. lecanii* densities was conducted from 6 to 8 June 2009. This was followed by a second census of the same plot from 8 to 11 July 2009. Each coffee bush was given a quick visual examination to determine whether there were less than twenty (0 category), twenty to fifty (50 category) or greater than fifty scales total. If the plant had greater than 50 scales, each individual branch was surveyed and placed into one of the following categories: low (0–6 scales), medium (7–30), high (31–70), or super (>70). For plants with greater than 50 scales, number of scales total was estimated by multiplying the number of branches in each of the above branch categories by 0, 15, 46, and 150, respectively, and summing. Otherwise, total number of scales was estimated at 0 or 50. This census protocol was previously established by other investigators using the same study system and found to have a 93% efficiency ($R^2 = 0.926$) when compared to direct counting methods (Jackson et al., 2012, Jackson et al., 2009; Perfecto and Vandermeer, 2006). Each plant was surveyed in sequential, numerical order. Logistical and geographical barriers prevented a random survey.

In order to control for effects of *C. viridis* density on infection rates, only data for bushes with an average of 50 scales in June were analyzed. For each of these bushes, *L. lecanii* infection was estimated for the entire bush from 0% to 100% in 5% intervals (Jackson et al., 2012, Jackson et al., 2009). To more accurately census *A. orbiger* populations, surveys were done about a week after *C. viridis* and *L. lecanii* surveys to minimize disturbance to the flying insect community. The first *A. orbiger* census was done from 16 to

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