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Food web associations among generalist predators and biological control agents of *Melaleuca quinquenervia*

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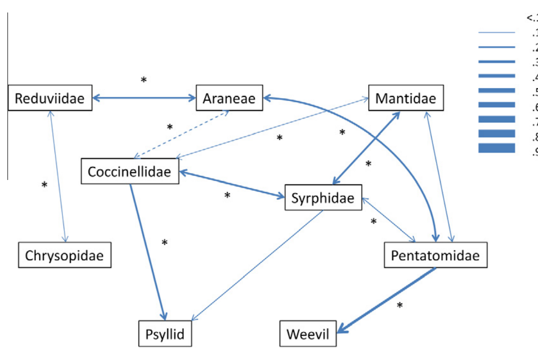
HIGHLIGHTS

- Generalist predators had little influence on two biological control agents.
- Coccinellids and pentatomids reduced densities of *Boreioglycaspis melaleucae* and *Oxyops vitiosa*, respectively.
- There was no evidence of mutualism between a subsocial spider and *B. melaleucae*.
- High levels of interactions among predators were evident within the food web.

GRAPHICAL ABSTRACT



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ABSTRACT

A partial food web that included two weed biological control species on *Melaleuca quinquenervia* and their associated generalist predators was examined by monitoring insect densities every two weeks for a year. The data were used to develop a theoretical path model that described directional relationships among predators and the two agents, *Boreioglycaspis melaleucae* and *Oxyops vitiosa*. Path analysis indicated that the model provided a good fit to the observed data and identified strong effects of Coccinellidae on *B. melaleucae* and Pentatomidae on *O. vitiosa*. The other six predator groups exhibited little or no influence on the agents. Relatively low r^2 values within the path model indicated that predators were more likely to be influencing each other (though intraguild predation) than the agents. Experiments were conducted to investigate causality with some of these associations including a small plot experiment that found that predation, primarily by coccinellids, reduced the density of *B. melaleucae* by 85.6%. Another experiment to examine a potential mutualistic relationship between the subsocial web spinning spider *Anelosimus studiosus* and *B. melaleucae* showed that, while *B. melaleucae* nymphs sometimes shelter within webs where they may avoid predators like coccinellids, the overall densities of *B. melaleucae* were greater away from webs and that webs frequently contained entrapped *B. melaleucae* adults. Overall, generalist predators explained little of the variance found in densities of both agents which indicates that predation had little impact on the population dynamics of the intentionally introduced herbivores.

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1. Introduction

Arthropod food webs in natural systems are dynamic and complex, making quantitative analysis challenging (Polis and Strong, 1996). Generalist predators in particular may engage in complicated predator-predator interactions like cannibalism and omnivory, resulting in poorly defined trophic levels (Rosenheim et al., 2004; Hunter, 2009). In addition to not interacting at all, predators may attack and kill each other, they may influence each other's foraging, or they may influence prey susceptibility for other predators (Losey and Denno, 1998). Intraguild predation is widespread in food webs with 58–87% of species engaged in this phenomenon in 113 food webs (Arim and Marquet, 2004). Halaj and Wise (2001) posited that because of intraguild predation and widespread trophic-level omnivory, most terrestrial food webs are strongly nonlinear trophic structures with the potential to buffer cascading effects. Ultimately, novel trophic groupings in food webs may weaken the effects of predation on herbivores as well as dampen the effect of trophic cascades on primary production (Finke and Denno, 2004; van Veen Frank et al., 2006).

Less complex food webs are often present on non-native plants, especially on those that were introduced without specialist herbivores and have become weedy (Burghardt et al., 2010; Proches et al., 2008). Biological control programs that target weeds with intentional introductions of host-specific herbivores may initiate or contribute to existing food webs by providing, at a minimum, subsidies to generalist predators (Paynter et al., 2010). Over time, more specialized natural enemies, including parasitoids, may accumulate on biological control agents, a process that can occur within the first 3 years of release (Cornell and Hawkins, 1993) and is expedited by the presence of native ecological analogues (Paynter et al., 2010). Critics of biological control argue that employing this tactic can influence food web interactions unpredictably, resulting in indirect effects that range from apparent competition to risks to human health (Willis and Memmott, 2005; Pearson and Callaway, 2006).

Melaleuca quinquenervia (Cav.) S. T. Blake (Myrtaceae) is a widespread ecological weed that threatens the integrity of wetlands and uplands in the greater Everglades region. This Australian tree was intentionally introduced in the late 1800s in southern Florida for use primarily as an ornamental landscape plant but subsequently spread into natural areas causing serious ecological degradation (Center et al., 2012). Eventually, this plant was targeted for classical biological control using insects as part of an integrated control program that led to the release of *Oxyops vitiosa* Pascoe (Coleoptera: Curculionidae) in 1997 and *Boreioglycaspis melaleucae* Moore (Hemiptera: Psyllidae) in 2002 (Center et al., 2000, 2006). *Oxyops vitiosa* is a defoliator whose larvae feed on both leaf surfaces and consume the tissue through to the cuticle on the other side, whereas *B. melaleucae* is a phloem feeder (Purcell and Balciunas, 1994; Purcell et al., 1997). Both species are widespread and have unique features, like *O. vitiosa* larvae being covered in a viscous layer of plant derived, essential oils that deters predators, whereas *B. melaleucae* nymphs secret waxy filaments that form highly visible flocculent masses on leaves (Purcell et al., 1997; Wheeler et al., 2002).

Food web interactions on non-native plants like *M. quinquenervia* may be further influenced by the presence of mutualism or commensalism within the community such as insects that use spider webs for protection from predators (Deyrup et al., 2004). A common spider found on *M. quinquenervia* is the subsocial spider *Anelosimus studiosus* (Hentz) (Araneida: Theridiidae), which constructs webs on the tips of *M. quinquenervia* branches. This spider ranges from New England, USA to Argentina where it spins irregular tangled webs in the outer reaches of trees and shrubs (Jones and Parker, 2002). A single female spider begins the web and is eventually accompanied by her offspring (Furey, 1998). Larger webs may be inhabited by inquilines like *Ranzovious clavicornis* (Knight) (Hemiptera: Miridae) and *Tallula watsoni* Barnes and McDunnough (Lepidoptera: Crambidae) (Wheeler and McCaffrey, 1984; Deyrup et al., 2004). Deyrup et al. (2004) posited that larvae of *T. watsoni* suffered reduced predation and parasitism as an obligate inquiline of A. *studiosus*. Numerous observations of these spider webs on *M. quinquenervia* noted copius amounts of flocculence from *B. melaleucae* within the webs with all stages of *B. melaleucae* observed alive within the webs. Potential explanations for this phenomenon include *B. melaleucae* actively sheltering and feeding within the webs to avoid predators, or the spiders simply spinning their webs around existing colonies of *B. melaleucae*.

The objectives of this paper were to: (1) quantify the direct and indirect effects of the predatory species within part of the food web on *M. quinquenervia* that interacted with *O. vitiosa* and *B. melaleucae*; (2) quantify the impact of coccinellids on *B. melaleucae*; and (3) determine the nature of the relationship between *B. melaleucae* and *A. studiosus*. We hypothesized that: (1) interactions among generalist predators and biological control agents will be weak in the food web on *M. quinquenervia*; (2) predation from coccinellids will not suppress densities of *B. melaleucae*; and (3) densities of *B. melaleucae* nymphs are not greater within webs of *A. studiosus* because they gained protection from predators.

2. Materials and methods

A number of sampling schemes were employed to quantify herbivore and predator densities on *M. quinquenervia*. Colonies of immature *B. melaleucae* are usually concentrated at branch tips and concealed beneath layers of a white flocculence while adults are active and readily fly when disturbed. Thus, in order to determine their densities, branch tips must be enclosed quickly to capture adults, and examined carefully under magnification to count nymphs. This was the method for estimating densities of *B. melaleucae*. When estimating arthropod abundances on upright plants growing in rows, beat sheets are often the method of choice, especially if the arthropods are easily distinguishable (Wade et al., 2006). This method was employed to sample herbivores other than *B. melalucae* and predators inhabiting the canopy of *M. quinquenervia* hedges.

2.1. Densities of B. melaleucae

Saplings of *Melaleuca quinquenervia* were planted in 2002 in eight 30 m-long hedges arranged 5 m apart at the USDA-ARS Invasive Plant Research Laboratory in Davie, Florida. Hedges were drip-irrigated and sheared periodically to keep them at a height and width of ca 2 m. Five of the eight hedges were sampled every two weeks from Oct. 2006 through Oct. 2007 by first randomly selecting a hedge then identifying a starting sample location based on the number of paces from the end of the hedge using a random number table. Subsequent sample locations along the hedge were based on the number of paces from the last sample locations. Surveyors that reached the end of the hedge reversed direction and sampled the opposite side until a total of 5 sample locations were identified. A 1 m-long piece of plastic tape was thrown over the surveyor's shoulder onto the hedge and the two closest plant tips to the tape ends were each enclosed quickly within zip lock bags to prevent the escape of active adults of *B. melaleucae*, clipped approximately 10 cm from the tip, and then the bags were sealed and returned to the lab for processing. The tips were examined under a dissecting microscope and the numbers of *B. melaleucae* and any generalist predators were recorded and removed. The dry weight biomass of the *M. quinquenervia* tip was determined