



Non-crop vegetation associated with chili pepper agroecosystems promote the abundance and survival of aphid predators

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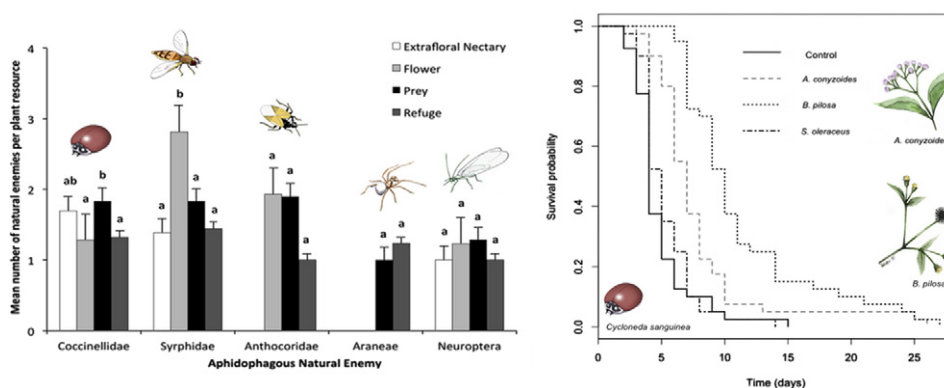
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HIGHLIGHTS

- ▶ We assessed the role of non-crop weeds for maintaining aphidophagous predators in tropical agroecosystems.
- ▶ We quantified the survival of two coccinellids feeding on weed floral resources.
- ▶ The interactions between non-crop weeds and natural enemies varied according to plant species and predators group.
- ▶ Native and exotic coccinellids survived differently according to flower resource.
- ▶ Non-crop weeds can affect aphid natural enemy abundance and survival.

GRAPHICAL ABSTRACT



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ABSTRACT

Habitat manipulation has long been used as strategy to enhance beneficial insects in agroecosystems. Non-crop weed strips have the potential of supplying food resources to natural enemies, even when pest densities are low. However, in tropical agroecosystems there is a paucity of information pertaining to the resources provided by non-crop weeds and their interactions with natural enemies. In this study we evaluated (a) whether weeds within chili pepper fields affect the diversity and abundance of aphidophagous species; (b) whether there are direct interactions between weeds and aphidophagous arthropods; and (c) the importance of weed floral resources for survival of a native and exotic coccinellid in chili pepper agroecosystems. In the field, aphidophagous arthropods were dominated by Coccinellidae, Syrphidae, Anthocoridae, Neuroptera and Araneae, and these natural enemies were readily observed preying on aphids, feeding on flowers or extrafloral nectaries, and using plant structures for oviposition and/or protection. Survival of native *Cycloneda sanguinea* (Coleoptera: Coccinellidae) differed between plant species, with significantly greater survival on *Ageratum conyzoides* and *Bidens pilosa*. However, no evidence was gathered to suggest that weed floral resources provided any nutritional benefit to the exotic *Harmonia axyridis* (Coleoptera: Coccinellidae). This research has provided evidence that naturally growing weeds in chili pepper agroecosystems can affect aphid natural enemy abundance and survival, highlighting the need for further research to fully characterize the structure and function of plant resources in these and other tropical agroecosystems.

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1. Introduction

The adoption of ecological practices aimed at strengthening trophic relationships within agroecosystems for regulation of herbivores is gaining prominence, especially in organic production systems (Zehnder et al., 2007). Top-down forces such as predation and parasitism directly influence agricultural communities, and can be managed to reduce pest outbreaks (Stireman et al., 2005; Macfadyen et al., 2009). From this perspective, the enhancement of natural enemies through habitat manipulation and increasing vegetational diversity can improve herbivore control (Landis et al., 2000; Gurr et al., 2003) and is associated with enhanced environmental heterogeneity which itself serves to sustain natural enemies in the environment. Indeed, such plant diversity not only functions as a refuge for many natural enemies, but can provide food such as nectar, pollen and alternative prey (Bugg and Pickett, 1998; Frank et al., 2007; Jonsson et al., 2008), all of which enhance natural enemy populations prior to pest arrival. However, natural enemy – pest interactions are complex and non-crop vegetation does not universally translate into improved levels of biological control (see Landis et al., 2000). Thus, understanding the complex interactions between natural enemies and non-crop resources forms a critical framework for the implementation of sound conservation biological control strategies.

A practice that has been widely adopted for habitat management in agroecosystems is the conservation of weed strips, which can enhance beneficial arthropod populations (Altieri and Whitcomb, 1978; Wyss, 1995; Nentwig, 1998; Liljeström et al., 2002; Gurr et al., 2003; Norris and Kogan, 2000, 2005). Although less predictable than managed wildflower plantings that promote populations of beneficial arthropods (Fielder et al., 2008) through the provisioning of food resources (Wäckers et al., 2005), natural weed strips provide the farmer with a low-investment option to enhance biological control. These weed strips are typically integrated into, and/or surrounding, crop fields, depending on habitat characteristics and the movement patterns of arthropod natural enemies (Corbett, 1998; Gurr et al., 2003; Skirvin et al., 2011). It is this interaction between weed strips and arthropods that can influence predator–prey interactions (Norris and Kogan, 2000, 2005), broaden the food resource base and increase the number of sites available for oviposition and shelter, thereby enhancing the pest suppression potential of natural enemies (Nentwig, 1998; Thies and Tschardtke, 1999; Landis et al., 2000). Specifically, flowers of weeds provide pollen and nectar that attracts and maintains a diverse community of arthropod predators such as syrphids (Tooker et al., 2006; Haenke et al., 2009), ladybirds (Cottrell and Yeagan, 1999; Burgio et al., 2006), lacewings (Nentwig, 1998) and predatory bugs (Atakan, 2010). Nutrients present in floral resources also improve natural enemy survival during their non-carnivorous life stage and are utilized as complementary food resource when prey are limiting.

An important component of successfully integrating weeds into pest management decision making processes is quantification of the mechanisms and resources that influence the response of natural enemies to such plants (Andow, 1988; Snyder et al., 2005). Here, we sought to examine such interactions in a tropical agroecosystem to clarify the role of weed strips in an important crop of South America, chili pepper. This cropping system is important in several regions of Brazil and is typically cultivated on small diverse farms (Ohara and Pinto, 2012). Crucially, there are currently no pesticides registered by the Brazilian government for use on pests attacking chili peppers, thus finding alternative management solutions to control pest species is critical. Given the lack of access to pest control technology, farmers rarely achieve efficient management of arthropod pests and can, during outbreak years, incur sig-

nificant economic losses. Two aphids, *Myzus persicae* (Sulzer) and *Aphis gossypii* Glover (Hemiptera: Aphididae), are particularly important pests of chili pepper and cause both direct and indirect damage to the crop (Venzon et al., 2006, 2011). Within these agroecosystems, coccinellids are highlighted as particularly important natural enemies (Venzon et al., 2006, 2007) and both *Cycloneda sanguinea* (L.) and *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) have a particularly close association with these aphids (Venzon et al., 2011). However, while the former has native range from the southern United States to Argentina (Gordon, 1985), thus encompassing the field sites in which this research was undertaken, the latter has an original distribution of Japan, Ryukyu [Ryukui Islands], Formosa [Taiwan], China, Saghalien [an island in the Russian Far East] and Siberia (after Sasaji, 1971) and is an exotic species in South America. In a multi-faceted approach, this study focused on the use of weed resources in chili pepper agroecosystems and clarified their role in influencing the abundance and diversity of aphid predators in the field. Additionally, the interactions between two coccinellids and weeds were quantified in laboratory feeding trials to quantify the effect of these non-prey resources on survival parameters of *C. sanguinea* and *H. axyridis*. Enhancing our understanding of such interactions could therefore establish an important framework for future conservation management in chili pepper (and other tropical) agroecosystems.

2. Material and methods

2.1. Field sampling of weeds

Field research was undertaken in five chili pepper fields located in the county of Piranga (Minas Gerais, Brazil, GPS coordinates 20° 45'45" S, 43° 18'10"W) during the main growing season (March–August). Chili pepper fields were selected based on their similarity in size (~1 ha) and small farmer agricultural practices. No insecticides were applied throughout the experiment and all fields were separated by at least 2 km. Sampling was conducted every 2-weeks from 29 March to 23 August 2011 (10 sampling dates) and the commencement of field collections corresponded to a reduction in weed control by farmers.

Total abundance of weed species was characterized using 0.25 m² quadrats (0.5 m × 0.5 m) (adapted from Smith et al., 2011) from 20 randomly selected sites within and surrounding all chili pepper fields. Predators present on weeds were sampled using three 100 m transects per field. This sampling approach incorporated a weed strip along a field border and transected the chili pepper field to the weed strip border on the opposite side of the field. To quantify arthropod abundance, each transect was meticulously inspected, all plant species recorded and all arthropods on the plant were collected (approximately 10 min collection/plant) and their location recorded based on the following parameters: (i) prey, when arthropods were feeding upon aphids or another prey; (ii) on/in plant flower parts, (iii) extrafloral nectaries, when arthropods were feeding on an extrafloral structure; and (iv) refuge, to categorize arthropods that were found on plants but were not feeding or associated with any plant food resource. After visual observation for arthropods, plants were also sampled by beating foliage over a collection tray to ensure comprehensive sampling of the fauna. All arthropods were transferred into 70% ethanol and returned to the laboratory for identification. Sampling was undertaken between 09:00 and 16:00 h.

2.1.1. Statistical analysis

The abundance of predators was analyzed using a generalized linear model (GLM), assuming a Poisson distribution and a log link

function (Crawley, 2007). In the analysis, models were created whereby the mean of arthropod abundance was included as a fixed effect in two-way ANOVA interactions between arthropod group (Coccinellidae, Syrphidae, Anthocoridae, Neuroptera and Araneae) and plant resource (prey, flowers, extrafloral nectaries and refuge). In further analyses, mean abundance was included as a fixed effect in two-way ANOVA interactions between coccinellid species versus plant resource and coccinellid species versus plant species. Distribution of residuals was tested for model assumptions and model simplification was done by removing non-significant interactions ($P > 0.05$) and then removing non-significant main effects (that were not consistent within significant interactions). The significance of each term was assessed using χ^2 test, based on an estimated mean deviance parameter. When significant interactions were observed between abundance at a resource or weed species, we tested the significance among abundance means (Crawley, 2007). Statistical analyses were performed using R software version 2.15 (R Development Core Team, 2012).

2.2. Laboratory experiments

The most common coccinellids found at the field site, *C. sanguinea* and *H. axyridis*, were used in laboratory feeding trials to quantify the role of pollen and nectar from weeds on their survival. Predators were collected in chili pepper fields in the county of Piranga (Brazil) and were subsequently reared in laboratory.

Adult mating pairs were maintained within plastic (400 mL) containers and maintained at 25 ± 1 °C on a 16:8 L:D cycle and $65 \pm 5\%$ RH. Coccinellid larvae were reared from eggs laid by field-collected adults and housed individually in plastic (10 mL) containers as above. Prior to the experiment, both larvae and adults were fed *ad libitum* with aphids (*M. persicae* and *A. gossypii*), eggs of *Anagasta kuehniella* (Zeller) (Lepidoptera: Pyralidae) and honey that was applied as a fine layer to the internal walls of vials. Water was provided as a moistened cotton ball. Upon pupation, larvae were maintained in an empty container as above, until emergence. Vials were inspected daily to document adult emergence. Aphids were reared in a greenhouse on cabbage plants (*Brassica oleracea* v. *capitata* L.) for *M. persicae* and cotton (*Gossypium hirsutum* L.) for *A. gossypii*.

Weeds were selected for laboratory experiments based on their abundance and association with coccinellids in chili pepper fields. For survival experiments, the following plant species were used: blue billygoat weed *Ageratum conyzoides* L. (Asteraceae), cobbler's pegs *Bidens pilosa* L. (Asteraceae) and sow thistle *Sonchus oleraceus* L. (Asteraceae). The sow thistle was selected to represent a flower resource that had no insect associates documented in the field. Plants were collected from the field, maintained in pots (2 L) in the greenhouse and filled with a 1:1 soil:substrate mix until the commencement of experiments.

Newly emerged coccinellid adults were also maintained individually in plastic vials (10 mL) and fed with 30 aphids/day, honey and water 48 h to reduce mortality due to starvation. Weeds were housed in transparent plastic vials (20 × 10 cm, 500 mL) with ventilation. All vials were secured with a post that was fixed in the soil close to the plant stem (Fig. 1). For each coccinellid, the three weeds (above) were tested and water was provided using moist cotton and replenished daily. Control treatments consisted of moistened cotton only. Coccinellids (48 h after emergence) were introduced into each vial cage, 20 replicates per treatment, and survival assessed daily for 30 days. Survival curves were estimated by Kaplan–Meier analysis (Kaplan and Meier, 1958), with equations adjusted to a non-linear model identity. A log-rank test was applied to compare survival rates and statistics were computed using R version 2.15.0 (R Development Core Team, 2012).

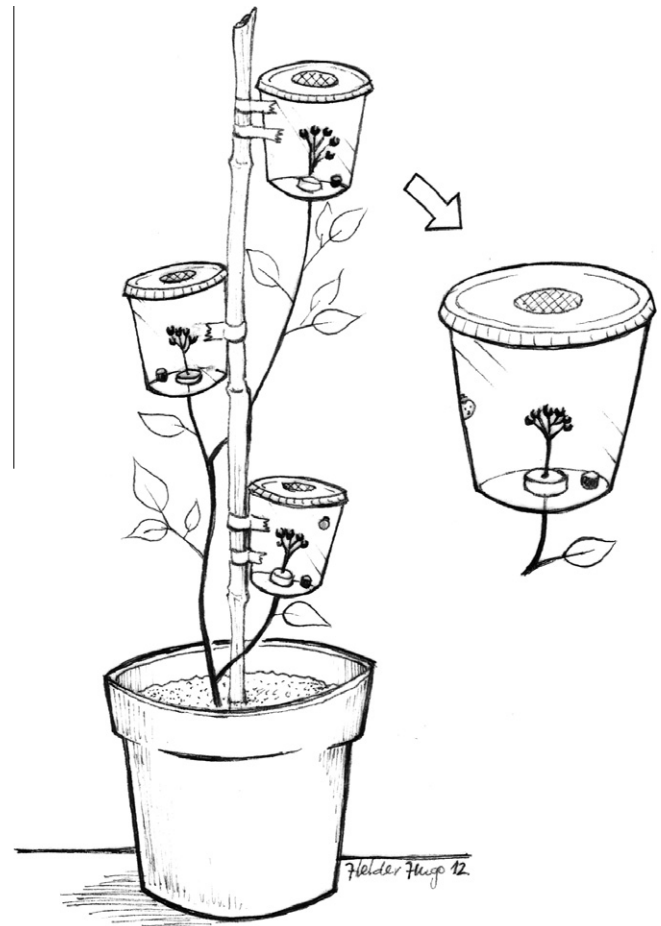


Fig. 1. Experimental design of laboratory experiments to quantify the effect of weeds on survival of Coccinellidae.

To quantify the role of non-crop plant flowers as a source of complementary food for immature coccinellids, first instar larvae ($n = 30$ replicates per treatment) of *C. sanguinea* or *H. axyridis* were held individually in 10 mL plastic vials, as above. All larvae were provided with one of the following diets: (a) weed flowers; (b) weed flowers plus frozen *A. kuehniella* eggs *ad libitum*; and (c) frozen *A. kuehniella* eggs *ad libitum*. Flowers from two weed species (*B. pilosa* and *A. conyzoides*) were selected and all treatments included water that was replenished daily. Larval survival and development were monitored daily. Statistical analysis was performed as above; Kaplan–Meier analysis was used to estimate survival curves and the log-rank test was applied to compare survival rates.

3. Results

3.1. Field sampling of weeds

A total of 40 species of weeds were associated with chili pepper fields, and were dominated by 25 species, representing 75% of all weeds present (Table 1). During extensive field observations, only 13 weed species harbored aphid natural enemies (Table 1), which were represented by the Coccinellidae, Syrphidae, Anthocoridae, Neuroptera (Chrysopidae and Hemerobidae) and Araneae.

The locations and utilization of specific food resources by aphid predators were recorded on all weeds. The abundance of aphid predators was significantly affected by resource ($\chi^2 = 534$, $df = 3$, $P < 0.001$), arthropod group or family ($\chi^2 = 467$, $df = 4$, $P < 0.001$) and there was a significant interaction between plant resource

Table 1

Abundant weeds associated with chili pepper fields in Piranga, Minas Gerais, Brazil (ordered by total number of natural enemies observed on weed plants). The status of each weed as native or exotic and native range are shown based upon Kissmann (1991).

Scientific name	Common name	Family	Predators observed	Native or exotic	Native range
<i>Ageratum conyzoides</i>	Tropic ageratum	Asteraceae	256	Native	Tropical America
<i>Sonchus oleraceus</i>	Annual sowthistle	Asteraceae	180	Exotic	Africa, Europe
<i>Bidens pilosa</i>	Hairy beggarticks	Asteraceae	146	Native	Tropical America
<i>Digitaria sp.</i>	Crabgrass	Poaceae	129	Native and exotic	Widespread distribution
<i>Solanum americanum</i>	American black	Solanaceae	129	Native	Americas
<i>Galinsoga sp.</i>	Galinsoga	Asteraceae	58	Native	Tropical America
<i>Melampodium divaricatum</i>	–	Asteraceae	50	Native	Americas
<i>Senna obtusifolia</i>	Sicklepod	Fabaceae–Caesalpinioideae	48	Native	Americas
<i>Leonurus sibiricus</i>	Siberian motherwort	Lamiaceae	47	Exotic	Asia
<i>Amaranthus sp.</i>	Low amaranth	Amaranthaceae	17	Native	Tropical America
<i>Buddleja stachyoides</i>	–	Scrophulariaceae	17	Native	Tropical America
<i>Euphobia heterophylla</i>	Wild poinsettia	Euphorbiaceae	11	Native	Americas
<i>Chloris sp.</i>	Windmillgrass	Poaceae	5	Native and exotic	Widespread distribution
<i>Baccharis sp.</i>	Eastern baccharis	Asteraceae	–	Native	Americas
<i>Emilia fosbergii</i>	Cupid's-shaving-brush	Asteraceae	–	Unknown	Unknown
<i>Blainvillea sp.</i>	–	Asteraceae	–	Native	Tropical America
<i>Brachiaria decumbens</i>	Sprawling panicum	Poaceae	–	Exotic	Africa
<i>Chaptalia nutans</i>	–	Asteraceae	–	Native	Americas
<i>Hypochaeris radicata</i>	Common catsear	Asteraceae	–	Exotic	Europe
<i>Commelina sp.</i>	Dayflower	Commelinaceae	–	Unknown	Unknown
<i>Cyperus esculentus</i>	Yellow nutsedge	Cyperaceae	–	Exotic	North America, Eurasia
<i>Erechtites valerianifolius</i>	Burnweed	Asteraceae	–	Native	Tropical America
<i>Gnaphalium purpureum</i>	Purple cudweed	Asteraceae	–	Native	Americas
<i>Leonotis nepetifolia</i>	Lionsear	Lamiaceae	–	Exotic	Africa
<i>Oxalis sp.</i>	Woodsorrel	Oxliadaceae	–	Native	Tropical America

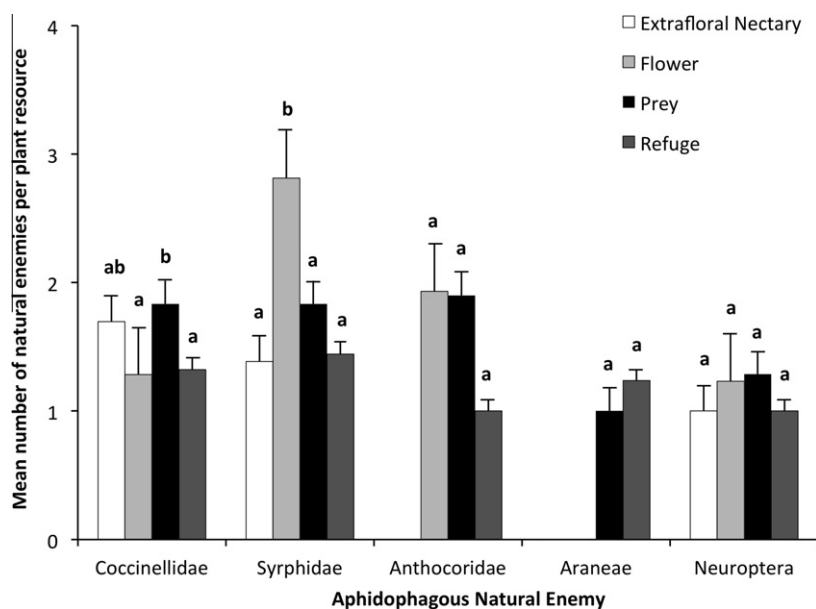


Fig. 2. Mean (+SE) number of natural enemies per plant recorded on different resources provided by weeds in chili pepper fields in Piranga, Minas Gerais, Brazil. Bars with different letters are statistically different from each other ($P < 0.05$) (comparisons within each insect taxa).

and arthropod group ($\chi^2 = 446$, $df = 9$, $P = 0.007$) (Fig. 2). Resource type also significantly affected the mean abundance of Coccinellidae ($\chi^2 = 336$, $df = 3$, $P < 0.001$), Anthocoridae ($\chi^2 = 50$, $df = 2$, $P < 0.001$) and Syrphidae ($\chi^2 = 174$, $df = 3$, $P < 0.001$). Unsurprisingly, coccinellids were more abundant when aphids were present ($\chi^2 = 334$, $df = 3$, $P = 0.030$), while no difference was observed between flowers, extrafloral nectar and refuge ($\chi^2 = 334$, $df = 3$, $P = 0.907$) (Fig. 2). Syrphids on the weeds were dominated by adults and were most frequently recorded on nectar and pollen from flowers compared to any other resource ($\chi^2 = 172$, $df = 3$, $P = 0.004$) (Fig. 2) and purely associated with *Digitaria sp.*, *B. pilosa* and *A. conyzoides*. Resource type had no effect on the distribution of Anthocoridae ($\chi^2 = 49$, $df = 1$, $P = 0.448$), Neuroptera (Chrysopidae

and Hemerobidae) ($\chi^2 = 26$, $df = 3$, $P = 0.506$) or Araneae ($\chi^2 = 38$, $df = 1$, $P = 0.162$) (Fig. 2). However, throughout the whole sampling period, the number of natural enemies varied significantly between non-crop plant species ($\chi^2 = 443$, $df = 4$, $P = 0.003$).

Given that coccinellids were the most abundant aphidophagous predator, the use of weed resources by the five species or genera of coccinellid were analyzed and found to be significantly affected by plant resource type ($\chi^2 = 282$, $df = 19$, $P < 0.001$) (Fig. 3). *C. sanguinea* was significantly more abundant on plants that provided prey compared to other resources ($\chi^2 = 131$, $df = 4$, $P = 0.018$) while *H. axyridis* ($\chi^2 = 58$, $df = 3$, $P = 0.329$), *Hyperaspis sp.* ($\chi^2 = 53$, $df = 3$, $P = 0.495$), *Scymnus sp.* ($\chi^2 = 31$, $df = 3$, $P = 0.252$) and other coccinellids ($\chi^2 = 39$, $df = 3$, $P = 0.993$) were unaffected by plant resource

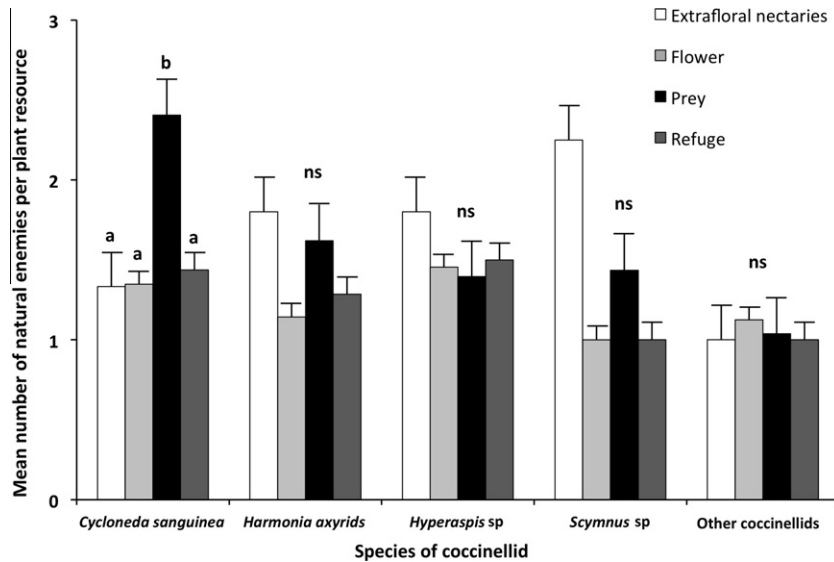


Fig. 3. Mean (+SE) numbers of coccinellid species per plant recorded on different resources provided by weeds in chili pepper fields in Piranga, Minas Gerais, Brazil. Bars with different letters are statistically different from each other ($P < 0.05$) (comparisons within each species).

type (Fig. 3). The abundance of *C. sanguinea* was also affected by weed species, with significantly more found on *S. americanum* and *S. oleraceus* plants compared to all other weeds ($\chi^2 = 131$, $df = 4$, $P = 0.018$) (Fig. 4). In contrast, no significant differences were observed in the other species of coccinellid.

3.2. Laboratory experiments

3.2.1. Survival of *Cycloneda sanguinea*

Adult survival varied between different weed flowers ($\chi^2 = 68.7$, $df = 3$, $P < 0.001$) (Fig. 5A), with a significant increase in survival on flowers of *B. pilosa* compared to *A. conyzoides* (log rank statistic = 29.5, $df = 2$, $P < 0.001$), *S. oleraceus* (log rank statistic = 44.7, $df = 2$, $P < 0.001$) and the control treatment (log rank statistic = 58.4, $df = 6$, $P < 0.001$). Meanwhile, *A. conyzoides* provided intermediate nutritional benefit to enhance survival compared to *S. oleraceus* (log rank statistic = 12.2, $df = 1$, $P < 0.001$) and the control (log rank statistic = 21.9, $df = 3$, $P < 0.001$). No oviposition was recorded for *C. sanguinea* in any treatment. The survival of *C. san-*

guinea larvae was also influenced by the provisioning of weed flowers ($\chi^2 = 118$, $df = 4$, $P < 0.001$) (Fig. 5B). Individuals subjected to a dietary mix of *B. pilosa* and *A. kuehniella* eggs or *A. conyzoides* and *A. kuehniella* eggs survived longer than eggs of *A. kuehniella* alone (*B. pilosa* and *A. kuehniella* eggs: log rank statistic = 44.3, $df = 3$, $P < 0.001$, *A. conyzoides* and *A. kuehniella* eggs: log rank statistic = 44.5, $df = 3$, $P < 0.001$). However, the survival of *C. sanguinea* larvae did not differ statistically between *A. conyzoides* and *B. pilosa* (log rank statistic = 1.7, $df = 2$, $P = 0.432$).

3.2.2. Survival of *Harmonia axyridis*

Survival parameters of *H. axyridis* varied considerably from those of *C. sanguinea*. Adult survival was not influenced by exposure to weed flowers (log rank statistic = 21.9, $df = 3$, $P = 0.95$) (Fig. 6A). In contrast, larvae were significantly affected by treatment, with eggs of *A. kuehniella* alone having the greatest effect on survival (log rank statistic = 45.9, $df = 3$, $P < 0.001$) (Fig. 6B). The survival of *H. axyridis* larvae did not differ between *B. pilosa* and *A. conyzoides* (log rank statistic = 23.0, $df = 1$, $P = 0.518$) but

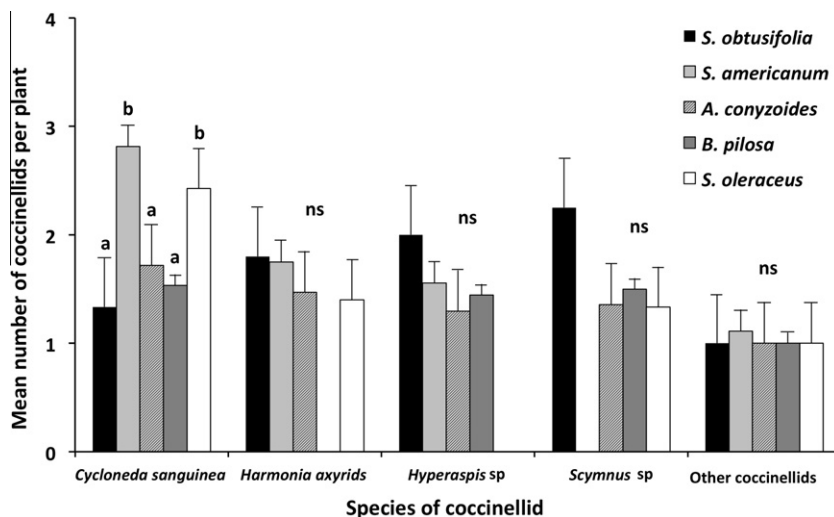


Fig. 4. Mean (+SE) numbers of coccinellid species per plant recorded on different weed species in chili pepper fields in Piranga, Minas Gerais, Brazil. Bars with different letters are statistically different from each other ($P < 0.05$) (comparisons within each species).

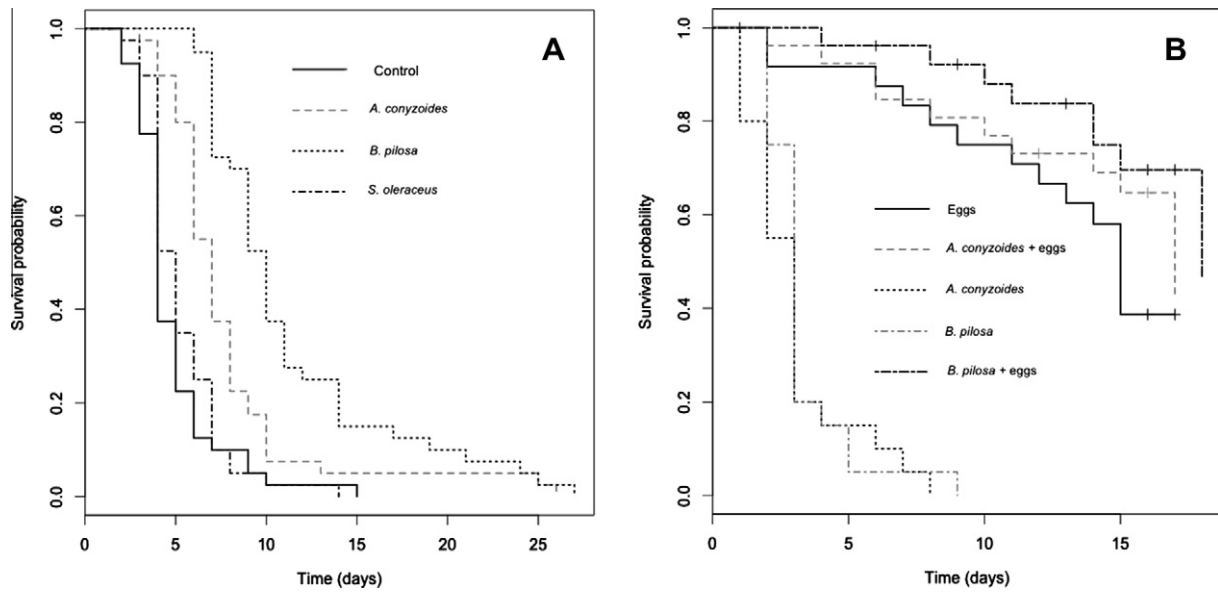


Fig. 5. (A) Kaplan–Meier estimates of survivorship function of *Cycloneda sanguinea* adults on flowers of three weeds and a control treatment. Median survival time was calculated as 10 days for coccinellids on *Bidens pilosa*, 7 days on *Ageratum conyzoides*, 5 days on *Sonchus oleraceus* and 4 days for the starvation control. (B) Kaplan–Meier estimates of survivorship function of *C. sanguinea* larvae on two weeds and *Anagasta kuehniella* eggs. Median survival time was calculated as 18 days (*B. pilosa* + eggs), 17 days (*A. conyzoides* + eggs), 15 days (eggs only), 3 days (*B. pilosa*, no eggs) and 3 days (*A. conyzoides*, no eggs).

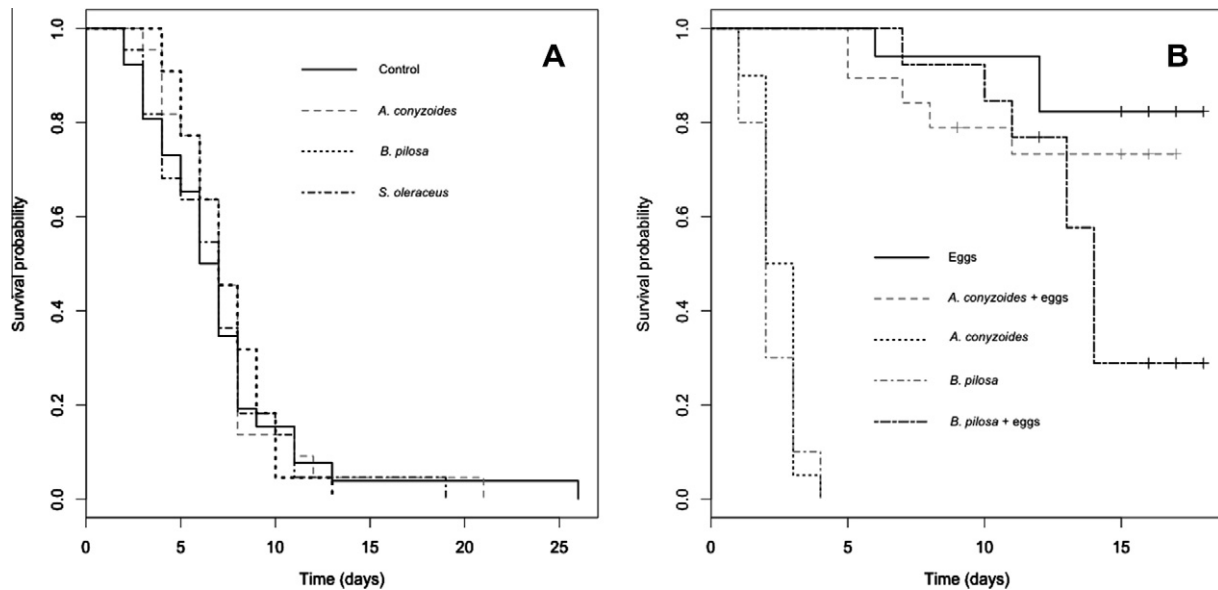


Fig. 6. (A) Kaplan–Meier estimates of survivorship function of *Harmonia axyridis* adults on flowers of three weeds and a control treatment. Median survival time was calculated as 7 days for coccinellids on *Bidens pilosa*, 7 days on *Ageratum conyzoides*, 7 days on *Sonchus oleraceus* and 6.5 days for the starvation control. (B) Kaplan–Meier estimates of survivorship function of *Cycloneda sanguinea* larvae on two weeds and *Anagasta kuehniella* eggs. Median survival time was calculated as 14 days (*B. pilosa* + eggs), 16 days (*A. conyzoides* + eggs), 18 days (eggs only), 3 days (*B. pilosa*, no eggs) and 3 days (*A. conyzoides*, no eggs).

was increased when eggs alone were offered, compared to eggs in combination with *A. conyzoides* (log rank statistic = 37.6, $df = 3$, $P < 0.001$) and *B. pilosa* (log rank statistic = 34.4, $df = 3$, $P < 0.001$). There was no significant difference in survival between the two weed species in combination with eggs (log rank statistic = 4.1, $df = 2$, $P = 0.013$). No oviposition was recorded for *H. axyridis* in any treatment.

4. Discussion

The presence of weeds within or surrounding chili pepper fields differentially affected the abundance of different groups of aphido-

phagous predators by providing alternative prey, nectar and pollen as a complementary resource. Other studies, typically conducted in temperate climates, have also reported beneficial effects of weeds on the distribution and abundance of beneficial arthropods (e.g., Wyss, 1995; Nentwig, 1998; Leather et al., 1999; Norris and Kogan, 2000; Showler and Greenberg, 2003; Silva et al., 2010). Ultimately, the food requirements of adult natural enemies can determine the importance of different non-crop plants to biological control and understanding these interactions forms an important framework to establish sound pest management recommendations. For example, the frequently observed increase of syrphids on weeds is probably associated to the availability of nectar and pollen (Gilbert,

1981; Frank, 1999; Haenke et al., 2009). Our results found that syrphids were more commonly observed visiting *B. pilosa*, a species of Asteraceae, a plant family known for providing pollen to syrphids (Irvin et al., 1999) which aids in sexual maturation and egg production (Irvin et al., 1999).

In chili pepper fields, both adult and larval coccinellids were commonly observed feeding on aphids on weeds but adult coccinellids were also frequently observed on plant flowers (*A. conyzoides*, *B. pilosa*) and on extrafloral nectaries (*S. obtusifolia*) of plants without aphids. However, the relative benefit of the utilization of such resources was limited and varied between species (Figs. 5 and 6). It is widely accepted that non-prey food items are associated with increased survival and reproduction in coccinellids (Lundgren, 2009a, 2009b), and floral and extrafloral nectaries on weeds supply pollen and nectar to adult coccinellids (e.g., Pember-ton and Vandenberg, 1993; Leather et al., 1999; Harmon et al., 2000; Bertolaccini et al., 2008; Lundgren, 2009b). However, in most cases it is unlikely to constitute an essential food that alone supports survival, growth and reproduction. In such instances, some coccinellids may use pollen and nectar as a supplemental resource to provide limited nutrients and energy, and ultimately prolong survival (Hodek and Evans, 2012) and reduce the likelihood of cannibalism and intraguild predation (Cottrell and Yeargan, 1999; Leather et al., 1999; Pell et al., 2008). In the context of biological control, the early season presence of coccinellids could be essential in restricting pest population outbreaks. Through these mechanisms to promote natural enemy population growth, weeds could be a suitable management tactic to attract and retain predators early in the season by providing alternative prey or non-prey food (Norris and Kogan, 2005; Lundgren, 2009b). Pest control efficacy may also be associated with higher density (Straub and Snyder, 2006) and diversity (Cardinale et al., 2003; Snyder et al., 2006; Letourneau et al., 2009) of predators. In our study, weeds supported higher coccinellid populations, compared with other arthropod groups, and conservation of habitat complexity has been shown to promote aphid control (Wyss, 1996; Gardiner et al., 2009). The wider diversity may therefore be related to complementary foraging strategies between species, differing nutritional requirements and aspects of niche partitioning (Obrycki et al., 2009; Snyder, 2009).

Understanding variation in food utilization between species is important in the development of conservation biological control that integrates naturally occurring weeds into pest management decision processes. For example, the presence of native *C. sanguinea* on weeds, compared to the relative scarcity of the exotic *H. axyridis*, reveals interesting variation in coccinellid population dynamics in chili pepper agroecosystems. *H. axyridis* has been considered a threat to native species (Osawa, 2011) and its success may be associated with the wide range of habitats available and its superior competitiveness with other coccinellids (Evans, 2004; Osawa, 2011). Such species may also negatively affect native populations due to their avoidance of prey-scarce habitats (facilitated by voracious feeding habits of *H. axyridis*) and the likelihood of abandoning crop fields (Alyokhin and Sewell, 2004; Evans et al., 2011). Weeds may therefore increase the potential for coexistence by reducing encounter risk and providing broader food resources (Pell et al., 2008; Osawa, 2011). Additionally, native species may be predisposed to utilize alternative resources due to life history relationships with plant species in their native range. This research supports the concept of enhanced utilization of some indigenous weed species by native species, given the greater abundance of *C. sanguinea* on non-crop plants. The management of non-crop plants could therefore reduce the possible negative effects of competition between predators for limited resources in tropical chili pepper agroecosystems.

In addition to understanding the role of natural weeds in supporting a community of natural enemies, quantifying resource utilization of non-prey foods is also important. The research presented here revealed that non-crop plant flowers increased survival of adults and larvae of native *C. sanguinea*, but not of the exotic *H. axyridis*. More significant was the apparent negative effect of *B. pilosa* and *A. conyzoides* to *H. axyridis* larvae, reducing survival compared to prey-only treatments. Pollen and nectar may serve as suitable nutrient resource during periods of low prey availability, by contributing to flight energy, sexual maturation and egg production (Hagen, 1962; Michaud and Grant, 2005; Lundgren, 2009a; Lundgren and Seagraves, 2011; Seagraves et al., 2011). Pollen and nectar may also be important for newly emerged coccinellid adults that may encounter unfavorable food conditions (Triltsch, 1999), thereby increasing coccinellid survival. The consumption of nectar and pollen undoubtedly varies between coccinellids and developmental stage. Adult *H. axyridis*, for example, experienced similar survival metrics whether or not weeds were provided as a supplemental resource. This contrasts with native species, such as *C. sanguinea*, which may utilize food supplies in weeds more efficiently, perhaps due to the variability in the digestibility of pollen and nectar, driven by long life-history associations between species.

In conclusion, this study provides an important framework for the utilization of weed strips in aphid biological control in chili pepper agroecosystems. It suggests that the management of specific weed species may provide an optimal strategy for the conservation of beneficial insects that utilize non-prey foods. Delineating the presence of weeds and their functional role to predator population dynamics is an important process in optimizing the integration of natural enemies into pest management in tropical agroecosystems. Upon the generation of such information, management approaches can be developed for farmers, aimed at selectively promoting beneficial weeds and increasing the diversity of such plants in chili pepper, and other agroecosystems. Identifying those traits of weeds that are compatible with biological control is particularly important in those systems where pesticide applications are tightly controlled. Further research, examining the effect of weeds on crop yield is clearly required, especially in many tropical systems where there is a dearth of information pertaining to biological control.

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