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# Non-crop plant to attract and conserve an aphid predator (Coleoptera: Coccinellidae) in tomato

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## ARTICLE INFO

## ABSTRACT

Pest control is an important ecosystem service that can be enhanced by increasing plant diversity. One of the simplest forms of plant diversification is making use of the occurring weeds that may benefit natural enemies of crop pests. We investigated the interaction between tomato plants, beggar-ticks (*Bidens pilosa*, Asteraceae), a common weed in Brazil and elsewhere, and the native ladybird beetle *Cycloneda sanguinea*, an important predator of aphids. The predators occurred on beggar-ticks in the field, independent of the presence of aphids, confirming that they obtained some benefit other than aphid prey from the plants. Predators were attracted to volatiles of clean, flowering beggar-ticks, and volatiles of flowering tomato plants plus flowering beggar-ticks were more attractive than volatiles of tomato plants alone. In the absence of aphids, *C. sanguinea* did not oviposit on tomato plants, beggar-ticks, or a combination of the two plants, but adult survival was higher on a combination of both plants than on tomato plants alone. These results show that the management of an abundant plant species in agricultural crops has potential for increasing pest control.

## 1. Introduction

The disturbance caused by agricultural production practices has induced dramatic changes in plant biodiversity and consequent deterioration of ecosystem services (Altieri and Letourneau, 1982; Tscharntke et al., 2005). One of the essential ecosystem services is natural pest control (Altieri and Letourneau, 1982; Myers, 1996; Van Emden, 1965). Approaches for restoring this ecosystem service form a continuum based on spatial scale (Gurr et al., 2017, 2003; Kremen and Miles, 2012; Landis et al., 2000; Tscharntke et al., 2005). The large-scale approach is diversification of the landscape, and this can indeed result in increased pest control (Bianchi et al., 2006; Gagic et al., 2011), although there are few studies on effects of landscape diversification on pest densities and crop damage (Chaplin-Kramer et al., 2011). At a smaller spatial scale, crops are combined with other plants that can benefit the natural enemies of pests and thus increase pest control (Altieri and Whitcomb, 1980; Landis et al., 2000). Plants are selected that may favor natural enemies by providing alternative prey or food such as pollen and nectar (Rezende et al., 2014; Wäckers et al., 2005), or that offer shelter or favorable microclimatic conditions (Diehl et al., 2012; Fiedler et al., 2008; Gurr et al., 2003). A meta-analysis showed that, overall, increasing plant diversity indeed resulted in increases of natural enemy densities and decreases of herbivore densities and of plant damage (Letourneau et al., 2011). To develop plant diversification practices to enhance natural pest control, detailed knowledge of specific associations of natural enemies with non-crop plants is required (Amaral et al., 2016, 2013; Fiedler et al., 2008; Landis et al., 2000).

Non-crop vegetation that provides alternative resources enables natural enemies to persist in crops when primary hosts or prey are scarce, and this may prevent outbreaks after pest invasions (Ehler and Miller, 1978; Murdoch et al., 1985). The existing weed vegetation can also provide these critical resources for natural enemies (Altieri and Whitcomb, 1979; Gurr et al., 2003; Norris and Kogan, 2005, 2000). Nevertheless, because modern agriculture generally considers weeds as harmful and because of the negative connotation of the term "weed", it is commonly thought that all weeds should be eliminated (Araj and Wratten, 2015; Chacon and Gliessman, 1982; Norris and Kogan, 2005). However, there are many instances in which weeds can be beneficial (Altieri and Koohafkan, 2004; Araj and Wratten, 2015). For example, some weeds can enhance soil fertility as well as prevent erosion by increasing moisture (Araj and Wratten, 2015). Associated to pest control, the presence of weed communities has been linked to an increase of natural enemy populations (Altieri and Whitcomb, 1979; Gurr et al., 2003; Nentwig, 1998; Norris and Kogan, 2005, 2000; Wyss, 1995).

Therefore, the management of existing weeds in agricultural crops is perhaps the simplest means to improve natural pest control and other ecosystem services, requiring low investments by the farmers (Altieri and Koohafkan, 2004; Amaral et al., 2013; Nentwig, 1998).

In this paper, we study the attractiveness and fitness effects of a common weed on an aphidophagous coccinellid. The weed *Bidens pilosa* L. (Asteraceae) is a tropical and subtropical plant, native to America (Needham, 1948) and commonly known as 'beggar-ticks'. This annual can flower continuously, and its flowers are visited by a rich diversity of insects, including predators (Needham, 1948). In Brazil, beggar-ticks is one of the most important species of weeds in annual and perennial crops (Santos and Cury, 2011). Although it has been mentioned as possible plant for diversification (Altieri and Whitcomb, 1980), it is not managed with the aim of improving natural control of pests.

One of the predators often encountered on beggar-ticks in Brazil is the native ladybird *Cycloneda sanguinea* L. (Amaral et al., 2013). It is one of the main coccinellid species in Brazil (Martins et al., 2009), feeds on various aphid species (Işıkber and Copland, 2002), and is considered a candidate for biological control of aphids on tomatoes (Oliveira et al., 2005; Sarmento et al., 2007). Feeding on beggar-ticks flower resources resulted in increased survival of *C. sanguinea* (Amaral et al., 2013). Among other cues, *C. sanguinea* uses volatiles to find plants with prey (Sarmento et al., 2007). It is repelled by the volatiles of clean tomato plants, but is highly attracted by volatiles from tomato plants with aphids (Sarmento et al., 2008). It is also attracted to clean coriander plants (*Coriandrum sativum* L.), and feeding on coriander flower resources increased adult female survival, but not oviposition (Togni et al., 2016). Here, we systematically investigated its occurrence on beggar-ticks with or without aphids in the field. Subsequently, we investigated attractiveness of beggar-ticks volatiles, either alone or in combination with tomato volatiles. Lastly, we investigated oviposition and survivorship of adult *C. sanguinea* on beggar-ticks, tomato plants, and their combination, as first steps towards integration of beggar-ticks and ladybirds in diversified tomato production systems.

## 2. Materials and methods

### 2.1. Predator rearing

*Cycloneda sanguinea* was collected from non-crop vegetation and on horticultural crops in three experimental fields (Fruticultura, Vale da Agronomia and Pomar do Fundão) located on the campus of the Federal University of Viçosa, Minas Gerais, Brazil (20° 45′24″S and 42° 52′30″W). Adults were taken to the laboratory and kept under controlled conditions (25 ± 2 °C, 70 ± 10% RH, 12:12 Light: Dark). They were placed in transparent plastic pots (500 ml) with an opening in the lid covered with mesh for ventilation. They were fed with aphids (*Myzus persicae* (Sulzer) and *M. euphorbiae* Thomas), and a solution of 10% honey water applied to a piece of cotton wool. *Myzus persicae* was reared in a greenhouse on cabbage plants (*Brassica oleracea* L. v. *capitata*), *M. euphorbiae* was collected from diverse weed plants in the field.

In each pot, three males and three females were confined together to produce eggs from which adults were obtained for all experiments. The eggs deposited in the pots were collected daily and transferred to other pots until egg hatching. The larvae were kept individually in transparent plastic pots (50 ml) and were fed with aphids until reaching adulthood.

### 2.2. Plant material

In a greenhouse, beggar-ticks and tomato seeds (*Solanum lycopersicum* L., var. Aguamiel, Vilmorin®) were sown in polystyrene trays (8 × 16 cells), using a commercial plant substrate (Bioplant®, Bioplant Misturadora Agrícola LTDA). After 20 days, the plants were transplanted to plastic pots (500 ml) containing the same substrate. The plants were kept inside cages (1.20 × 1.20 × 1.20 m) covered with a fine mesh (90 μm) to prevent insect and mite infestation. The plants were watered daily and were fertilized with a solution of 10 g of N-P-K (4-14-8) and 20 g of superphosphate simple in 20 of water every two weeks. For the experiments, we selected plants at the reproductive stage, with similar numbers of flowers. We verified that tomato pollen became available from the flowers upon slight vibration, which could easily be achieved by coccinellids.

### 2.3. Field sampling

To assess the probability of co-occurrence of ladybirds with aphids on beggar-ticks, sampling was conducted at irregular intervals, between 08:00 and 12:00 h, from 14 March to 13 June 2013, at randomly selected sites surrounding orchards and horticultural crops in the experimental fields mentioned above. All fields contained a mixture of weed vegetation including beggar-ticks, but coccinellids were mainly found on beggar-ticks. During each visit to each area, forty randomly selected beggar-ticks plants were sampled *in situ* for the presence of adults of *C. sanguinea*, of aphids and both together on the plants. The first field (Fruticultura), consisting of an orchard with *Plinia cauliflora* (DC.) Kausel (jabuticaba) and *Psidium guajava* L. (guava) trees, was sampled 15 times; the second field (Vale de Agronomia), containing mainly potatoes (*Solanum tuberosum* L.), pumpkin (*Cucurbita maxima* Duchesne) and cassava (*Manihot esculenta* Crantz), was sampled 14 times and the third field (Pomar), containing cabbage and a citrus (*Citrus* spp. L.) orchard, six times, resulting in a total of 1400 sampled plants. The probability of co-occurrence was calculated following Griffith et al. (2016), assuming a hypergeometric distribution:

$$P_j = \frac{\binom{N_1}{j} \times \binom{N - N_1}{N_2 - j}}{\binom{N}{N_2}},$$

with $N_i$ the number of plants with species $i$ (= 1, 2) and $N$ the total number of plants sampled, and $j$ ranging from 1 to $N_1$ (Griffith et al., 2016). This probability shows whether two species are positively, negatively or randomly associated. A positive association would be the result of attraction and/or arrestment of *C. sanguinea* to plants with aphids, the absence of a positive or negative association would show that the predators are not arrested or attracted to plants with aphids, suggesting that they receive some benefit from visiting plants without aphids.

### 2.4. Olfactometer

To study the attraction of adult females of *C. sanguinea* by volatiles of beggar-ticks and beggar-ticks plus tomato plants, two-choice tests were done in a Y-tube olfactometer (Janssen, 1999; Sabelis and van de Baan, 1983). The olfactometer consists of a Y-shaped glass tube (27 cm in length × 3.5 cm in diameter), with a black Y-shaped metal wire in the middle to guide the predator, with the base of the tube connected to a pump that causes an airflow from the arms of the tube to the base (Janssen, 1999). Each arm was connected to a glass container (50 × 36 × 43 cm) where pots containing beggar-ticks and/or tomato plants were placed. The wind speed in each arm of the Y-tube was measured with a hot-wire anemometer and calibrated to 0.45 m/s, which is the best wind speed to assess the foraging behavior of *C. sanguinea* in a Y-tube olfactometer (Sarmento et al., 2007). When wind speeds in both arms are equal, the air coming from the containers form two separated fields in the base of the Y-tube (Sabelis and van de Baan, 1983).

Prior to the experiments, mated adult females of *C. sanguinea*, judged by the production of eggs, were starved for 24 h, because starved females need to find suitable food and oviposition sites (Obrycki and Kring, 1998). They were tested in the olfactometer by introducing

them one at a time by disconnecting the pump and putting the female on the metal wire at the base of the Y-tube. After reconnecting the pump, the female started moving upwind to the junction of the wire, where she had to choose for one of the two arms. Each female was observed from the time that it was introduced until it reached the end of one of the arms or for a maximum of 5 min and was subsequently removed, after which the next female was introduced.

Females that did not make a choice within 5 min were scored as having made no choice and were excluded from further analysis. Three replicates were done per combination of volatile sources, each with a new set of plants and a new group of predators. Each replicate was terminated after 20 females had responded to either of the volatile sources. To correct for any unforeseen asymmetry in the experimental set-up, volatile sources were switched to the opposite arm of the olfactometer after each 5 females tested. The following choices were offered: (i) beggar-ticks vs. clean air; (ii) beggar-ticks vs. tomato plants; (iii) beggar-ticks vs. tomato plants plus beggar-ticks plants (each in a separate pot) and (iv) tomato plants vs. tomato plants plus beggar-ticks plants (again in a separate pot).

We first assessed whether the choice of the predators differed significantly among replicates, using a satiated log-linear model for contingency tables with Generalized Linear Models (GLM) using a Poisson error distribution (log link) (Crawley, 2013) with volatile source, replicate and their interaction as factors. A significant interaction between the volatile and replicate would indicate that the preference of the predators varied significantly among replicates, and a significant effect of replicate on the preference would indicate that the overall preference was more strongly determined by some replicates. This was never the case. The significance of the preference was subsequently assessed with a simple binomial test with an expected proportion of predators choosing each volatile of 0.5. This statistical analysis was done using R (R Development Core Team, 2014).

### 2.5. Oviposition

This experiment was conducted to verify whether beggar-ticks combined with tomato plants supply sufficient resources for egg production by *C. sanguinea*. Adult ladybird beetles were placed with flowering beggar-ticks and tomato plants in cages (l × w × h = 0.60 × 0.60 × 1.20 m) made of PVC tubes covered with mesh, outside the laboratory. Only pairs of females and males that previously produced eggs on a diet of aphids and water in plastic pots (500 ml) in the laboratory were used. Three pairs were released in each cage. There were four replicates of three treatments: (i) one beggar-ticks plant; (ii) one beggar-ticks plus one tomato plant; and (iii) one tomato plant. The twelve cages were placed alternately in the sequence as above. Oviposition rates were assessed daily by checking the entire plant plus the cage during five days, and the plants were replaced daily to facilitate the counting of eggs. After five days, the females had stopped ovipositing. We subsequently added ample amounts of aphids to each cage in a Petri dish. This Petri dish was placed inside a larger Petri dish containing wet cotton wool. This cotton wool served as barrier to prevent the wingless aphids from going to the plants, yet allowing access of flying predators to the aphids. The oviposition rate was then evaluated for five more days. Oviposition data in the absence and in the presence of aphids were analyzed separately using linear mixed-effects models (LME, package nlme of R, Pinheiro et al., 2017) with plant species, time and their interaction as fixed factors and replicate as a random factor. Numbers of eggs were log(x + 1) transformed, and the distribution of the residuals was checked for normality and heteroscedasticity. Non-significant interactions and factors were removed until a minimal adequate model was reached (Crawley, 2013).

### 2.6. Survivorship

We evaluated the survival of adults of *C. sanguinea* with flowering beggar-ticks, flowering tomato plants, and a combination of these two as food source. Newly-emerged adults were fed in the laboratory with aphids and water for 6 days to reduce mortality due to starvation. Subsequently, pairs of adult females and males were released in cages (as above) under a roof outside the laboratory. There were four treatments, each with four replicates: (i) a cage with one beggar-ticks; (ii) a cage with one beggar-ticks plus one tomato plant; (iii) a cage with one tomato plant and (iv) a control, i.e. an empty cage. The sixteen cages were placed alternately in the sequence mentioned above. Survival was assessed daily until most individuals had died.

Survival data were analyzed with a Cox mixed effects proportional hazards model (package Coxme in R, Therneau, 2015) with plant species as fixed factor and replicate as random factor. Contrasts were obtained through general linear hypothesis testing (package lsmeans of R, Lenth, 2016). The Kaplan–Meier estimator, which takes censored data into account, was used to produce estimates of the survival through time.

## 3. Results

### 3.1. Field sampling

In all three fields, most beggar-ticks did not harbor aphids or ladybirds (Fig. 1). The observed number of plants with both aphids and ladybirds did not differ significantly from expected assuming that they distributed themselves independently over the plants (P values above bars in Fig. 1). This implies that the ladybirds often occurred on plants without aphids, perhaps because they encountered other rewards on these plants (Amaral et al., 2013).

### 3.2. Olfactometer experiments

In the olfactometer, *C. sanguinea* females showed a significant preference for volatiles from beggar-ticks when ambient air was given as alternative (Fig. 2, top bar). When given a choice between volatiles from beggar-ticks and volatiles from tomato plants, *C. sanguinea* showed no preference (Fig. 2, 2nd bar). Volatiles from beggar-ticks and volatiles from tomato plants plus beggar-ticks were equally attractive (Fig. 2, 3rd bar), but tomato plants plus beggar-ticks were somewhat
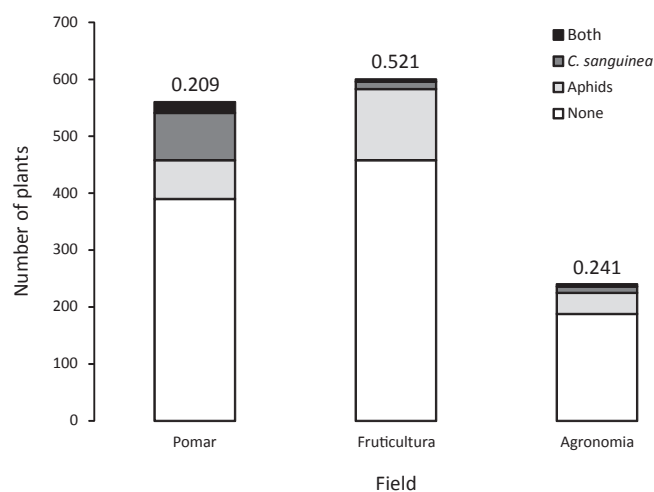


**Fig. 1.** Co-occurrence of *C. sanguinea* with aphids on beggar-ticks in 3 fields. Shown are frequencies of occurrence of plants without aphids or *C. sanguinea* (Empty, white bars), plants with aphids (light grey bars), plants with *C. sanguinea* (dark grey bars), and plants with both (black bars). Fields were sampled 14 (Pomar), 15 (Fruticultura) and 6 (Agronomia) times, 40 plants were inspected for each sample (1400 plants in total). The probability of finding the observed proportion of plants with both aphids and *C. sanguinea* or more extreme proportions was assessed assuming a hypergeometric distribution (Griffith et al., 2016), probabilities are given above the bars.
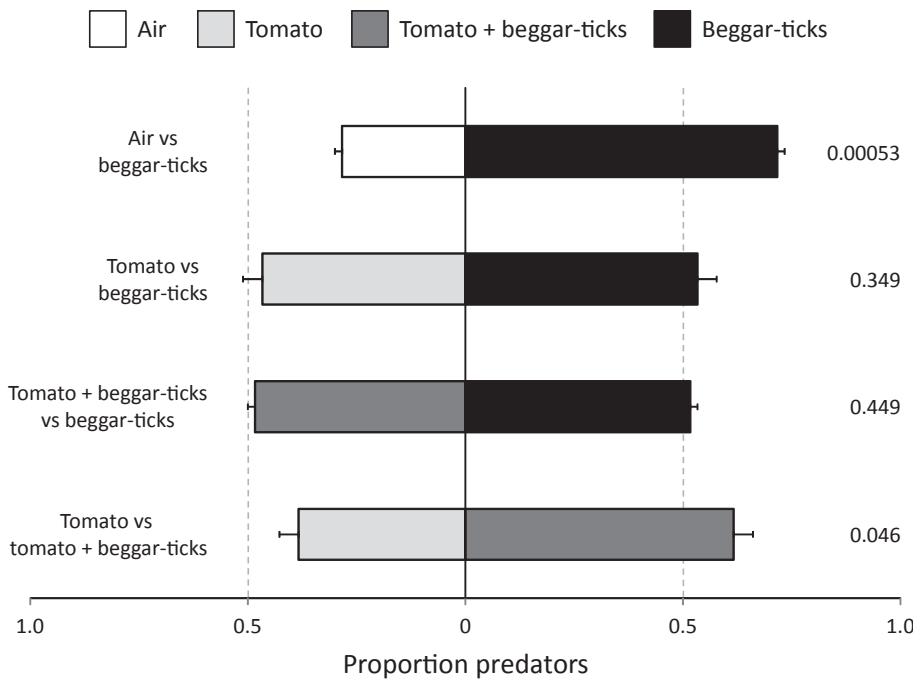
more attractive than tomato plants alone (Fig. 2, 4th bar).

### 3.3. Oviposition

Oviposition of *C. sanguinea* did not differ significantly among plants, neither in the absence (Fig. 3, day 1–5, LME: $Chi^2 = 0.15$, d.f. = 2, P = 0.56) nor in the presence of aphids (Fig. 3, day 6–10. LME: $Chi^2 = 0.07$, d.f. = 2, P = 0.96). In the absence of aphids, ladybird oviposition decreased over time and stopped completely after 3 days. Oviposition observed during the first 3 days was likely due to the previous diet consisting of aphids. The females resumed oviposition only after they were supplied with aphids (Fig. 3, days 6–10), showing that they could still reproduce. Thus, the plant resources alone were not sufficient for oviposition of the ladybirds. Most oviposition occurred on the cage walls.
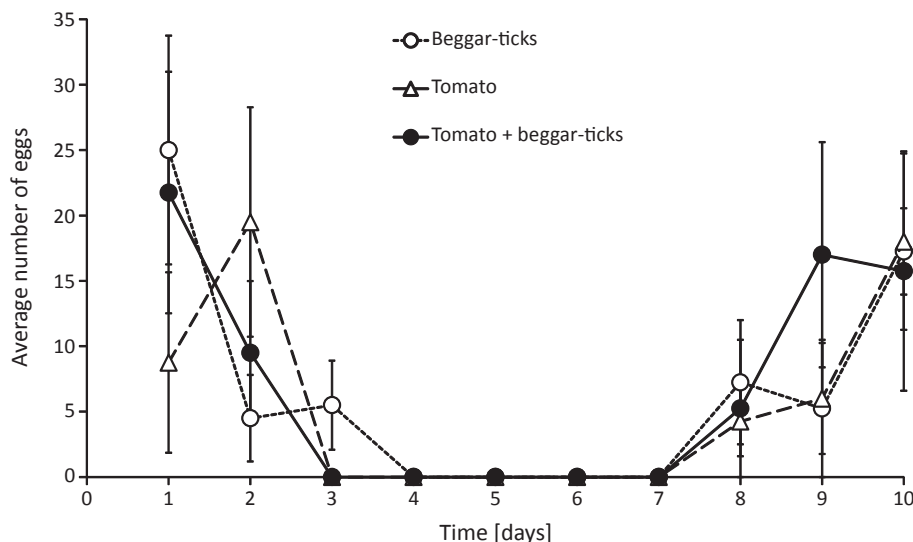
### 3.4. Survival

Survival of adult ladybird beetles differed significantly among plants (Fig. 4, Cox proportional hazards, $Chi^2 = 25.0$, d.f. = 3, P < 0.001). Cumulative survival was highest with the combination of tomato plants plus beggar-ticks, somewhat lower with beggar-ticks, and lowest with tomato plants and without plants.

### 4. Discussion

There is a plethora of publications showing that predators and parasites are attracted by plant volatiles induced by herbivore feeding, but much less on the attraction by volatiles constitutively produced by plants that are not under attack by herbivores (Elzen et al., 1983; Salamanca et al., 2015; Takabayashi et al., 1991; Togni et al., 2016). Here we add another case, that of beggar-ticks that attract *C. sanguinea*. Predators were mainly found on beggar-ticks in the field and were hardly encountered on other plants. On beggar-ticks, they were not



**Fig. 3.** Average oviposition ( ± s.e.) of *C. sanguinea* on tomato plants (open triangles), beggar-ticks (open circles) and on a combination of beggar-ticks and tomato plants (closed circles). During the first 5 days, the ladybirds were offered clean plants, aphids were added as food during the last 5 days.
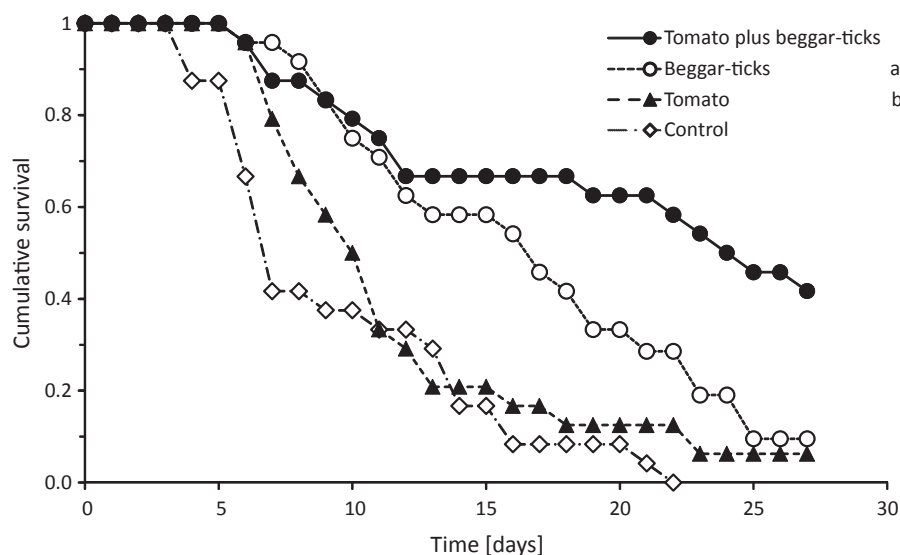
**Fig. 4.** Cumulative survival of adult *C. sanguinea* on tomato plants (closed triangles), beggar-ticks (open circles), tomato plus beggar-ticks (closed circles) and without plants (control, open diamonds). Treatments with different letters in the legend are significantly different (contrasts after a mixed effects Cox proportional hazards model). Standard errors are not shown for reasons of clarity.

significantly associated with aphids, suggesting that they did not specifically search for aphids on these plants. Although we could not rule out that the beggar-ticks in the field had been attacked by aphids or other herbivores before we sampled them, hence, that the ladybirds were attracted to herbivore-induced plant volatiles, the olfactometer experiments clearly showed that undamaged beggar-ticks were attractive. The response of predators to plant volatiles can only be preserved over evolutionary time if the predators benefit from visiting the plant (van Baalen and Jansen, 2003). Coccinellids frequently use plant resources to complement their diet, hence, there may be selection to respond to volatiles associated with these resources (Giorgi et al., 2009; Lundgren, 2009). Thus, the attraction of *C. sanguinea* to beggar-ticks can be understood because this plant offers resources that can increase adult survival (this study and Amaral et al., 2013). Our field results confirm earlier findings of coccinellids visiting plants without prey and feeding on non-prey foods (Amaral et al., 2013; Lundgren, 2009).

Sarmento et al. (2008) found that *C. sanguinea* was repelled by volatiles of clean tomato plants, which led us to expect that the volatiles of beggar-ticks would be preferred over those of tomato plants. However, this was not the case (Fig. 2). Contrary to the present study, Sarmento et al. (2008) used plants in the vegetative stage. Hence, the flowering tomato plants used here may have been less repellent than plants without flowers. Another reason for the difference in attractiveness may be the different tomato varieties used here and by Sarmento et al. (2008). This remains to be tested.

We found that a mixture of volatiles of beggar-ticks and tomato plants was somewhat more attractive than volatiles of tomato plants (Fig. 2), suggesting that combining these two plants will attract more ladybird beetles, which may increase natural control of aphids. In the olfactometer experiments, we offered *C. sanguinea* the choice between volatiles of one tomato plant vs. one tomato plant plus one beggar-ticks. Arguably, the volatiles of the combination were more attractive because there were more plants present. The experimental design of this kind of experiments is a difficult issue, because it is not clear how to compare the quantity of plants of different species, and should arguably be based on numbers, biomass, or on leaf area. We chose to add a beggar-ticks plant to a tomato plant because this is what growers could do: they will not voluntarily replace a tomato plant with a beggar-ticks, but they can opt to leave some beggar-ticks in their tomato field instead of weeding them.

There is one other example of a combination of a weed and a crop plant being more attractive than crop plants alone (Ninkovic and Pettersson, 2003). Moreover, several studies have shown an increase in coccinellid densities in the field as a result of plant diversification with weeds (Burgio et al., 2006; Cottrell and Yeargan, 1998; Harmon et al., 2000; Sengonca et al., 2002; Wyss, 1995). There are also examples of increased control of pests as a result of such increase in plant diversity. For instance, the presence of three weed species in lettuce cultures increased the density of three species of ladybirds, which resulted in a reduction of infestation by aphids (Sengonca et al., 2002). Also, increased densities of the weed *Taraxacum officinalis* (dandelion) in alfafa fields resulted in higher ladybird densities, which in turn was associated with lower aphid densities (Harmon et al., 2000). Hence, there is potential for using weeds to promote the control of pests by natural enemies.

Because the beggar-ticks associated with tomato plants studied here did not result in increased reproduction of *C. sanguinea*, but only in increased survival, the densities of coccinellids in the field will not necessarily increase when beggar-ticks are allowed in or around tomato fields. This can be gleaned from simple models of predator-prey dynamics. For example, the Lotka-Volterra predator-prey model shows that reduced predator mortality does not result in increased equilibrium predator densities (Volterra, 1928), and the Rosenzweig-McArthur model (Rosenzweig and MacArthur, 1963) can show increases or decreases of predator densities with decreasing predator mortality. Indeed, there are several examples where increased predator survival due to increased plant biodiversity did not result in increased predator densities in the field (Bianchi et al., 2006; Letourneau et al., 2011). However, the increased survival will result in increased persistence of coccinellid populations in the field in times of prey scarcity, and will form a buffer against new pest invasions. Because beggar-ticks are a common weed at the borders and within field crops, this increase in persistence is gained at low costs: it only requires adequate management of this weed.

In conclusion, we show that beggar-ticks can play an important role in conservation of *C. sanguinea* in tomato crops. Field experiments should be done to investigate the effects of combining tomato plants with beggar-ticks on aphid dynamics and damage on tomato. Like other studies, our results suggest that the management of specific species of weeds may favour the conservation of natural enemies (Altieri and Whitcomb, 1979; Amaral et al., 2016, 2013; Landis et al., 2005).

## References

Altieri, M., Whitcomb, W., 1979. The potential use of weeds in the manipulation of beneficial insects. HortScience 14, 12–18.

Altieri, M.A., Koohafkan, P., 2004. Globally important ingenious agricultural heritage systems (GIAHS): extent, significance, and implications for development. In: Proceedings of the Second International Workshop and Steering Committee Meeting for the Globally Important Agricultural Heritage Systems (GIAHS) Project. FAO, Rome, Italy, pp. 7–9.

Altieri, M.A., Letourneau, D.K., 1982. Vegetation management and biological control in agroecosystems. Crop Prot. 1, 405–430.

Altieri, M.A., Whitcomb, W.H., 1980. Weed manipulation for insect pest management in corn. Environ. Manage. 4, 483–489. http://dx.doi.org/10.1007/BF01876885.

Amaral, D.S., Venzon, M., dos Santos, H.H., Sujii, E.R., Schmidt, J.M., Harwood, J.D., 2016. Non-crop plant communities conserve spider populations in chili pepper agroecosystems. Biol. Control 103, 69–77.

Amaral, D.S.S.L., Venzon, M., Duarte, M.V.A., Sousa, F.F., Pallini, A., Harwood, J.D., 2013. Non-crop vegetation associated with chili pepper agroecosystems promote the abundance and survival of aphid predators. Biol. Control 64, 338–346.

Araj, S.-E., Wratten, S.D., 2015. Comparing existing weeds and commonly used insectary plants as floral resources for a parasitoid. Biol. Control 81, 15–20.

Bianchi, F., Booij, C.J.H., Tscharntke, T., 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proc. R. Soc. B-Biol. Sci. 273, 1715–1727.

Burgio, G., Ferrari, R., Boriani, L., Pozzati, M., van Lenteren, J., 2006. The role of ecological infrastructures on Coccinellidae (Coleoptera) and other predators in weedy field margins within northern Italy agroecosystems. Bull. Insectol. 59, 59.

Chacon, J., Gliessman, S.R., 1982. Use of the "non-weed" concept in traditional tropical agroecosystems of south-eastern Mexico. Agro-Ecosyst. 8, 1–11.

Chaplin-Kramer, R., O'Rourke, M.E., Blitzer, E.J., Kremen, C., 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. Ecol. Lett. 14, 922–932.

Cottrell, T.E., Yeargan, K.V., 1998. Effect of pollen on *Coleomegilla maculata* (Coleoptera: Coccinellidae) population density, predation, and cannibalism in sweet corn. Environ. Entomol. 27, 1402–1410.

Crawley, M.J., 2013. The R book. John Wiley & Sons, Chichester, UK.

Diehl, E., Wolters, V., Birkhofer, K., 2012. Arable weeds in organically managed wheat fields foster carabid beetles by resource-and structure-mediated effects. Arthropod-Plant Interact. 6, 75–82.

Ehler, L., Miller, J., 1978. Biological control in temporary agroecosystems. Biocontrol 23, 207–212.

Elzen, G.W., Williams, H.J., Vinson, S.B., 1983. Response by the parasitoid *Campoletis sonorensis* (Hymenoptera: Ichneumonidae) to chemicals (synomones) in plants: Implications for host habitat location. Environ. Entomol. 12, 1873–1877. http://dx.doi.org/10.1093/ee/12.6.1873.

Fiedler, A.K., Landis, D.A., Wratten, S.D., 2008. Maximizing ecosystem services from conservation biological control: the role of habitat management. Biol. Control 45, 254–271.

Gagic, V., Tscharntke, T., Dormann, C.F., Gruber, B., Wilstermann, A., Thies, C., 2011. Food web structure and biocontrol in a four-trophic level system across a landscape complexity gradient. Proc. R. Soc. Lond. B Biol. Sci. 278, 2946–2953.

Giorgi, J.A., Vandenberg, N.J., McHugh, J.V., Forrester, J.A., Ślipiński, S.A., Miller, K.B., Shapiro, L.R., Whiting, M.F., 2009. The evolution of food preferences in Coccinellidae. Biol. Control 51, 215–231.

Griffith, D.M., Veech, J.A., Marsh, C.J., 2016. COOCCUR: Probabilistic species co-occurrence analysis in R. J Stat Softw 69, 1–17.

Gurr, G.M., Wratten, S.D., Landis, D.A., You, M., 2017. Habitat management to suppress pest populations: Progress and prospects. Annu. Rev. Entomol. 62.

Gurr, G.M., Wratten, S.D., Luna, J.M., 2003. Multi-function agricultural biodiversity: pest management and other benefits. Basic Appl. Ecol. 4, 107–116.

Harmon, J., Ives, A., Losey, J., Olson, A., Rauwald, K., 2000. *Coleomegilla maculata* (Coleoptera: Coccinellidae) predation on pea aphids promoted by proximity to dandelions. Oecologia 125, 543–548.

Işıkber, A., Copland, M., 2002. Effects of various aphid foods on *Cycloneda sanguinea*. Entomol. Exp. Appl. 102, 93–97.

Janssen, A., 1999. Plants with spider-mite prey attract more predatory mites than clean plants under greenhouse conditions. Entomol. Exp. Appl. 90, 191–198.

Kremen, C., Miles, A., 2012. Ecosystem services in biologically diversified versus conventional farming systems: benefits, externalities, and trade-offs. Ecol. Soc. 17.

Landis, D.A., Menalled, F.D., Costamagna, Alejandro C., Wilkinson, Tammy K., 2005. Manipulating plant resources to enhance beneficial arthropods in agricultural landscapes. Weed Sci. 53, 902–908.

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

Lenth, R., 2016. Least-squares means: The R package lsmeans. J. Stat. Softw. 69, 1–33.

http://dx.doi.org/10.18637/jss.v069.i01.

Letourneau, D.K., Armbrecht, I., Rivera, B.S., Lerma, J.M., Carmona, E.J., Daza, M.C., Escobar, S., Galindo, V., Gutierrez, C., Lopez, S.D., Mejia, J.L., Rangel, A.M.A., Rangel, J.H., Rivera, L., Saavedra, C.A., Torres, A.M., Trujillo, A.R., 2011. Does plant diversity benefit agroecosystems? a synthetic review. Ecol. Appl. 21, 9–21. http://dx.doi.org/10.1890/09-2026.1.

Lundgren, J.G., 2009. Nutritional aspects of non-prey foods in the life histories of predaceous Coccinellidae. Biol. Control 51, 294–305.

Martins, C.B., Almeida, L.M., Zonta-de-Carvalho, R.C., Castro, C.F., Pereira, R.A., 2009. *Harmonia axyridis*: a threat to Brazilian Coccinellidae? Rev. Bras. Entomol. 53, 663–671.

Murdoch, W.W., Chesson, J., Chesson, P.L., 1985. Biological control in theory and practice. Am. Nat. 125, 344–366.

Myers, N., 1996. Environmental services of biodiversity. Proc. Natl. Acad. Sci. 93, 2764–2769.

Needham, J.G., 1948. Ecological notes on the insect population of the flower heads of *Bidens pilosa*. Ecol. Monogr. 18, 431–446.

Nentwig, W., 1998. Weedy plant species and their beneficial arthropods: potential for manipulation in field crops. In: Pickett, C.H., Bugg, R.L. (Eds.), Enhancing Biological Control: Habitat Management to Promote Natural Enemies of Agricultural Pests. University of California Press, Berkeley, CA, USA, pp. 49–67.

Ninkovic, V., Pettersson, J., 2003. Searching behaviour of the sevenspotted ladybird, *Coccinella septempunctata* - effects of plant-plant odour interaction. Oikos 100, 65–70.

Norris, R.F., Kogan, M., 2005. Ecology of interactions between weeds and arthropods. Annu. Rev. Entomol. 50, 479–503.

Norris, R.F., Kogan, M., 2000. Interactions between weeds, arthropod pests, and their natural enemies in managed ecosystems. Weed Sci. 48, 94–158.

Obrycki, J.J., Kring, T.J., 1998. Predaceous Coccinellidae in biological control. Annu. Rev. Entomol. 43, 295–321.

Oliveira, E., Oliveira, C., Sarmento, R., Rezende, L., Fadini, M., 2005. Biological aspects of the predator *Cycloneda sanguinea* Linnaeus, 1763 (Coleoptera: Coccinellidae) fed with *Tetranychus evansi* Baker & Pritchard, 1960 (Acari: Tetranychidae) and *Macrosiphum euphorbiae* Thomas, 1878 (Homoptera: Aphididae). Biosci. J. 21, 33–39.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2017. NLME: Linear and Nonlinear Mixed Effects Models. http://CRAN.R-project.org/package=nlme.

R Development Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rezende, M.Q., Venzon, M., Perez, A.L., Cardoso, I.M., Janssen, A., 2014. Extrafloral nectaries of associated trees can enhance natural pest control. Agric. Ecosyst. Environ. 188, 198–203.

Rosenzweig, M.L., MacArthur, R.H., 1963. Graphical representation and stability conditions of predator-prey interactions. Am. Nat. 97, 209–223.

Sabelis, M.W., van de Baan, H.E., 1983. Location of distant spider mite colonies by phytoseiid predators: demonstration of specific kairomones emitted by *Tetranychus urticae* and *Panonychus ulmi*. Entomol. Exp. Appl. 33, 303–314.

Salamanca, J., Pareja, M., Rodriguez-Saona, C., Resende, A., Souza, B., 2015. Behavioral responses of adult lacewings, *Chrysoperla externa*, to a rose–aphid–coriander complex. Biol. Control 80, 103–112.

Santos, J., Cury, J., 2011. Picão-preto: uma planta daninha especial em solos tropicais. Planta Daninha 29, 1159–1172.

Sarmento, R.A., de Lemos, F., Dias, C.R., Pallini, A., Venzon, M., 2008. Infoquímicos induzidos por herbivoria mediando a comunicação entre plantas de tomate e o predador *Cycloneda sanguinea* (Coleoptera: Coccinellidae). Rev. Ceres 55, 439–444.

Sarmento, R.A., Venzon, M., Pallini, A., Oliveira, E.E., Janssen, A., 2007. Use of odours by *Cycloneda sanguinea* to assess patch quality. Entomol. Exp. Appl. 124, 313–318.

Sengonca, C., Kranz, J., Blaeser, P., 2002. Attractiveness of three weed species to polyphagous predators and their influence on aphid populations in adjacent lettuce cultivations. Anz. Für Schädlingskunde 75, 161–165.

Takabayashi, J., Noda, T., Takahashi, S., 1991. Plants produce attractants for *Apanteles kariyai*, a parasitoid of *Pseudaletia separata*; cases of "communication" and "misunderstanding" in parasitoid-plant interactions. Appl. Entomol. Zool. 26, 237–243.

Therneau, T.M., 2015. COXME: mixed effects Cox models.

Togni, P.H.B., Venzon, M., Muniz, C.A., Martins, E.F., Pallini, A., Sujii, E.R., 2016. Mechanisms underlying the innate attraction of an aphidophagous coccinellid to coriander plants: Implications for conservation biological control. Biol. Control 92, 77–84.

Tscharntke, T., Rand, T.A., Bianchi, F., 2005. The landscape context of trophic interactions: insect spillover across the crop-noncrop interface. Ann. Zool. Fenn. 42, 421–432.

van Baalen, M., Jansen, V.A., 2003. Common language or Tower of Babel? On the evolutionary dynamics of signals and their meanings. Proc. R. Soc. Lond. B Biol. Sci. 270, 69–76.

Van Emden, H., 1965. The role of uncultivated land in the biology of crop pests and beneficial insects. Sci. Hortic. 17, 121–136.

Volterra, V., 1928. Variations and fluctuations of the number of individuals in animal species living together. J. Cons. Int. Explor. Mer. 3, 3–51.

Wäckers, F., van Rijn, P.C.J., Bruin, J., 2005. Plant-provided food for carnivorous insects: a protective mutualism and its applications. Cambridge University Press, Cambridge, UK.

Wyss, E., 1995. The effects of weed strips on aphids and aphidophagous predators in an apple orchard. Entomol. Exp. Appl. 75, 43–49.