DANY SILVIO SOUZA LEITE AMARAL

MORE THAN WEEDS: NON-CROP PLANTS, ARTHROPOD PREDATORS AND CONSERVATION BIOLOGICAL CONTROL

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Entomologia, para obtenção do título de *Doctor Scientiae*.

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APROVADA: 27 de fevereiro 2014.

Irene Maria Cardoso

Cleide Maria Ferreira Pinto

Angelo Pallini Filho
(Co-orientador)

Edison Ryoiti Sujii
(Co-orientador)

Madelaine Venzon
(Orientadora)
(EPAMIG)

De noite há uma flor que corrige os insetos

Manoel de Barros – Livro: Anotações de Andarilho.

A esperança não vem do mar
Nem das antenas de TV
A arte de viver da fé
Só não se sabe fé em quê

Paralamas do Sucesso – Música: Alagados.

… a Universidade deve ser flexível, pintar-se de negro, de mulato, de operário,
de camponês, ou ficar sem porta, pois o povo a arrombará e
ele mesmo a pintará, a Universidade. com
as cores que lhe pareça mais adequadas.

Ernesto "Che" Guevara – Discurso: Universidade de Las Villas, dezembro de 1959.

À Fê, que tem sido o amor que inspira minha vida,
Ao João, meu filho, meu "Gesù Bambino", meu "Sítio do Pica-Pau Amarelo",
dedico cada letra, pingo e ponto desta tese.
Sem vocês nada aqui faria sentido.

À **tudo** aquilo que não sabemos o que é, mas mesmo assim vive, pulsa e movimenta dentro de nós, da natureza e do universo;

Aos meus pais, **Carlos e Maria Helena**, pelo amor, carinho e dedicação irrestritos que sempre tiveram comigo. Amo vocês;

À minha **família**, que mesmo com a distância tem sido presente em minha vida;

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A **todos agricultores e agricultoras familiares**, que constroem este país com suor, sangue e sentimento, desejo que todos encontrem solo fértil e água viva para realizar seus sonhos e lutas.

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BIOGRAFIA

DANY SILVIO SOUZA LEITE AMARAL, filho de Carlos Soares do Amaral e Maria Helena de Souza Leite, nasceu em Barbacena – MG, no dia 19 de junho de 1976. Em 1991, iniciou o curso de Técnico em Agropecuária, na Escola Agrotécnica Federal de Barbacena (MG), concluindo-o em dezembro de 1993. Em 1996, iniciou o curso de Agronomia na Universidade Federal de Viçosa (MG), concluindo-o em agosto de 2001. Em agosto de 2003, finalizou o curso de mestrado em Entomologia na Universidade Federal de Viçosa, sob orientação do professor Angelo Pallini. Assessor Parlamentar no Mandato do Deputado Estadual Padre João, no período de 2003 a 2008, trabalhou com a apoio à Agricultura Familiar, Agricultura Urbana e Agroecologia. Atualmente, é técnico da Secretaria Municipal de Meio Ambiente de Belo Horizonte, atuando no licenciamento ambiental. Em 2010 iniciou o doutorado em Entomologia na Universidade Federal de Viçosa, sob supervisão e orientação da pesquisadora Madelaine Venzon.

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Chapter 4: Coccinellid interactions mediated by spatial plant heterogeneity

RESUMO

AMARAL, Dany Silvio Souza Leite, D.Sc., Universidade Federal de Viçosa, fevereiro de 2014. **Mais do que plantas daninhas: plantas espontâneas, artrópodes predadores e controle biológico conservativo.** Orientadora: Madelaine Venzon. Coorientadores: Angelo Pallini e Edison Ryoiti Sujii.

A diversidade de plantas dentro das áreas de plantio tem sido uma das principais estratégias utilizadas para o aumento e conservação do controle biológico. Dentre tais técnicas, o manejo de plantas espontâneas seja em faixas de vegetação, seja nas entrelinhas da cultura, promove a oferta de recursos e heterogeneidade do habitat, o que pode garantir a manutenção de populações de inimigos naturais. A conservação de plantas espontâneas pode se tornar uma estratégia de fácil adoção em diversos sistemas de cultivo, sobretudo cultivos anuais. Como modelo de estudo do uso dessa estratégia, foram utilizados os cultivos de pimenta-malagueta (*Capsicum frutenses)* e abóbora (*Cucurbita pepo* L.), caracterizados por pequenas áreas de plantio, alta susceptibilidade ao ataque de artrópodes herbívoros e alto potencial para instalação de sistemas de produção agroecológicos. Portanto, o objetivo desta tese foi avaliar o papel das plantas espontâneas na manutenção de populações de inimigos naturais e efeitos no controle biológico conservativo. Para isso, investigou-se a hipótese de plantas espontâneas apresentarem correlação com artrópodes predadores principalmente nestes cultivos; bem como verificou-se efeitos na controle biológico de afídeos. Dentre os artrópodes predadores, destacam-se os coccinelídeos, que pela especificidade de predação em afídeos encontrados nos cultivos avaliados. Dessa forma, foram avaliadas as seguintes hipóteses de trabalho: a) as plantas espontâneas afetam diferentemente grupos distintos de artrópodes predadores, fornecendo recursos diferentes a estes; b) a sobrevivência de coccinelídeos predadores pode ser afetada pelo fornecimento de alimento alternativo (pólen e néctar) advindo de plantas espontâneas; c) as interações entre duas espécies de coccinelídeos pode ser afetada pela presença de plantas espontâneas em cultivo de abóbora, reduzindo a competição e a predação intraguilda; d) em sistema de cultivo de pimenta, a abundância de artrópodes predadores pode aumentar com o manejo de plantas espontâneas, refletindo na redução da infestação de afídeos e no aumento da produtividade; e) a distribuição espacial de artrópodes predadores e afídeos pode ser diretamente relacionada com a presença de plantas espontâneas; e f) a estrutura da comunidade e das guildas de forrageamento de artrópodes predadores, espacialmente aranhas, pode ter influencia direta das espécies e do manejo de plantas espontâneas. Como resultados, verificou-se, primeiramente, que artrópodes predadores (coccinelídeos, sirfídeos, crisopídeos e aracnídeos) foram influenciados diferentemente pelo fornecimento de recursos das plantas espontâneas, como pólen, presas e refúgio. Os coccinelídeos foram afetados de maneira distinta, de acordo com cada espécie. Adultos e larvas da *Cycloneda sanguinea* sobreviveram por mais tempo quando expostas a inflorescências de mentrasto (*Ageratum conizoides*) e de picão (*Bidens pilosa*), enquanto que a sobrevivência de larvas e adultos de *Harmonia axyridis* não foi influenciada. Por outro lado, verificou-se que a presença de plantas espontâneas alterou o comportamento de oviposição e de forrageamento de *Hippodamia convergens,* além de reduzir a predação intraguilda por *H. axyridis*. Em experimento de campo no sistema de cultivo de pimenta-malagueta, verificou-se que a abundância da maioria dos inimigos naturais estudados aumentou e as populações de afídeos diminuíram com o manejo de plantas espontâneas, embora não tenha sido verificado efeitos na produtividade de pimenta. Com relação à distribuição espacial, o manejo de plantas espontâneas seja em faixas de vegetação no entorno do área de cultivo, seja em faixas nas entrelinhas das plantas de pimenta, teve efeitos diretos na distribuição de inimigos naturais. Verificou-se, também, agregação de populações de aranhas e de coccinelídeos mais próximas das faixas de plantas espontâneas. Em análise de guildas e famílias de aranhas, A composição de comunidades de aranhas variou de acordo com cada espécies de plantas espontâneas. Adicionalmente, verificou-se que o manejo de plantas espontâneas promoveu alterações na frequência de grupos funcionais de aranhas, aumentando a diversidade de estratégias de forrageamento dentro das áreas de cultivo. Em conclusão, a partir dos experimentos e resultados desta tese, verificou-se que as plantas espontâneas tem amplo potencial de manejo em sistemas de cultivo, beneficiando diretamente inimigos naturais e promovendo o controle de pragas em sistemas de produção de alimentos.

ABSTRACT

AMARAL, Dany Silvio Souza Leite, D.Sc., Universidade Federal de Viçosa, February 2014. **More than weed: non-crop plants, arthropod predators and conservation biological control.** Adviser: Madelaine Venzon. Co-advisers: Angelo Pallini e Edison Ryoiti Sujii.

The management of non-crop plants, by increasing biodiversity, may influence positively populations of natural enemies in agroecosystems. A common strategy of enhancing plant diversity in cropping system has been the manipulation and restoration of non-crop plants. The management of non-crop plants may easily adopt by farmers due to characteristics such as rapid plant grows and low investment. To understanding the mechanisms correlated to management of non-crop plants and the increasing of arthropods predator abundance, we used chili pepper and squash agroecosystems as model. Specially, chili pepper production is an economically important crop in several regions of Brazil and the chili peppers are attacked by a variety of pestilent arthropod species. Moreover, legislation from the Brazilian government restricts the used of broad spectrum pesticides in chili pepper production, thus finding sustainable management solutions to pest control pest is critical issue. Strategies to enhance beneficial arthropods may be the way to minimize the drastic reduction of horticultural crop systems. On these crop systems, predaceous ladybirds (Coleoptera: Coccinellids) have special importance because of their biocontrol potential against aphids. On this thesis we examined the following hypothesis: a) whether non-crop plants affects different arthropod predators, by supplying different resource for them; b) whether survival parameters of coccinelids is affected to non-prey food found in non-crop plants; c) whether non-crop plants affected interaction between two species of coccinelids on squash plant crop, reducing competition and intraguild predation; d) Evaluate the abundance and the aphids and arthropod predators in chili pepper plants system managed with non-crop plants; e) whether the spatial distribution of herbivore and arthropod predators is related to presence of non-crop plants; f) whether the spider community and spiders functional groups differ according to different species of non-crop plants. Therefore, we firstly found that the presence of weeds within or surrounding chili pepper fields differentially affected the abundance of different groups of aphidophagous predators by providing alternative prey, nectar and pollen as a complementary resource. Survival of native *Cycloneda sanguinea* (Coleoptera: Coccinellidae) differed between plant species, with 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). In other study, we observed the influence of spatial heterogeneity mediated by non-crop plant on interaction between

H. convergens and *H. axyridis,* reducing intraguild predation and completion between species. The foraging and oviposition behavior of *H. convergens* was altered on presence of spatial heterogeneity. The reduction of intraguild predation varied according to size and time period of experiments. On chili pepper systems, we found that the presence of non-crop plants was able to increase the abundance of most of beneficial arthropods studied and reduce herbivore populations. On spatio-temporal experiment, non-crop plants presence affected positively the distribution of coccinelids and spiders, promoting more densities of arthropods in non-crop plants patches. Finally, We study found intrinsic association between non-crop plants and spider guild composition and abundance of spiders on chili pepper agroecosystem. The frequency of group of spider families was direct affected by presence and composition of non-crop plants. 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.

Introdução Geral

A agricultura convencional, baseada na monocultura e uso no intensivo de insumos, tem o potencial de causar mudanças e perturbações ambientais que refletem diretamente sobre a sustentabilidade dos agroecossistemas. As monoculturas, amplamente utilizadas em sistemas de produção de alimentos, provocam efeitos diretos na biodiversidade local e regional. Embora a biodiversidade possa ter vários efeitos sobre os sistemas de produção, a sua perda está associada a surtos populacionais de pragas. Para o manejo de agroecossistemas mais sustentáveis deve-se pensar na adoção de práticas que favoreçam componentes biológicos e determinadas funções capazes de evitar o ataque severo de pragas (Sujii *et al* 2010). Nessa perspectiva, o controle biológico conservativo caracteriza-se pelo manejo e pela modificação do sistema agrícola com o objetivo de aumentar as populações de inimigos naturais e, consequentemente, realizar o controle biológico de artrópodes que potencialmente podem se tornar pragas (Pickett & Bugg 1998; Landis *et al* 2000). Uma das práticas utilizadas no controle biológico conservativo consiste no aumento da diversidade de plantas nas áreas de cultivo, utilizando espécies que possam manter predadores e parasitoides capazes de reduzir a intensidade do ataque de herbívoros (Landis *et al* 2000; Wilkinson & Landis 2005). No entanto, a simples diversificação de plantas em um agroecossistema não é uma garantia de efetividade do controle biológico.

O conhecimento de plantas mais adequadas para serem introduzidas ou preservadas em sistemas de produção dependerá diretamente da cultura, da espécie ou espécies de herbívoro-alvo e, finalmente, dos inimigos naturais a serem manejados. Por isso, não basta que um agroecossistema seja somente diversificado, deve-se levar em conta que a diversidade seja funcional (diversidade de interações), buscando espécies de plantas que deem suporte à comunidade de inimigos naturais (Altieri 1999; Gurr *et al* 2012). Primeiramente, deve-se compreender quais as relações entre as espécies vegetais utilizadas e os artrópodes que se desejam manter no sistema, com foco nas características das plantas que favoreçam os inimigos naturais (Gurr *et al* 2005). Em seguida, as estratégias de diversificação da vegetação devem compreender o arranjo de espécies no espaço e tempo, a composição e abundância de vegetação alternativa dentro e ou no entorno das áreas de cultivo; e o tipo e intensidade de manejo das espécies empregadas (Gurr *et al 2005*).

A diversidade de plantas dentro das áreas de cultivo tem sido uma das principais técnicas utilizadas para o aumento e conservação do controle biológico (Landis *et al* 2000, Venzon & Sujii 2009). Dentre tais técnicas, utiliza-se o manejo de plantas espontâneas, as quais são normalmente eliminadas dos plantios convencionais devido aos seus impactos negativos, sobretudo de competição com cultivo principal (Altieri & Whitcomb 1978). A abundância de insetos pode ser aumentada e influenciada pela manipulação da comunidade de plantas espontâneas, pois somente uma planta possibilita a criação de habitat a um conjunto de artrópodes (Nentwig 1998). De forma geral, quando se promove o manejo de plantas, seja em faixas de vegetação, seja nas entrelinhas da cultura, pode-se promover a oferta de alimento derivado de plantas, como pólen e néctar, que atuam como fonte alternativa de alimento a insetos predadores e parasitoides (Stansly *et al* 1997; Broufas & Koveos 2000; Venzon *et al* 2006a), de presas ou hospedeiros alternativos (Tingle *et al* 1978; Qureshi *et al* 2010), de local alternativo para oviposição (Cottrell & Yeargan 1999; Griffin & Yeargan 2002) ou para a construção de teias por aranhas predadoras (Nentwig 1998).

O uso de espécies de plantas espontâneas para o controle biológico conservativo deve partir primeiramente do conhecimento de quais espécies melhor proporcionam o manejo ecológico de herbívoros (Isaacs *et al* 2009). Posteriormente, deve-se determinar quais mecanismos envolvidos nas interações de plantas, pragas e inimigos naturais, objetivando a seleção de espécies que serão manejadas (Barberi *et al* 2010). A seleção de plantas deve ser criteriosa, pois a vegetação espontânea associada a cultivos comerciais também podem atuar como hospedeira alternativa de artrópodes herbívoros. A manutenção dessas plantas no sistema de cultivo pode ter efeitos negativos ao manter populações de herbívoros em épocas de entressafra, ou positivo, se estas atuarem como plantas armadilhas, afastando herbívoros do cultivo principal (Norris & Kogan 2005; Capinera 2005; Winkler *et al* 2009).

Embora a presença de plantas espontâneas tenha o potencial de aumentar a presença de insetos benéficos nos agroecossistemas, é necessário entender como estas plantas devem ser manejadas para se evitar a competição com a cultura principal (Altieri & Whitcomb 1978), concomitantemente com o manejo para aumento de inimigos naturais. Duas estratégias tem sido utilizadas, uma empregando a manutenção da vegetação no entorno das áreas de cultivo, com a preservação de faixas de vegetação natural; e outra com a manutenção de plantas nas entrelinhas de cultivo, com o mínimo de competição com a cultura. Para a escolha da estratégia mais viável deve-se avaliar as interferências de plantas espontâneas na cultura comercial e a capacidade de dispersão dos artrópodes benéficos estudados, correlacionando estes fatores para maximizar o controle biológico e a produção de alimentos (Nentwig 1998; Altieri 1999). Por isso, além do conhecimento das espécies de plantas relacionadas com inimigos naturais, deve-se atentar para o efeito da vegetação na colonização e distribuição espacial de artrópodes benéficos para se pensar na estratégia mais eficiente de manejo das plantas espontâneas (Barberi *et al* 2010).

Nesse campo de pesquisa ainda não são bem conhecidos os efeitos diretos e indiretos da vegetação espontânea e do manejo da complexidade do habitat sobre o comportamento de inimigos naturais e suas interações multitróficas. Mesmo com o aumento das informações sobre os efeitos da diversidade da vegetação sobre inimigos naturais, a maioria dos estudos não investigam porque a população de inimigos naturais é influenciada pelo manejo desta diversidade; e nem como são as interações tróficas em sistemas diversificados (Coll 1998; Greenstone *et al* 2010). Existem evidências de que habitats estruturalmente complexos influenciam o comportamento de forrageamento de predadores (Grabowski 2004; Finke & Denno 2006; Burgio *et al* 2006). Por exemplo, coccinelídeos são capazes de forragear melhor e, consequentemente, alcançam maior taxa de predação em plantas com arquitetura mais complexa (Kareiva & Sahakian 1990). O impacto de diversidade de plantas sobre inimigos naturais vai depender não somente da presença de plantas, mas da capacidade de locomoção e dispersão dos artrópodes de interesse. Por isso a manipulação de inimigos naturais depende do entendimento da correlação das dinâmicas espaço-temporal destes organismos, suas presas e a estrutura do ambiente.

Quando se busca a implementação de técnicas que aumentem de diversidade de plantas para o controle de possíveis pragas, espera-se uma maior eficiência devido ao incremento no número e na diversidade de inimigos naturais. Embora a diversificação possa aumentar as populações de inimigos naturais, o somatório de artrópodes predadores e parasitoides pode não resultar necessariamente na redução da população de herbívoros. Esse aumento pode ter múltiplos efeitos na supressão de herbívoros, atuando então de forma sinérgica, aditiva, não aditiva, ou mesmo antagônica (Losey & Denno 1998; Cardinale *et al* 2003; Snyder *et al* 2005). Assim, torna-se necessário conhecer, quando se busca estratégias de controle biológico conservativo, o impacto da diversidade de vegetação espontânea sobre a comunidade de inimigos naturais relacionados com a planta de interesse comercial. O número e identidade de espécies pertencentes a teias de interações tróficas pode determinar o nível de supressão de pragas (Root 1973; Ives *et al* 2005). Em agroecossistemas, o manejo de plantas, além do aumento da diversidade *per si*, deve adotar estratégias que mantenham e conservem de agentes de controle biológico nas áreas de cultivo, resultando em incremento na eficiência do controle de pragas.

Ao se pensar em adaptação das estratégias de cultivo para a promoção de manejo ecológico de pragas, a manipulação de plantas espontâneas pode se tornar uma estratégia de fácil adoção em diversos agroecossistemas, sobretudo sistemas de produção orgânicos ou agroecológicos. Mais especificamente, no cultivo de hortaliças, geralmente realizado em pequenas áreas de cultivo e caracterizado pela predominância da mão de obra familiar e diversidade de atividades agrícolas, têm-se o potencial de utilizar o manejo de plantas de espontâneas como promotor de serviços ecológicos dentro das propriedades. Dessa forma, o conhecimento das espécies de plantas espontâneas mais eficientes na promoção do controle biológico e quais são os mecanismos específicos que garantam a presença de inimigos naturais pode ser uma importante área de estudo, sobretudo quando se pensa na aplicação de técnicas de cultivo ou mesmo aplicação em políticas públicas voltadas para a sustentabilidade de sistemas de produção familiares.

No presente trabalho estudou-se o papel da diversidade de plantas espontâneas sobre as populações de inimigos naturais e os reflexos desta biodiversidade no controle biológico conservativo de pragas e na produção da cultura da pimenta-malagueta (*Capsicum frutescens)* na Zona da Mata Mineira. Complementarmente, em áreas de cultivo do Estado de Kentucky, EUA, estudou-se a manipulação de plantas espontâneas para se verificar alterações no comportamento entre artrópodes predadores, reduzindo, assim, interações negativas como competição e predação intraguilda.

O cultivo da pimenta-malagueta vem crescendo em várias regiões brasileiras, com destaque para as regiões Sudeste e Nordeste (Rufino & Penteado 2006). No estado de Minas Gerais, segundo dados da Central de Abastecimento de Minas Gerais (CEASA – Minas), no ano de 2013, foram são comercializados 1.011,14 toneladas de pimenta. Na Zona da Mata Mineira, destacam-se como produtores de pimenta os municípios de Guarani, Tabuleiro, Piranga, Paula Cândido, Matipó, Oratórios, dentre outros. Nesta região, cultivo de pimenta tem sido principalmente realizado por agricultores familiares que apresentam dificuldade de manejo de pragas, devido a problemas de identificação das pragas e seus sintomas e, principalmente, a falta de tecnologias agroecológicas apropriadas. Estratégias de manejo que buscam o controle preventivo e complementar de herbívoros podem gerar redução dos impactos de organismos indesejáveis na cultura, além de ser uma alternativa sustentável para agricultores.

Uma das principais causas de perdas de produtividade no cultivo da pimenta está associada ao conjunto de pragas que atacam folhas, flores e frutos em diferentes fases do ciclo da cultura (Venzon *et al* 2006b, Venzon *et al* 2011). Com o aumento das áreas de cultivo de pimenta, geralmente, verifica-se perda de diversidade e simplificação da matriz agrícola, o que facilita surtos populacionais de insetos que se tornam pragas na lavoura (Venzon *et al* 2011). De acordo com os coeficientes técnicos de cultivo, a controle de pragas e doenças pode alcançar até 10% do custo de produção (Vilela & Junqueira 2006).

Dentre os artrópodes que atacam a cultura da pimenta, pode-se destacar o pulgão verde *Myzus persicae* Shulzer e o pulgão-do-algodoeiro *Aphis gossypii* (Hemiptera: Aphididae). Em sistemas de cultivo da pimenta é bem comum observar presença de predadores afidófagos, que mesmo em reduzidas populações podem contribuir para o controle de algumas pragas. Em sistemas agroecológicos, que preconiza o uso de medidas alternativas para controle de organismos prejudiciais, a atração e manutenção de inimigos naturais tem papel estratégico na redução de surtos populacionais de pulgões. O controle biológico pode ser uma estratégia importante para evitar o surto populacional de artrópodes herbívoros na cultura da pimenta, reduzindo ou eliminando a aplicação de agrotóxicos. Estratégias de diversificação do ambiente, como a preservação de áreas de vegetação espontâneas no entorno das áreas de cultivo, podem proteger e manter os artrópodes benéficos, reduzindo o impacto de herbívoros na cultura da pimenta. Por ser um prática de fácil compreensão e que pode ser adotada sem grande custos nas propriedades, a manutenção de plantas espontâneas como promotora do controle biológico conservativo tem o potencial de ser tornar uma técnica com aplicabilidade em agroecossistemas da pimenta-malagueta. Por isso, torna-se necessário entender o papel das espontâneas no incremento do controle biológico, como o objetivo de desenvolver sistemas de produção mais eficientes e que ao mesmo tempo possibilitem maior sustentabilidade.

O objetivo deste trabalho foi avaliar as contribuições do manejo de plantas espontâneas para o incremento e manutenção de predadores artrópodes, além de reduzir possíveis efeitos negativos entre estes organismos. No capítulo I foi avaliada a composição de espécies de plantas espontâneas no cultivo da pimenta-malagueta, determinando associação com inimigos naturais e o tipo de recursos fornecido aos insetos benéficos. Adicionalmente, foi avaliada a sobrevivência de adultos e larvas de coccinelídeos expostos à inflorescência de plantas espontâneas mais comuns nos cultivos de pimenta estudados. No capítulo II, estudou-se o efeito da presença de faixas de plantas espontânea circundando cultivo de pimenta-malagueta na abundância de populações de afídeos e de artrópodes predadores, e na produtividade da pimenta. Adicionalmente, avaliou-se a distribuição espaço-temporal de artrópodes predadores em sistema de cultivo de pimenta com diferentes manejos de plantas espontâneas (presença e ausência de plantas espontâneas; e faixas de plantas fora e dentro do sistema de cultivo). No capítulo III, avaliou-se, detalhadamente, a interação entre plantas espontâneas e grupos de aranhas, com levantamento de famílias de aranhas relacionadas com as espécies de plantas espontâneas. Também, avaliou-se o efeito do plantas espontâneas associadas com o cultivo de pimenta-malagueta na estrutura de guildas e abundância de aranhas. Por fim, no capítulo IV, investigou-se o papel da heterogeneidade do habitat mediada pelo manejo de plantas espontâneas em interações de competição, canibalismo e predação intraguilda entre uma espécie nativa e uma exótica de coccinelídeo, no cultivo de abóbora.

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Chapter I

Non-crop vegetation associated with chili pepper agroecosystems promote the abundance and survival of aphid predators[1]

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 agro- ecosystems. 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

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[1] **Ver Anexo:** 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**. *Biological Control*, **64**, 338–346.

fully characterize the structure and function of plant resources in these and other tropical agroecosystems.

Keywords: aphidophagous species, alternative food, conservation biological control

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 & Whitcomb 1978; Wyss 1995; Nentwig 1998; Liljesthröm *et al* 2002; Gurr *et al* 2003; Norris & 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 & 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 Tscharntke 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 & Yeargan 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 & 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 significant 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 agro- ecosystems, 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 under- taken, the latter has an original distribution of Japan, Ryukyus [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 agro- ecosystems 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 re- sources 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 & 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 m^2 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±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 & 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).

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 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 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. sanguinea* 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 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 aphidophagous 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 & Kogan 2000; Showler & 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., Pemberton & 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 & Evans 2012) and reduce the likelihood of cannibalism and intraguild predation (Cottrell & 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 & Kogan 2005; Lundgren 2009b). Pest control efficacy may also be associated with higher density (Straub & 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 & 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 & Grant 2005; Lundgren 2009a; Lundgren & 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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Table 1. Abundant spontaneous weeds associated with chili pepper fields in Piranga, Minas Gerais, Brazil (ordered by total number of natural enemies observed on weed plants).

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

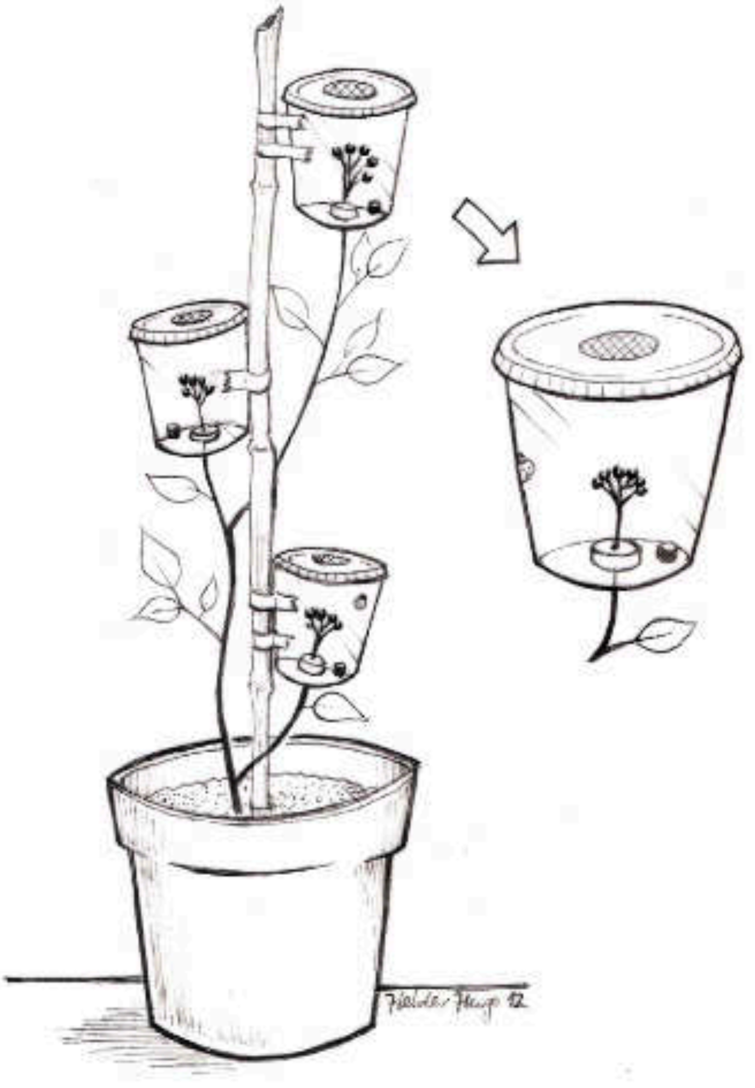

Figure 1. Experimental design of laboratory experiments to quantify the effect of spontaneous weeds on survival of Coccinellidae.

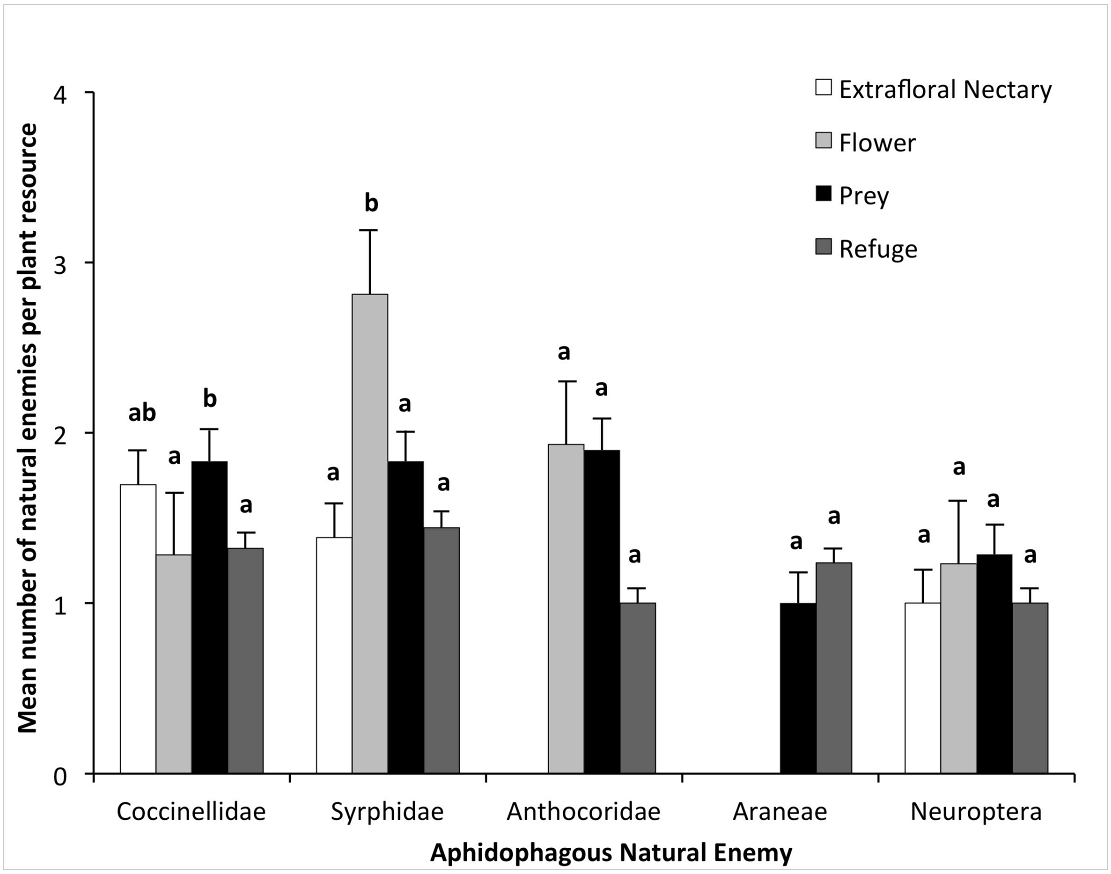

Figure 2. Mean (+SE) number of natural enemies per plant recorded on different resources provided by spontaneous weeds in chili pepper fields in Piranga, Minas Gerais, Brazil. Bars with different letters are statistically different from each other ($P < 0.05$) (comparisons within each insect taxa).

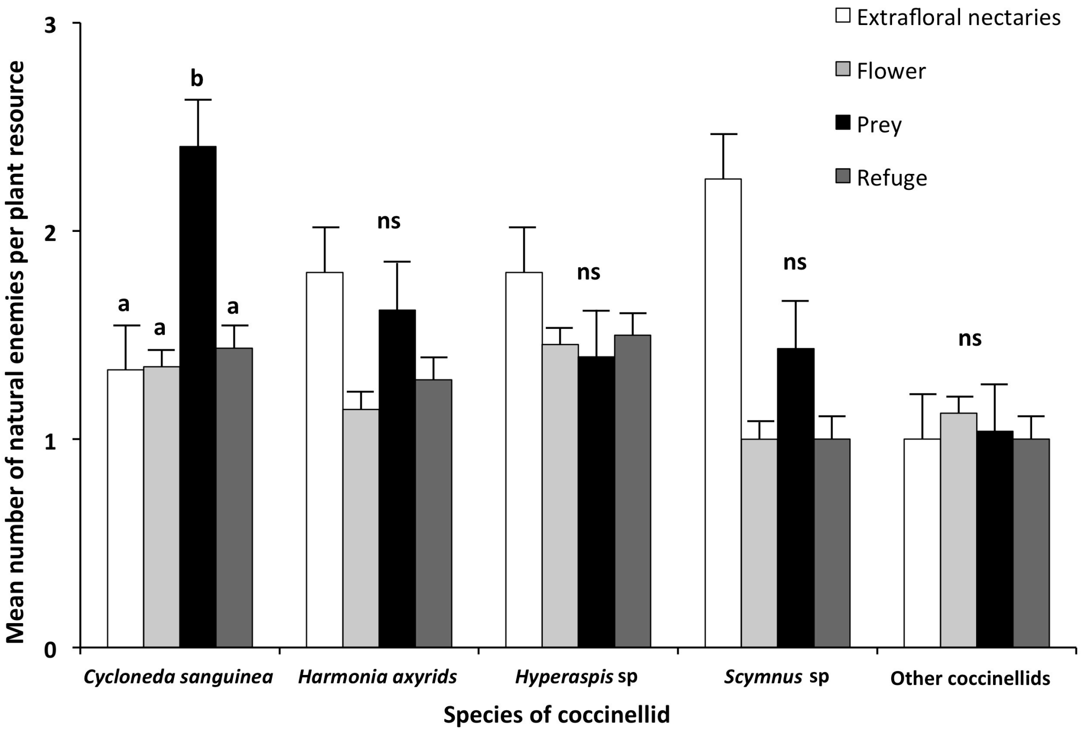

Figure 3. Mean (+SE) numbers of coccinellid species per plant recorded on different resources provided by spontaneous weeds in chili pepper fields in Piranga, Minas Gerais, Brazil. Bars with different letters are statistically different from each other ($P < 0.05$) (comparisons within each species).

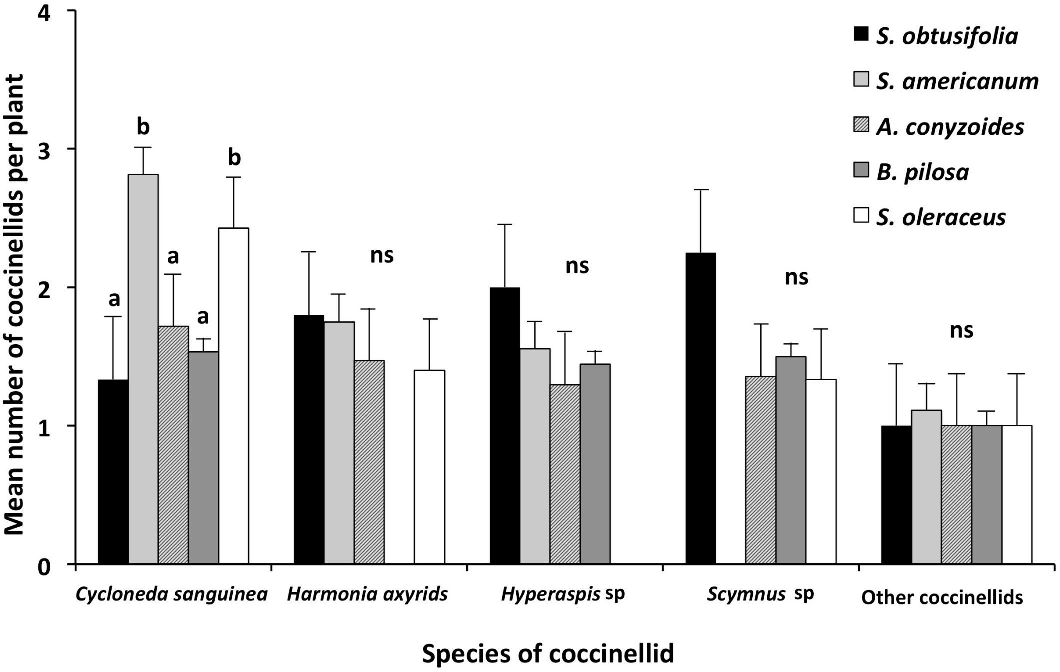

Figure 4. Mean (+SE) numbers of coccinellid species per plant recorded on different spontaneous weed species in chili pepper fields in Piranga, Minas Gerais, Brazil. Bars with different letters are statistically different from each other ($P < 0.05$) (comparisons within each species).

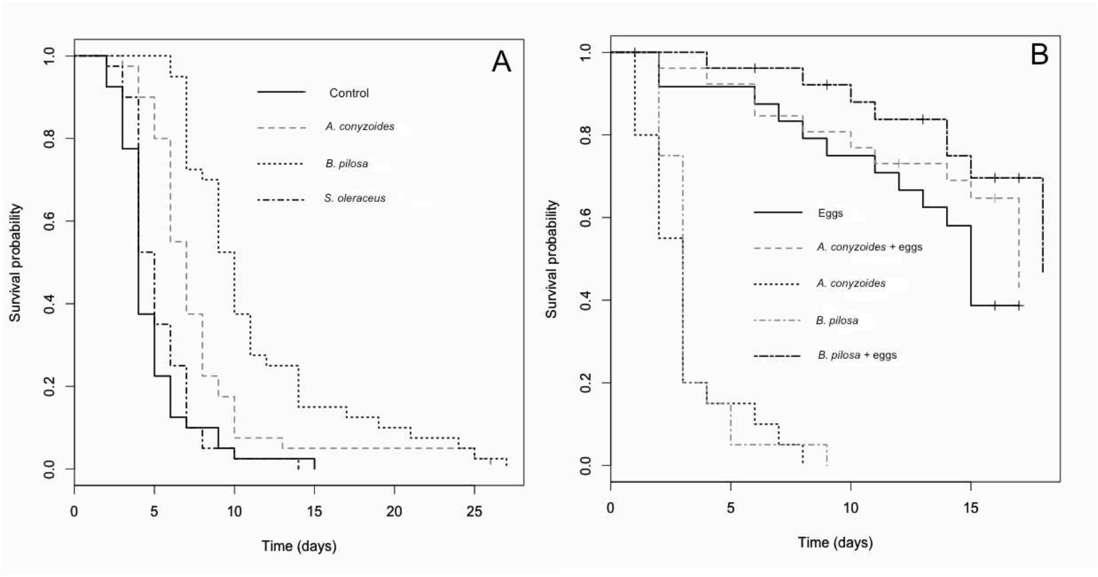

Figure 5. (a) Kaplan–Meier estimates of survivorship function of *Cycloneda sanguinea* adults on flowers of three spontaneous weeds and a control treatment. Median survival time was calculated as 10 days for coccinellids on *Bidens pilosa*, 7 days on *Ageratum conyzoides*, 5 days on *Sonchus oleraceus* and 4 days for the starvation control. (b) Kaplan–Meier estimates of survivorship function of *Cycloneda sanguinea* larvae on two spontaneous 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).

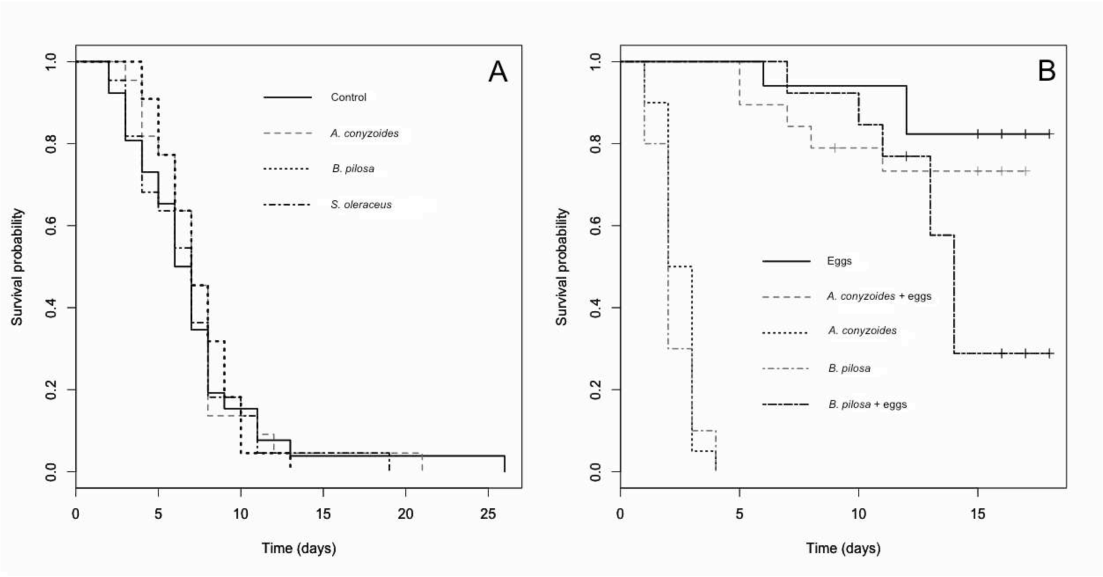

Figure 6. (a) Kaplan–Meier estimates of survivorship function of *Harmonia axyridis* adults on flowers of three spontaneous weeds and a control treatment. Median survival time was calculated as 7 days for coccinellids on *Bidens pilosa*, 7 days on *Ageratum conyzoides*, 7 days on *Sonchus oleraceus* and 6.5 days for the starvation control. (b) Kaplan–Meier estimates of survivorship function of *Cycloneda sanguinea* larvae on two spontaneous 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).

Chapter II

The abundance and spatio-temporal distribution of arthropods predators in chili pepper is affected by non-crop plants management

Abstract

The management of non-crop plants, by increasing biodiversity, may influence positively populations of natural enemies in agroecosystems. The correlation between increase of beneficial arthropods and pest reduction is important to better plain strategies to augment the associated non-crop vegetation. More specifically, the strength of plant manipulation on biological control may be affected by the pattern of movement and spatial distribution of natural enemies on crop fields. Here, we evaluated how abundance of aphid and arthropod predator populations is affect by presence of non-crop plants during all chili pepper season. The crop yield was used to determine the possible positive effects of increasing of beneficial arthropods. We also investigated spatial distribution of arthropod predators influenced by non-crop plants manipulation. Spatial Analyses by Distance Indices (SADIE) was used to compare chili pepper areas (i) without non-crop plants, (ii) with strip of non-crop plants at margin crop and (iii) with strip of non-crop plants at margin crop and with non-crop plants within field. Grids inside crop were sampled during the chili pepper season. We found that in the presence of non-crop plants, there was an increase of abundance of most beneficial arthropods studied and a reduction of herbivore populations. Despite of this, the presence of non-crop plants strip did not influence chili pepper yield. On spatio-temporal experiment, non-crop plants presence affected positively the distribution of coccinelids and spiders, promoting more densities of arthropods in non-crop plant patches. Our results indicate that manipulation of non-crop plants around or inside cropping systems may contribute to abundance and distribution of natural enemies.

Understanding the movement pattern or diffusion rate of key natural enemies may contribute to choose the appropriate strategy of non-crop management in crop fields.

Keywords: spatial patterns, SADIE analysis, conservation biological control, arthropod predators

1. Introduction

The use of monoculture in modern agriculture disturb ecosystems through reduction of connections among organisms that negatively affect ecological process and services (Tilman *et al* 2002; Power 2010; Bommarco, Kleijn & Potts 2012). In general, the monoculture systems are more susceptible to pest outbreaks mainly due to reduced natural enemies community richness and evenness (Wilby & Thomas 2002; Crowder *et al* 2010). Conservation biological control strategies such as plant diversification may modify agroecosystem conditions to support natural enemies, enhancing their efficiency to capture pests (Andow 1991; Landis, Wratten & Gurr 2000; Snyder *et al* 2005, Jonsson *et al* 2008; Bianchi, Booij & Tscharntke 2008). Management of plant diversity should enhance the abundance and diversity of natural enemies that result on strong trophic cascade and direct outcome on crop production (Cardinale *et al* 2003; Letourneau *et al* 2011). Beneficial arthropods can profit from diversified agroecosystems because they can provide resources other than prey for survival and even reproduction (Gurr, Wratten & Luna 2003; Jonsson *et al* 2010).

The vegetational diversity management may vary depending on the type of crop (perennial or annual), region (temperate or tropical) and landscape structure (Thies & Tscharntke 1999; Letourneau *et al* 2011). A common strategy of enhancing plant diversity in cropping system has been the manipulation and restoration of non-crop plants (Altieri & Whitcomb 1978; Wyss 1995; Nentwig, Frank, & Lethmayer 1998; Norris & Kogan 2000; 2005). Non-crop plant diversity distributed temporally or spatially on cropping systems can impact beneficial arthropods dynamics (Altieri & Letourneau 1982; Norris 2005). Moreover, the management of non-crop plants may be easily adopted by farmers due to characteristics such as rapid plant grows and low investment (Nentwig 1998, Norris & Kogan 2000; Barberi *et al* 2010).

Non-crop plants might harbored several species of aphids (Souza-Silva & Ilharco 1995) and they may represent important source of alternative prey in times of low crop aphid abundance (Nentwig 1998). Certain groups of non-crop plants (*p.e.* Apiaceae or Astereracea) are fundamental to provide pollen, nectar, shelter and oviposition places that affects positively the arthropod predators survival (Altieri 1999; Norris & Kogan 2005). Additionally, different groups of arthropods are affected in singular way by non-crop plant resources. Coccinellids use mostly alternative prey and extra floral nectar, while syrphids feed on flower resources (Amaral *et al* 2013). Adult lacewings gut analyses found grains of pollen belonging to 21 botanical families (Medeiros *et al* 2010). Additionally, lacewings have preference for specific non-crop plants during the oviposition period, with almost all eggs found on four plant species (Nentwig 1998). Spiders may use non-crop plants as substrate to building webs, thereby increasing the prey capture (Sunderland & Samu 2000).

Although plant diversity has been considered attractive and ‘hospitable’ for natural enemies, few studies presented correlation between increase of beneficial abundance and effective population pest regulation (Wyss 1995; Halaj & Cady 2000; Sengonca, Kranz & Blaeser 2002). In some cases, plant diversity may improve increase natural enemies abundance, but decrease crop yield (Poveda, Gómez & Martínez 2008). The presence of non-crop plants is mainly important on early season to attract natural enemies before pest outbreaks. However, in some cases there is the risk of such plants to reduce the efficiency of pest management, for instance when arthropods remain feeding on alternative food or using non-crop plant as habitat source (Prasad & Snyder 2006; Spellman, Brown & Mathews 2006). Additionally, the trophic cascade may be disrupted by negative interactions among natural enemies such as intraguild predation (Straub, Finke & Snyder 2008; Letourneau *et a.* 2009). Thus, it is important to measure whether increasing of arthropod predators abundance and diversity reflect on crop production.

The spatial distribution should be also considered when evaluating possible benefits of management of non-crop plants, by determining the natural enemy cover span from source of plant diversity (Holland *et al* 2004, Thomson & Hoffmann 2013). More than intrinsic characteristic among species or life stages, the movement behavior may be influenced by environmental heterogeneity (Corbett 1998, Winder *et al* 2001; Perry 2002; Park & Obrycki 2004). To understand the efficiency of presence of non-crop plant strips on biological control, we should take into account the movement of beneficial arthropods from strips towards crop plants, by measuring how far insects may be found into field (Perry 2002; Hogg & Daane 2010; Thomson & Hoffmann 2013). For instance, abundance of natural enemies reduces when the distance from non-crop plants increases (Altieri & Todd 1981; Thomson & Hoffmann 2009; Hogg & Daane 2010). Spatial pattern may help to plan distance between non-crop vegetation and crop in order to that affects positively pest control.

To access the impact of non-crop plant management as practice to promote biological control, we used chili pepper crops, a common horticulture system in tropical region, as model to understanding the effects of non-crop plants on natural enemies abundance and spatial distribution. Pest control is a multifaceted problem in this system because pest arthropods can cause damage during different phenological crop phases and so far there is no an efficient method of control (Venzon *et al* 2006). The aphids are particularly important pests of chili pepper and can cause both direct and indirect damage to the crop on all phenological stages (Venzon *et al* 2006, 2011). Previous observation in predatory arthropods in chili pepper crops has shown interactions between non-crop plants and natural enemies, mainly due to provision of alternative food and oviposition sites (Amaral *et al* 2013). However it is not clear whether the presence of non-crop plants influence the action of natural enemies inside field crop, promoting trophic cascade and benefits in yield.

Our study focused on analyzes aphid and aphidophagous group populations (Coccinellidae, Syrphidae, Araneae, Neuroptera) to answer the following questions: (i) Does the presence of non-crop plant strip enhance natural enemy abundance and reduces herbivore outbreaks? (ii) Does plant diversified agroecosystem have superior chili pepper production than monoculture of chili pepper? (iii) Are spatial temporal distribution of arthropod pests and natural enemies influenced by the presence of non-crop plants on chili pepper systems?

2. Material & Methods

2.1. Field experiment 1: Abundance sampling and chili pepper yield

In 2012, a field study was carried out to examine the effects of non-crop plant strip around to chili pepper plots on abundance of aphids and arthropod predators and its effect on the crop productivity, in 2012. The experiment was carried out in the experimental farm of Empresa de Pesquisa Agropecuária de Minas Gerais (EPAMIG), located at Oratórios'county (20° 25' 05" S, 42° 48' 08" W) in the state of Minas Gerais, Brazil. The region is characterized by semi intensive agricultural use, with small farms ranging from 1 to 10 ha. The average temperature and total rainfall during the study period from February to June was 24,7 ° C and 719 mm.

Chili pepper seedlings were transplanted, in February, into 10 X 10 m plots with plants spaced in 1 m. Four replications of each treatment (non-crop plants strip and control, without non-crop plants) were randomly assigned in the experimental area. Plots were separated from each other by 20 m of bare ground, in order to reduce the inter-plot movement of arthropods within experimental field. During the experiment, the areas within and among the plots were maintained in bare soil by using mechanic control when necessary. The plots with non-crop plants had a strip of 3 m around the plots where the weeds were growing freely, after seedlings transplant. All plots were irrigated during periods of low precipitation with an overhead sprinkler system. The plants were maintained under standard agronomic practices with organic and mineral fertilization. A compound fertilizer NPK (20:5:20) was applied at the rate of 50 g per plant at monthly intervals. No insecticides were applied. Each treatment was replicated four times.

The community of non-crop plant species was characterized by sampling with quadrats measuring 0.5 m X 0.5 m in eight randomly assigned sites per plot of chili pepper with these treatments. Unknown plants were collected for later identification in laboratory. The non-crop plants were sampled twice during the crop season.

The abundance of arthropods was evaluated through 10 samplings done from March until July (03 March 2012, 21 March, 04 April, 18 April, 02 May, 16 May, 30 May, 13 June, 27 June and 11 July 2012). The abundance of aphids and aphidophagous was assessed on 20 plants randomly assigned on each sampling per plot. Each assigned plant was observed for 1 min to access arthropod predators flying around the plant. The insects observed were registered and collected to identification *ex post*. To determine aphid abundance, firstly four sprouting were randomly select for plant, and they were checked for the presence of aphids. Additionally, the same plant was sampled by beating foliage on collection tray, counting and collecting the aphids. Numbers of adult and nymph aphids were registered.

Predatory arthropod abundance on each plant was evaluated by beating the foliage over a plastic collection tray to ensure comprehensive sampling of arthropods. For predator abundance, it was sampled 20 plants/plot. The immature and adult arthropods were collected and identified in the Laboratory of Entomology (EPAMIG). Samplings were conducted in the between 9:00 to 15:00 h and only in sunny days. Chili pepper yield on each treatment was evaluated harvesting fruits from 10 undisturbed plants per plot. The weight of the fruits per sampled chili pepper plant was registered on four-harvest date in each plot (20 May, 21 June, 23 July and 2 August 2012). The same assigned plants had all mature fruits harvested along the whole crop season.

The abundance of arthropods was analyzed using Generalized Linear Model, assuming a quasipoisson distribution and a log link function (Crawley 2012). To stabilize variances, absolute data were square root transformed prior to analysis. In this analysis, the arthropod abundance was included as a fixed effect in one-way ANOVA associated to vegetational diversity (presence and absence of non-crop plants). Chili peppers fruit yield data were analyzed by Student’s t test.

2.2. Field experiment 2: Spatio-temporal analysis and arthropods distribution

A chili pepper field was set at an experimental area located on a small farm in Piranga County, state of Minas Gerais, Brazil (20°45’45”S, 43°18’10”W). The experimental area was divided in three plots with 15 X 40 m each one. On 14 December 2011, seven weeks-old chili pepper seedlings were transplanted into plot areas with spacing of 1.0 m within and between rows. The plants were maintained under standard agronomic practices with organic and mineral fertilization. A compound fertilizer NPK (20:5:20) was applied at the rate of 50 g per plant at monthly intervals. Insecticide was not applied in the studied field. An initial infestation of broad mite, *Polyphagotarsonemus latus* (Banks) (Acari: Tarsonemidae), was controlled by spraying lime sulfur in a concentration of 10 mL L^{-1} one month after the chili pepper transplant (Venzon *et al* 2013).

The experimental area was divided in the following treatments: (i) control, chili pepper plants in bare soil; (ii) strip, chili pepper with non-crop plants strip outside crop area, (iii) intercropped, chili pepper non-crop plants strip on both outside and inside of plot area. To maintain control plots, the area around (at least 50 m apart) the field and the area between chili pepper rows were weeded using manual equipment. The treatments with non-crop plants strip consisted of 15 x 10 m area attached to a face of experimental plot. The other faces (at least 50 m apart) and inside chili pepper lines were kept without non-crop plants. Intercropped experimental plot contained a non-crop strip outside the plot (15 x 10 m) and non-crop plants between among chili pepper lines. The non-crop plants were separated from the chili pepper rows by 0.25 m with bare soil. The other plot faces were maintained in bare soil by using mechanic control when necessary, at least 50 m around the experimental plot.

Each experimental chili pepper plot was divided into 3 X 3 m area, totalizing 48 quadrants. For each quadrant, two plants were selected and sampled biweekly from December 2011 to May 2013. The aphids usually present on chili pepper systems and the four more common arthropod predators (coccinelids, lacewings, syrphids and spiders) were sampled to assess the spatial distribution of arthropods. The arthropods on plants were sampled by beating the foliage over a white plastic tray (300 X 500 X 100 mm deep). The number of selected predatory arthropod was recorded and collected to posterior identification. The abundance of aphids on each quadrant was estimated through the aphids collected on a tray after beating the foliage. The samplings were carried out from

9:00 to 15:00 h in sunny days during eight sampling days (22 December 2011, 18 January 2012, 15 February, 12 March, 23 March, 16 April, 06 May and 29 May 2012).

The spatial distribution of aphids and predatory arthropods sampled within the experimental plots were characterized using Spatial Analyses by Distance Indices (SADIE) (Perry 1995; Perry, Winder & Holland 1999; Winder, Perry & Holland 1999). SADIE provides mechanisms to analysis the spatial distribution pattern of organism, by testing whether data are either organized randomly or regularly distributed (Perry & Dixon 2002). Initially, the overall spatial pattern of organisms was determined by the index of aggregation (I_a). Values I_a significantly lower than 1 indicates a regular pattern and I_a higher than 1 indicates aggregation of observed data. The spatial analyze indicates a random distribution of organisms studied when the expected value is 1. Additionally, to identify and quantify clustering in the distributions of aphids and each arthropod predator group we used SADIE Shell (version 1.22) graphic interface (Conrad 2006). According to Perry et al (1999), SADIE analyzes are based on referenced points that create clustering index able to show how distributed in "*i*" in patch clusters (high density near each other) or "*j*" in gap clusters (low or zero density). Positive index (vi) occurs when the counts are higher than the mean, indicating patch clusters. Differently, negative index (vj) is described for the counts lower the mean and indicates gasp cluster. Surfer mapping software (version 8; Golden Software, Inc. 2008, Golden, Colorado, USA) was used to interpolate the index values into a contoured surface map of v significantly above or bellow ±1.5, representing significant patches and gaps (Perry *et al* 1999). Two-dimensional maps with sample coordinates were constructed using SURFER software to indicate significant patches and gasp (ANON 1999).

When we found significant patched distribution of herbivore and natural enemies on the same sampling date, it was used SADIE local association. These analyzes were used to test the hypothesis of aggregation due predator-prey interactions instead of relation between non-crop and natural enemies. The association is measured by correlation between two clusters indices calculated prior for each studied organism (Winder *et al* 2001). The correlation results an overall index of association (X), which is able to show the degree of association between two organisms population, through the specific probability (*P*). The P-value should be less than 0.025 for significant positive association, or greater than 0.975 for significant dissociation (Winder *et al* 2001).

3. Results

3.1. Field experiment 1: Abundance sampling and chili pepper yield

A total of 21 different non-crop plants represented 80 % of total species and genera found on chili pepper system in Oratórios (Table 1). The most common groups of aphidophagous predators were coccinellids, syrphids, spiders and lacewings. The presence of non-crop plants showed positive impact on abundance of these arthropods. The abundance of these aphidophagous arthropods was significantly greater when they were collected on chili pepper plants with non-crop plants ($F_{1,\ 472} = 20.35$, $P < 0.001$) (Fig 1). The temporal abundance of aphids was significantly higher on plots with only chili pepper than on diversified fields with strip of non-crop plants around chili pepper fields ($F_{1,\ 472} = 20.35$, $P < 0.001$) (Fig 2). The mean density of aphids per plant was always low, varying from 0.15 to 2.14 per plant.

Spiders were the more common arthropod groups sampled, and they were significantly more abundant in plots with non-crop plants than on plots with only chili pepper plants ($F_{1,\ 305} = 15.66$, $P < 0.001$). Also, syrphids ($F_{1,\ 41} = 7.97$, $P = 0.007$) and Neuroptera (hemerobids and lacewings) ($F_{1,\ 82} = 32.07$, $P < 0.001$) were more abundant in the presence of non-crop plants associated to chili pepper system (Fig. 3 and 4). However, the coccinelid populations did not show significant difference on abundance when plots with and without non-crop plants were compared ($F_{1,\ 38} = 1.58$, $P = 0.753$) (Fig 4). The mean fruit weight per chili pepper plant in all harvest dates did not show significant difference between the chili pepper experimental plots with and without strips of non-crop plants (t=0,205 df =445 $P = 0.842$).

3.2. Field experiment 2: Spatio-temporal analysis and arthropods distribution

The total of 20 different non-crop plants represented 75 % of total species and genera found on chili pepper system in Piranga (Table 2). The spatial distribution pattern of aphids on plants in experimental plots on chili pepper crop was mainly random during crop season. However, the aphid populations showed aggregation (*Ia*) twice on plots with strip of non-crop plants and one occasion on intercropped non-crop and chili pepper plants. See Tables 3 a 7 with a summary of the aggregation index *(Ia)* and clustering indices (*vi* and *vj*). On two samples date (2/15/12 and 3/12/12) the aphid population showed a gap on area with the strip of non-crop plant at one side of the chili pepper crop (Fig. 8). At end of crop season, the aphid population was significantly aggregated (*Ia*=1.511) on the area with non-crop intercropped with chili pepper, showing patchiness far from area with strip of non-crop plants and large gaps nearby this area (Fig 9, strip of non-crop plant on page bottom).

The results of SADIE analysis also showed that coccinellid populations were directly influenced by presence of non-crop plants on chili pepper crop. The sample of coccinellids on experimental plot with non-crop plants (control) showed random distribution (Table 2). High values of the patch-clustering index (vi) within the chili pepper (>1.5) indicate patches of strong coccinellid aggregation. From beginning to middle of season, the coccinellids showed significant aggregation (Table 2) on 3 sampling dates with large patch of individuals nearby strip of non-crop plants (Fig. 10 and 11). The patchiness was higher on area on the middle of chili pepper plants and gaps were more frequent at end of sampling area. On the experimental plot with intercropped non-crop plants, the coccinellid populations presented spatial aggregation on 5 sampling dates, from middle to the end of chili pepper season (Fig 12 to 14).

The spider populations presented more spatial pattern aggregation on diversified chili pepper systems (see result summary on Table 5). Although it was observed spiders aggregation as on control plot (two sampling dates, 01/18/12 and 02/15/12) as chili pepper associated only strip of non-crop plants (three sampling dates, 12/22/11, 05/06/12 and 05/29/12), the aggregation was more common when chili pepper was intercropped with non-crop plants mainly from the middle to end of crop season (Table 5). When chili pepper plants were associated to plant diversity, the strong aggregation of spiders on strip and on intercropped non-crop plants concentrated from beginning to middle of sampling plot, and larger gaps on the ending of plot (Figures from 16 to 19). Syrphidae and Neuroptera displayed random spatial distribution when sampled within the fields of chili pepper only, or with strip with of non-crop plant (Table 6 and 7).

The SADIE association index (*X*) between aphid populations and natural enemies was significant only on two sample dates in different treatment. The aggregation index was significant for aphids and coccinelids at same time on two samples date on strip on non-crop plant (2/15/12 and 3/12/12) and one date to experimental plot with intercropped non-crop plants (05/29/12). On sampling date 02/15/12 the association index was not statistically significant (X = -0.0748, P = 0.691). However, the association between aphid and coccinelids was significant on experimental plot with strip of non-crop plants on 03/12/12 (X = 0.3988, P = 0.0053); and the dissociation was significant on plot with intercropped non-crop plants (X = -0.3769, P = 0.9961). When we compare association between aphids and spider aggregation index was significant to both arthropods only on experimental plot with intercropped at sampling date 05/29/12. However the association between arthropods was not statistically significant (X = -0.1461, P = 0.8354).

4. Discussion

The maintenance of a strip with non-crop plants around chili pepper plots increase the abundance of some aphidophagous groups. Syrphids, spiders and lacewings, enhanced their abundance for overall sampling date, differently of coccinelids. These abundance enhancement of natural enemies resulted on reduction of aphid populations on overall chili pepper season period. The increase of plant diversity through the maintenance of non-crop plants around the crop field was able to enhance the abundance of beneficial arthropods as showed by other studies done in different crops and regions, confirming the importance of this practice to conservation biological control (Shelton & Edwards 1983;

Wyss 1995, 1996; Leather *et al* 1999; Sengonca, Kranz & Blaeser 2002; Showler & Greenberg 2003; Caballero-López *et al* 2011). Despite of increasing natural enemy population and decreased pest population, the presence of non-crop plant strips was not influenced chili pepper yield in our experiment. The same productivity on both treatments, with and without non-crop plants, can be associated to infestation of aphids that was lower than threshold, not affecting significantly the crop yield. Although, the two systems showed the same production, the management of non-crop plants reduces the agricultural labor and in put energy for over all crop systems.

Coccinellid populations did not show significant increase on abundance on chili pepper systems with or without non-crop plants. In all sampling dates, the number of coccinelids collected was lower than other arthropod predators. Weather conditions, as excessive rainfall, may have contributed to reduce the coccinellid populations overall. Although coccinellids may be benefited by non-crop plants due to supply of alternative food (Lundgren 2009; Amaral *et al* 2013), the most common species of non-crop plants found in Oratórios (Poaceae) were usually not associated with these predators. Coccinellids are known to feed preferentially on some Asteraceae or Apiaceae plants (Medeiros *et al* 2009; Berkvens *et al* 2010; Lixa *et al* 2010). Additionally, on sampling date, aphids never achieved high densities either on chili pepper or on non-crop plants, which could have reduced the chance to attract coccinellids on the systems.

Spider populations showed abundance on plots with management of non-crop plants around chili pepper crop. Generalist predators as spiders may be benefited by habitat-structured systems, usually associated to an increase on vegetal diversity (Langelloto & Denno 2004, Sunderland & Samu 2000). The higher abundance of spider on a vegetational diversified crops is mainly due to the presence of additional area of refuge, provision of complementary or supplementary food, favorable microclimate and increased chance of preying (Mcnett & Rypstra 2000; Langellotto & Denno 2006; Peterson, Romero & Harwood 2010; Chen, You & Chen 2011). The benefits of more spiders in the field may reflect on suppression of aphid populations. For instance, web-building spiders in the strip-managed area may have reduced the winged aphids that colonize crop fields (Wyss 1995).

On this context, the reduction of local disturbance through the conservation of non-crop plants implies on presence of spider all over the crop season.

Syrphidae and Neuroptera populations also responded positively to manipulation of non-crop plants strip and the results showed the importance of selecting specific non-crop species to increase beneficial arthropods abundance. The most significant life stage found for both predator groups was adult. The presence and survival of non-carnivore lacewings and syrphids adults depends on the presence of floral resources, because they feed exclusively on pollen and nectar that provide energy and proteins (Villenave *et al* 2005; Laubertie & Wratten 2011; Gillespie *et al* 2011). The occurrence of blooming plants from Asteraceae and Apiaceae in non-crop plant strips favored the population of syrphids in the same way as it was previously observed in other studies (Tooker, Hauser & Hanks 2006; Burgio & Sommaggio 2007). Additionally, for lacewings, pollen gut analysis revealed that this predators displayed preference for Apiaceae, Asteraceae, Amaranthaceae and Fabaceae plants (Villenave *et al* 2005; 2006; Medeiros *et al* 2009).

The spatio-temporal distribution of aphids and their natural enemies varied differently in response to strip of non-crop plants. Aphids showed random spatial distribution inside chili pepper fields for most of plots and collection dates. The populations of aphids just presented clumped spatial distribution on the experimental plot with non-crop strips outside cropping fields in two sampling dates. The spatial distribution of some groups of arthropods predator were affected by the presence of non-crop plants on chili pepper system. Non-crop plants may affect positively the distribution of natural enemies, promoting higher densities of arthropods in non-crop plants patches (Holland, Perry & Winder 1999; Holland *et al* 2004; Thomson & Hoffmann 2009). In our study, coccinellids concentrate their distribution nearby the strip of non-crop plants, mainly after establishment of non-crop plants. Usually, the adult coccinelids was observed on non-crop plant inflorescence and feeding on plants harbored aphids, such as *Ageratum conyzoides* and *Sonchus oleraceus*. It is known the influence of non-crop plants as resource of shelter, alternative prey and complementary food as pollen and nectar (Leather *et al* 1999; Bertolaccini, Nunez-Perez & Tizado 2008; Lundgren 2009; Lundgren & Seagraves 2011, Amaral *et al* 2013). Barely on one sampling date (03/12/12) the association between populations of aphids and coccinelids was observed. Differently of this result, the other significant aggregation of coccinelids was related to factors related to non-crop plants. At 29 May sampling date, on experimental plot of intercropped non-crop plants, aphid and coccinelids showed significant dissociation with coccinelids nearby strip of non-crop plants and aphids far from this point. The dissociation indicates the role of non-crop plants on coccinelids spatial distribution. Usually, the spatial distribution of coccinellids is directly correlated to local abundance of aphids (*p. e.* Ives, Kareiva & Perry 1993; Schellhorn & Andow 2005), but non-crop plants may attract these predators and contribute to keep them nearby cropping systems (Harmon *et al* 2000; Griffin & Yeargan 2002; Sengonca, Kranz & Blaeser 2002). The existence of non-target aphid populations on non-crop plants associated to non-crop alternative food source (pollen and nectar) certainly contribute to aggregate coccinellids that may move to cropping plants lately. Non-crop plant flowers are known to increase survival of adults and larvae of native *Cycloneda sanguinea* L. (Coleoptera: Coccinelidae), even without presence of prey (Amaral *et al* 2013).

Similarly to coccinellids distribution, SADIE analysis showed that spiders have aggregation related to non-crop plant strips. The experiment with non-crop strip inside chili pepper system presented significant aggregation of spider in more sampling times than experiments with only chili pepper and chili pepper with outside strip of non crop plants. The vegetation surrounding crop fields may affect positively spider colonization and distribution (Sunderland & Samu 2000). For instance, Linyphiidae showed strong correlation with non-crop patches found on winter wheat crops (Holland *et al* 2004). Although with reduced capacity to move between habitat, spiders are able to rapidly colonize fields from non-crop habitats by walking (Öberg & Ekbom 2006). The colonization may be improved by manipulation of non-crop plants within-crop which could facilitate the movement or web-building (Balfour & Rypstra 1998; Mcnett & Rypstra 2000). The presence of resource habitat, such as non-crop plant management, affects the amount and the dispersion of spider, increasing their population size, specially for slowing disperse species (Halley, Thomas & Jepson 1996).

While Syrphidae and Neuroptera (lacewings and hemerobids) did not show any spatial distribution pattern, coccinellids and spiders have generally concentrate their distribution on patches nearby strip of non-crop plants and gaps was created far from these points. The spatial pattern of cluster and gaps to both arthropod predators was common from the middle to the end of chili pepper cropping season. These results may be associated to more appropriate climatic conditions and the establishment of non-crop plant communities.

We found intrinsic correlation between the presence of non-crop plant and abundance and spatial distribution of natural enemies. Beyond act as resource of alternative food and shelter, the manipulation of non-crop plants around or inside cropping systems may affect positively pest control, by keeping beneficial arthropods on agroecosystem for over all season. In the development to conservative biological control strategies, an interesting aspect is associated to movement of predators between crop and non-crop vegetation (Thomson & Hoffmann 2009; Hogg & Daane 2010). Our studies shown that the distribution and effective 'colonization' of target crops depend on natural enemies group and their relation with non-crop plant. On this context, future researches may develop models to explain correlation of vegetation, arthropods life states and organism movement behavior to create habitat manipulation strategies that improve conservative biological control. More specifically on arthropod species, the understanding of the movement pattern or diffusion rate of key natural enemies may contribute to choose the appropriate strategy of non-crop management on crop field. From this knowledge, we have a possibility to select plant species or group of them that keep target natural enemies on system, managing the local biodiversity according to specific necessities. Depending on agroecosystems, pest and key natural enemies interactions, it would be possible to manipulate strategically plant diversity (Landis, Wratten & Gurr 2000; Fiedler & Landis 2007).

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Table 1. Abundant non-crop plants associated with chili pepper fields in Oratórios, state of Minas Gerais, Brazil. Plants were ordered from the more to the less abundant specie plants.

Scientific name	**Common name**	**Family**
Pennisetum purpureum	Napiergrass	Poaceae
Blainvillea biaristata	-	Asteraceae
Commelia spp.	Dayflower	Commelinaceae
Digitaria sp	Crabgrass	Poaceae
Ageratum conyzoides	Tropic ageratum	Asteraceae
Asclepia curassavia	bloodflower	Apocynaceae
Galinsoga parviflora	Galinsoga	Asteraceae
Setaria sp	Foxtail	Poaceae
Bidens pilosa	Hairy beggarticks	Asteraceae
Aeschynomene sp	Jointvetch	Fabaceae
Brachiaria spp	Paragrass	Poaceae
Ipomoea cairica	Morningglory	Convolvulaceae
Cyperus distans L	Sedge	Cyperaceae
Artemisia verlotorum	Artemisia	Asteraceae
Sonchus oleraceus L.	Annual sowthistle	Asteraceae
Ipomoea quamoclit	morningglory	Convolvulaceae
Amaranthus sp	Low amaranth	Amaranthaceae
Leonurus sibiricus L	Siberian motherwort	Lamiaceae
Parthenium sp	parthenium, ragweed	Asteraceae
Aspilia pascalioides	-	Asteraceae
Lepidium virginicum	Pepperweed	Brassicaceae

Table 2. Abundant non-crop plants associated with chili pepper fields in Piranga, Minas Gerais, Brazil (Spatial Distribution experiment)

Scientific name	**Common name**	**Family**
Blainvillea sp	-	Asteraceae
Ageratum conyzoides	tropic ageratum	Asteraceae
Chloris sp	windmillgrass	Poaceae
Digitaria sp	crabgrass	Poaceae
Commelina sp	dayflower	Commelinaceae
Cyperus esculentus	nutsedge, yellow	Cyperaceae
Senna obtusifolia	sicklepod	Fabaceae-Caesalpinioideae
Melampodium divaricatum	sn	Asteraceae
Brachiaria decumbens	panicum, sprawling	Poaceae
Oxalis sp	woodsorrel	Oxlidaceae
Sonchus oleraceus	sowthistle, annual	Asteraceae
Baccharis sp.	baccharis, eastern	Asteraceae
Bidens pilosa	beggarticks, hairy	Asteraceae
Leonurus sibiricus	motherwort, Siberian	Lamiaceae
Euphobia heterophylla	poinsettia, wild	Euphorbiaceae
Hypochaeris radicata	catsear, common	Asteraceae
Galinsoga sp	galinsoga	Asteraceae
Solanum americanum	nightshade, American black	Solanaceae
Emilia fosgergii	Cupid's-shaving-brush	Asteraceae
Amaranthus sp	amaranth, low	Amaranthaceae

Table 3. Summary data of Spatial Analyses by Distance Indices (SADIE) of aphid populations colonizing chili pepper crop during 2012 season in different experimental plots (control, strip non-crop plant and intercropped).

Control

Sample Date	*Pa*	*Ia*	mean *vj*	mean *vi*	P(mean *vj*)	P(mean *vi*)
12/22/11	0.8842	0.735	-0.724	0.803	0.8912	0.7277
1/18/12	0.2256	1.134	-1.159	1.097	0.202	0.2381
2/15/12	0.8007	0.812	-0.801	0.797	0.8346	0.8756
3/12/12	0.1026	1.313	-1.365	1.528	0.1282	0.0513
3/23/12	0.3505	1.021	-1.002	1.224	0.3874	0.1512
4/16/12	0.5408	0.914	-0.914	0.869	0.5351	0.6337
5/6/12	0.6496	0.864	-0.897	0.876	0.5755	0.6402
5/29/12	0.3655	1.011	-0.985	0.971	0.4062	0.4289

Strip Non-Crop

Sample Date	*Pa*	*Ia*	mean *vj*	mean *vi*	P(mean *vj*)	P(mean *vi*)
12/22/11	0.4108	1.04	-1.048	1.003	0.3769	0.5643
1/18/12	0.3374	1.052	-1.049	0.902	0.3498	0.5591
2/15/12	**0.0157**	**1.728**	**-1.686**	**1.696**	**0.0241**	**0.0198**
3/12/12	**0.0387**	**1,569**	**-1.456**	**1.576**	**0.0590**	**0.0322**
3/23/12	0.4414	0.97	-0.954	1.021	0.4544	0.3408
4/16/12	0.7640	0.812	-0.81	0.788	0.7612	0.8215
5/6/12	-	-	-	-	-	-
5/29/12	-	-	-	-	-	-

Intercropped

Sample Date	*Pa*	*Ia*	mean *vj*	mean *vi*	P(mean *vj*)	P(mean *vi*)
12/22/11	0.5693	0.895	-0.886	0.9	0.5726	0.5629
1/18/12	0.2955	1.083	-1.099	0.923	0.281	0.5229
2/15/12	0.1163	1.299	-1.318	1.342	0.1068	0.0917
3/12/12	0.8329	0.783	-0.781	0.798	0.8329	0.8205
3/23/12	0.8874	0.764	-0.756	0.766	0.9103	0.9068
4/16/12	0.6735	0.846	-0.849	0.806	0.6791	0.7803
5/6/12	0.5782	0.892	-0.902	0.873	0.5604	0.6435
5/29/12	**0.0466**	**1.511**	**-1.578**	**1.56**	**0.039**	**0.0362**

Control was chili pepper in bare soil. Strip non-crop consisted in chili pepper with strip of non-crop plants; and Intercropped consisted of strip of weedy plants and intercropped weedy plants among chili pepper plants. *Ia* is an index of aggregation and *Pa* the associated probability, *vi* and *vj* are cluster indices and refer to patch and gaps, respectively. Indices are significant when $P < 0.05$. Significant indices and the associated probability values are shown in bold.

Table 4. Summary data of Spatial Analyses by Distance Indices SADIE analysis of coccinelids populations colonizing chili pepper crop during 2012 season in different experimental plots (control, strip non-crop plant and intercropped).

Control

Sample Date	*Pa*	*Ia*	mean *vj*	mean *vi*	P(mean *vj*)	P(mean *vi*)
12/22/11	0.9026	0.744	-0.736	0.756	0.9015	0.8487
01/18/12	0.9982	0.651	-0.645	0.696	0.9978	0.9889
02/15/12	0.3999	0.988	-0.997	0.943	0.3627	0.4501
03/12/12	0.4909	0.934	-0.956	0.859	0.4444	0.6782
03/23/12	0.0680	1.449	-1.419	1.452	0.0712	0.0578
04/16/12	0.3774	1.005	-0.989	1.154	0.4066	0.2157
05/06/12	0.4765	0.954	-0.987	0.895	0.4304	0.5978
05/29/12	0.4367	0.966	-0.968	0.949	0.4347	0.4771

Strip Non-Crop

Sample Date	*Pa*	*Ia*	mean *vj*	mean *vi*	P(mean *vj*)	P(mean *vi*)
12/22/11	**0.0112**	**1.810**	**-1.826**	**1.67**	**0.0097**	**0.0292**
01/18/12	0.9412	0.717	-0.712	0.746	0.9351	0.8973
02/15/12	**0.0213**	**1.658**	**-1.695**	**1.592**	**0.0206**	**0.0258**
03/12/12	**0.0260**	**1.668**	**-1.723**	**1.44**	**0.0196**	**0.0458**
03/23/12	0.0949	1.334	-1.377	1.314	0.0882	0.1022
04/16/12	0.3166	1.047	-1.061	1.03	0.2981	0.3283
05/06/12	0.3414	1.027	-1.038	0.872	0.3305	0.6715
05/29/12	0.3518	1.041	-1.017	0.972	0.3923	0.4359

Intercropped

Sample Date	*Pa*	*Ia*	mean *vj*	mean *vi*	P(mean *vj*)	P(mean *vi*)
12/22/11	0.5693	0.895	-0.886	0.9	0.5726	0.5629
1/18/12	0.9995	0.648	-0.651	0.711	0.9985	0.9834
02/15/12	**0.0002**	**2.292**	**-2.33**	**2.137**	**0.0002**	**0.0012**
03/12/12	**0.0127**	**1.803**	**-1.76**	**1.758**	**0.0137**	**0.0139**
03/23/12	0.4421	0.967	-0.983	0.947	0.4042	0.4657
04/16/12	**0.0007**	**2.363**	**-2.193**	**2.129**	**0.001**	**0.0023**
05/06/12	**0.0002**	**2.309**	**-2.337**	**2.538**	**0.0003**	**0.0000**
05/29/12	**0.0005**	**2.250**	**-2.201**	**2.242**	**0.0007**	**0.0007**

Control was chili pepper in bare soil. Strip non-crop consisted in chili pepper with strip of non-crop plants; and Intercropped consisted of strip of weedy plants and intercropped weedy plants among chili pepper plants. *Ia* is an index of aggregation and *Pa* the associated probability, *vi* and *vj* are cluster indices and refer to patch and gaps, respectively. Indices are significant when $P < 0.05$. Significant indices and the associated probability values are shown in bold.

Table 5. Summary data of Spatial Analyses by Distance Indices SADIE analysis of Araneae populations colonizing chili pepper crop during 2012 season in different experimental plots (control, strip non-crop plant and intercropped).

Control

Sample Date	*Pa*	*Ia*	mean *vj*	mean *vi*	P(mean *vj*)	P(mean *vi*)
12/22/11	0.5453	0.906	-0.886	1,003	0.5936	0.4022
01/18/12	**0.0136**	**1.751**	**-1.779**	**1.527**	**0.0134**	**0.0415**
02/15/12	**0.0007**	**2.185**	**-2.228**	**2.260**	**0.0015**	**0.0010**
03/12/12	0.099	1.325	-1.349	1.442	0.0892	0.0501
03/23/12	0.6967	0.847	-0.850	0.849	0.6972	0.7200
04/16/12	0.6524	0.863	-0.859	0.976	0.665	0.4091
05/06/12	0.3461	1.023	-1.041	0.944	0.3241	0.4922
05/29/12	0.8830	0.771	-0.787	0.751	0.8435	0.9306

Strip Non-Crop

Sample Date	*Pa*	*Ia*	mean *vj*	mean *vi*	P(mean *vj*)	P(mean *vi*)
12/22/11	**0.0020**	**2.717**	**-2.742**	**2.567**	**0.0001**	**0.0001**
01/18/12	0.5916	0.884	-0.87	0.927	0.6278	0.5108
02/15/12	0.9385	0.734	-0.752	0.843	0.9147	0.7334
03/12/12	0.6496	0.867	-0.873	0.869	0.6368	0.6657
03/23/12	0.4069	0.984	-1,001	0.934	0.3838	0.5177
04/16/12	0.5249	0.922	-0.934	0.847	0.4954	0.7288
05/06/12	**0.0392**	**1.538**	**-1.574**	**1.519**	**0.0362**	**0.0407**
05/29/12	**0.0027**	**2.020**	**-2.065**	**1.902**	**0.0030**	**0.0069**

Intercropped

Sample Date	*Pa*	*Ia*	mean *vj*	mean *vi*	P(mean *vj*)	P(mean *vi*)
12/22/11	0.416	0.976	-0.959	0.970	0.4555	0.4344
1/18/12	0.216	1.141	-1.141	1.087	0.2269	0.2723
02/15/12	**0.0357**	**1.558**	**-1.557**	**1,542**	**0.0372**	**0.0399**
03/12/12	0.8423	0.793	-0.793	0.863	0.8502	0.6714
03/23/12	0.5319	0.919	-0.918	0.885	0.5455	0.6171
04/16/12	**0.0238**	**1.630**	**-1.664**	**1.526**	**0.020**	**0.0952**
05/06/12	**0.0008**	**2,169**	**-2,212**	**1,883**	**0.0008**	**0.006**
05/29/12	**0.0002**	**2,111**	**-2,079**	**2,248**	**0.0017**	**0.005**

Control was chili pepper in bare soil. Strip non-crop consisted in chili pepper with strip of non-crop plants; and Intercropped consisted of strip of weedy plants and intercropped weedy plants among chili pepper plants. *Ia* is an index of aggregation and *Pa* the associated probability, *vi* and *vj* are cluster indices and refer to patch and gaps, respectively. Indices are significant when $P < 0.05$. Significant indices and the associated probability values are shown in bold.

Table 6. Summary data of Spatial Analyses by Distance Indices SADIE analysis of syrphid populations colonizing chili pepper crop during 2012 season in different experimental plots (control, strip non-crop plant and intercropped).

Control

Sample Date	*Pa*	*Ia*	mean *vj*	mean *vi*	P(mean *vj*)	P(mean *vi*)
12/22/11	-	-	-	-	-	-
01/18/12	-	-	-	-	-	-
02/15/12	0.1939	1.1890	-1.1980	1.1460	0.1864	0.2264
03/12/12	0.2585	1.1080	-1.1250	1.0820	0.2372	0.2775
03/23/12	0.8691	0.7490	-0.7470	0.7070	0.8751	0.9522
04/16/12	0.4317	0.9740	-0.9630	1.0110	0.4515	0.3714
05/06/12	0.1428	1.2550	-1.2690	1.1050	0.1230	0.2355
05/29/12	0.6315	0.8640	-0.8670	0.8130	0.6246	0.7481

Strip Non-Crop

Sample Date	*Pa*	*Ia*	mean *vj*	mean *vi*	P(mean *vj*)	P(mean *vi*)
12/22/11	0.0980	1.366	-1.380	1.316	0.0985	0.1264
01/18/12	-	-	-	-	-	-
02/15/12	0.2926	1.085	-1.081	1.180	0.2787	0.1922
03/12/12	0.2041	1.158	-1.147	1.246	0.2207	0.1421
03/23/12	0.4069	0.984	-1.001	0.934	0.3838	0.5177
04/16/12	-	-	-	-	-	-
05/06/12	0.2157	1.142	-1.161	1.093	0.2103	0.2727
05/29/12	-	-	-	-	-	-

Intercropped

Sample Date	*Pa*	*Ia*	mean *vj*	mean *vi*	P(mean *vj*)	P(mean *vi*)
12/22/11	-	-	-	-	-	-
1/18/12	0.2160	1.141	-1.141	1.087	0.2269	0.2723
02/15/12	0.6430	0.721	-0.723	0.728	0.9596	0.9737
03/12/12	0.9206	0.740	-0.739	0.751	0.9224	0.9212
03/23/12	0.6492	0.861	-0.859	0.866	0.6564	0.6347
04/16/12	0.2026	1.171	-1.204	1.061	0.1741	0.2877
05/06/12	0.1428	1.255	-1.269	1,105	0.1230	0.2355
05/29/12	0.2154	1.168	-1.181	1.069	0.2051	0.3141

Control was chili pepper in bare soil. Strip non-crop consisted in chili pepper with strip of non-crop plants; and Intercropped consisted of strip of weedy plants and intercropped weedy plants among chili pepper plants. *Ia* is an index of aggregation and *Pa* the associated probability, *vi* and *vj* are cluster indices and refer to patch and gaps, respectively. Indices are significant when $P < 0.05$. Significant indices and the associated probability values are shown in bold.

Table 7. Summary data of Spatial Analyses by Distance Indices SADIE analysis of Neuroptera populations colonizing chili pepper crop during 2012 season in different experimental plots (control, strip non-crop plant and intercropped).

Control

Sample Date	*Pa*	*Ia*	mean *vj*	mean *vi*	P(mean *vj*)	P(mean *vi*)
12/22/11	-	-	-	-	-	-
01/18/12	-	-	-	-	-	-
02/15/12	-	-	-	-	-	-
03/12/12	0.5255	0.919	-0.919	0.984	0.552	0.4326
03/23/12	0.4500	0.953	-0.957	0.925	0.4555	0.511
04/16/12	0.8344	0.822	-0.791	1,005	0.8131	0.1197
05/06/12	0.2767	1,090	-1,088	1,123	0.2733	0.2328
05/29/12	0.1896	1,227	-1,226	1,207	0.1935	0.2525

Strip Non-Crop

Sample Date	*Pa*	*Ia*	mean *vj*	mean *vi*	P(mean *vj*)	P(mean *vi*)
12/22/11	0.2501	1,182	-1.207	1.004	0.2242	0.2678
01/18/12	-	-	-	-	-	-
02/15/12	0.6612	0.87	-0.853	1,008	0.6601	0.2314
03/12/12	0.9705	0.676	-0.68	0.742	0.9626	0.9475
03/23/12	-	-	-	-	-	-
04/16/12	0.9746	0.69	-0.681	0.736	0.9757	0.9215
05/06/12	0.9198	0.791	-0.76	1.001	0.8951	0.3796
05/29/12	0.9170	0.788	-0.757	0.998	0.8764	0.4043

Intercropped

Sample Date	*Pa*	*Ia*	mean *vj*	mean *vi*	P(mean *vj*)	P(mean *vi*)
12/22/11	-	-	-	-	-	-
1/18/12	-	-	-	-	-	-
02/15/12	-	-	-	-	-	-
03/12/12	0.3779	1	-1.012	1.052	0.364	0.3469
03/23/12	0.5314	0.922	-0.925	0.873	0.5072	0.5805
04/16/12	0.425	0.976	-0.984	0.972	0.4179	0.4325
05/06/12	0.7054	0.839	-0.847	0.807	0.6819	0.7882
05/29/12	0	0	0	0	0	0

Control was chili pepper in bare soil. Strip non-crop consisted in chili pepper with strip of non-crop plants; and Intercropped consisted of strip of weedy plants and intercropped weedy plants among chili pepper plants. *Ia* is an index of aggregation and *Pa* the associated probability, *vi* and *vj* are cluster indices and refer to patch and gaps, respectively. Indices are significant when $P < 0.05$. Significant indices and the associated probability values are shown in bold.

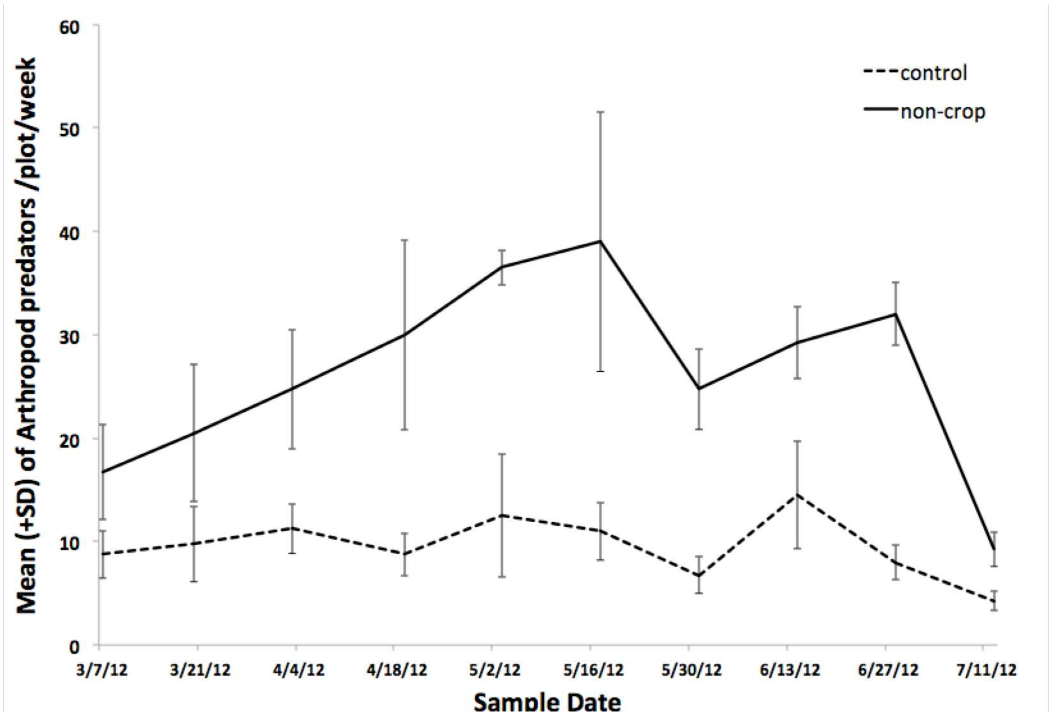


Figure 1. Mean (+SE) number of arthropod predators per plot (n=4) on chili pepper plots with strip of non-crop plants (non-crop) or bare soil (control) at different sample date recorded in Oratórios, Minas Gerais, Brazil.

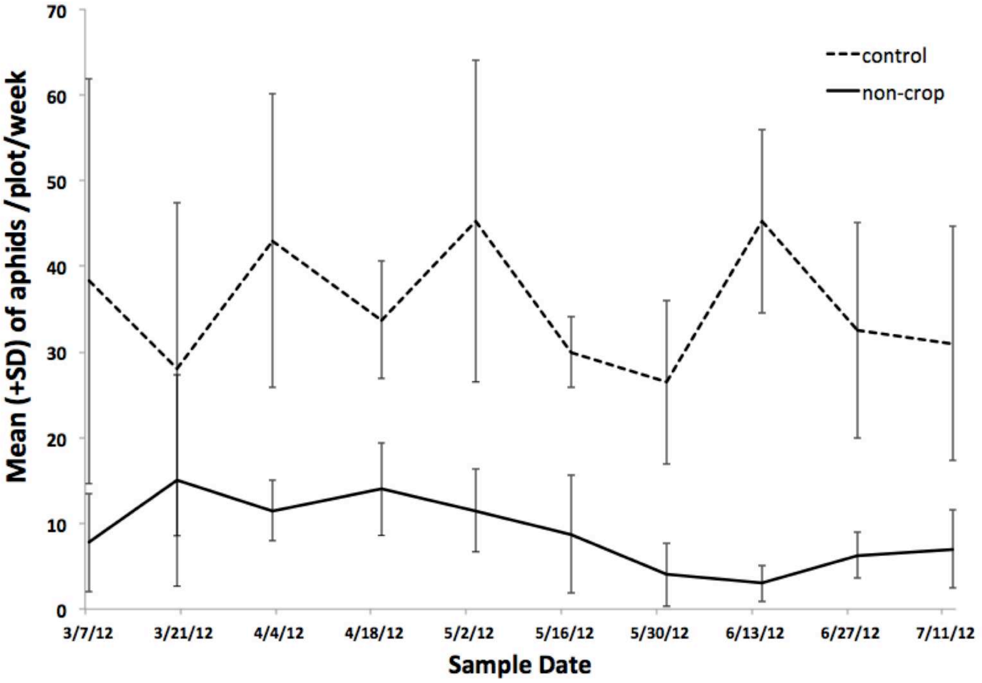


Figure 2. Number of aphids (mean ± SE) collected on 20 chili pepper plants per plot (n=4) with strip of non-crop plants (non-crop) or bare soil (control) at different sample date recorded in Oratórios, Minas Gerais, Brazil.

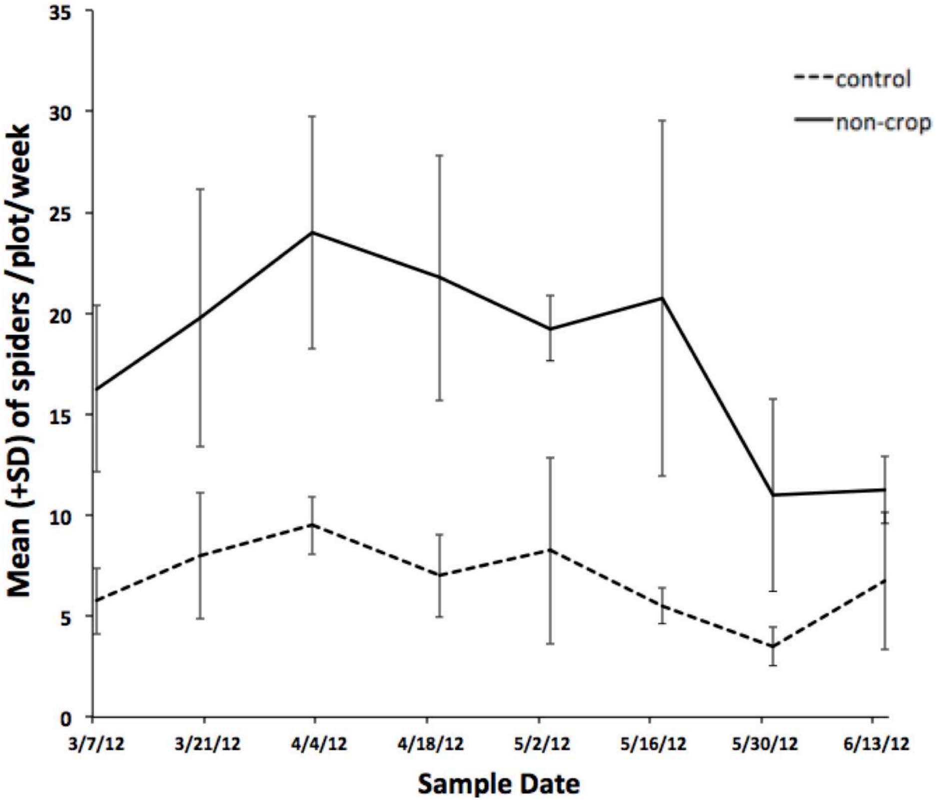


Figure 3. Mean (+SE) number of spiders collected on 20 chili pepper plants per plot (n=4) with strip of non-crop plants (non-crop) or bare soil (control) plant at different sample date recorded in Oratórios, Minas Gerais, Brazil.

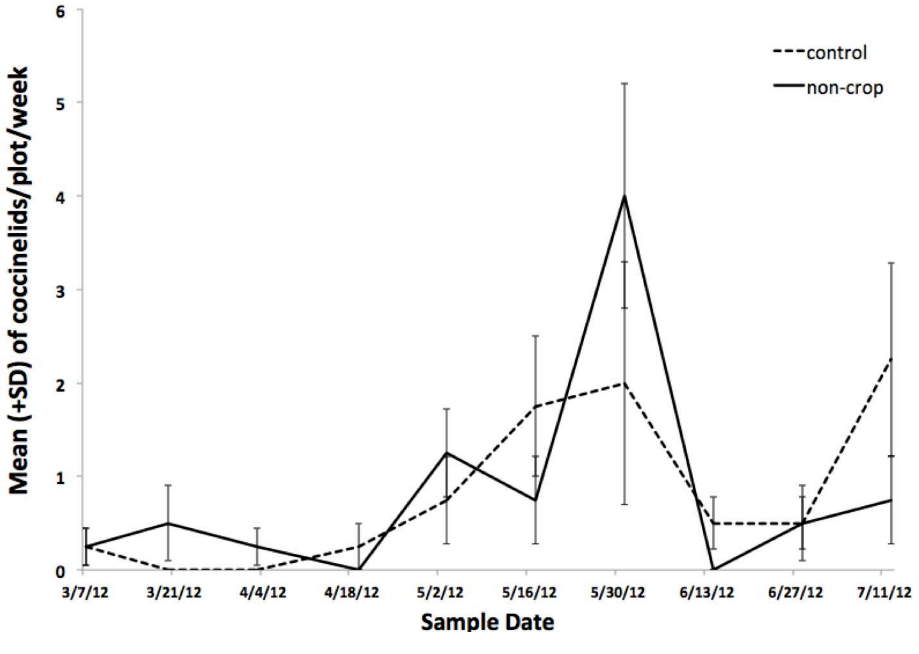


Figure 4. Number of coccinellids (Mean ± SE) collected in 20 chili pepper plants per plot (n=4) with strip of non-crop plants (non-crop) or bare soil (control) plant at different sample date recorded in Oratórios, Minas Gerais, Brazil.

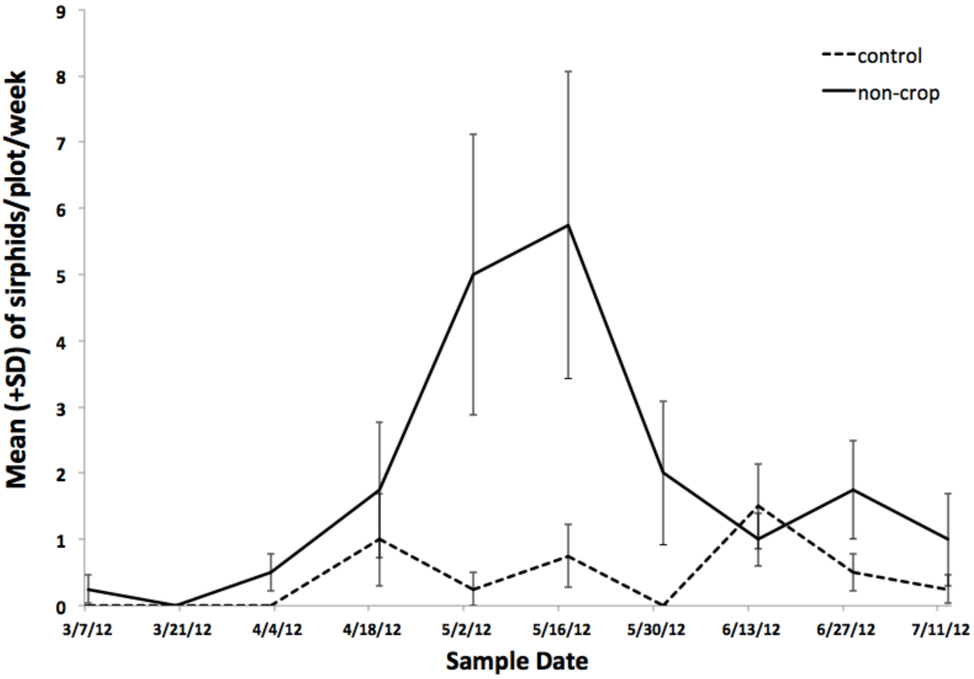


Figure 5. Number of sirphids (Mean ± SE) collected on 20 chili pepper plants per plot (n=4) with strip of non-crop plants (non-crop) or bare soil (control) plant at different sample date recorded in Oratórios, Minas Gerais, Brazil.

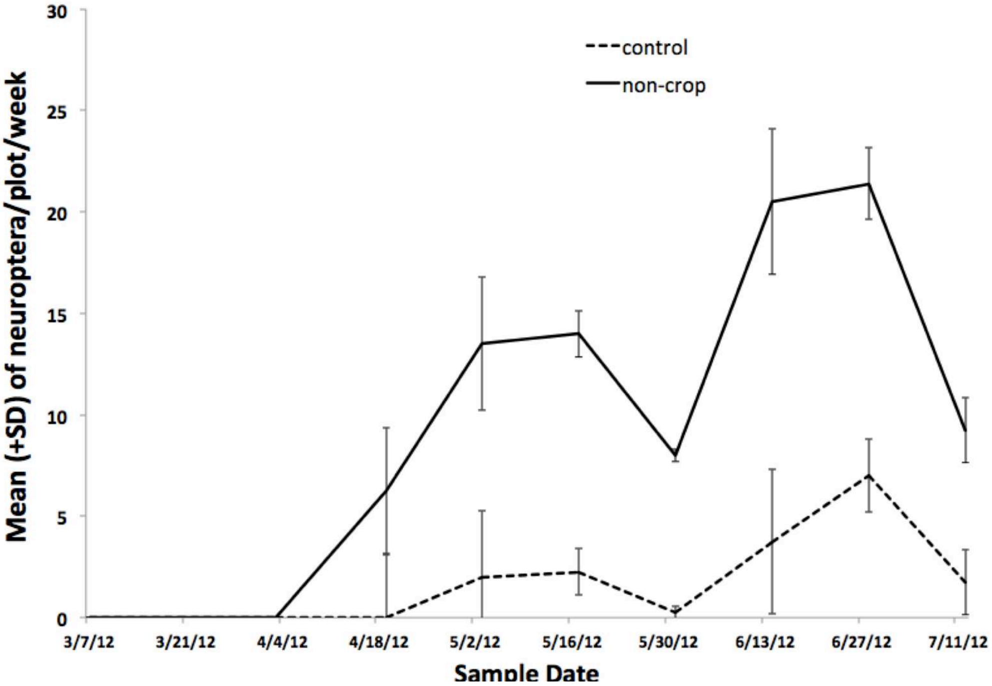


Figure 6. Number of coccinellids (Mean ± SE) collected on 20 chili pepper plants per plot (n=4) with strip of non-crop plants (non-crop) or bare soil (control) plant at different sample date recorded in Oratórios, Minas Gerais, Brazil.

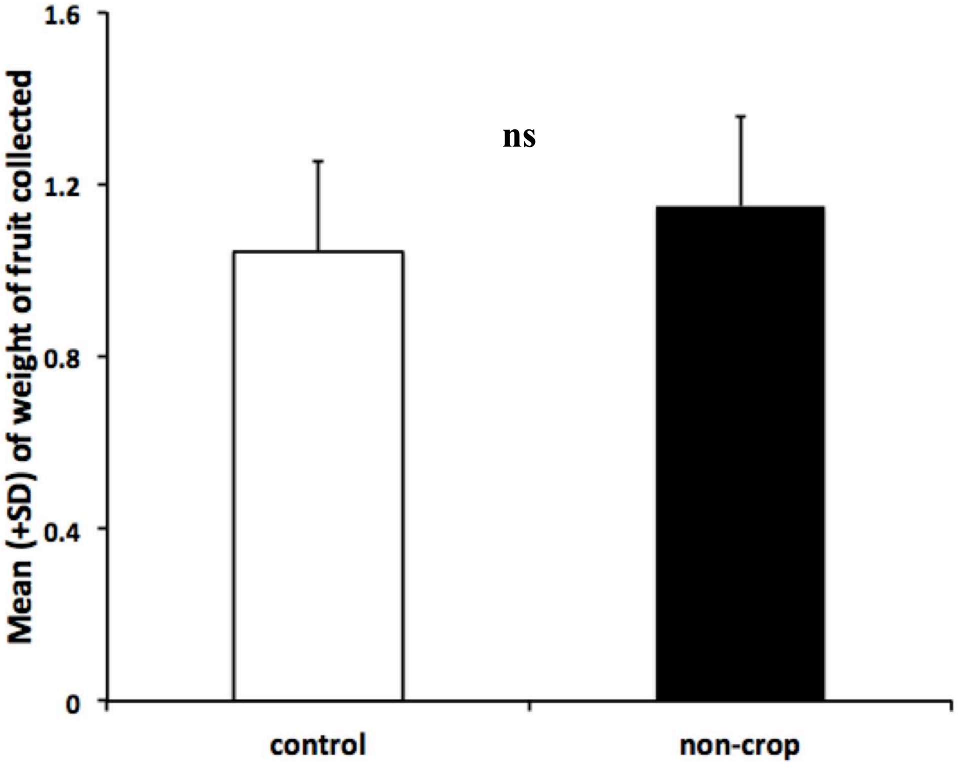


Figure 7. Mean (+SE) weight of chili pepper fruits collected of plants in experimental crop with strip of non-cro plants (non-crop) or bare soil (control). NS. Not significantly

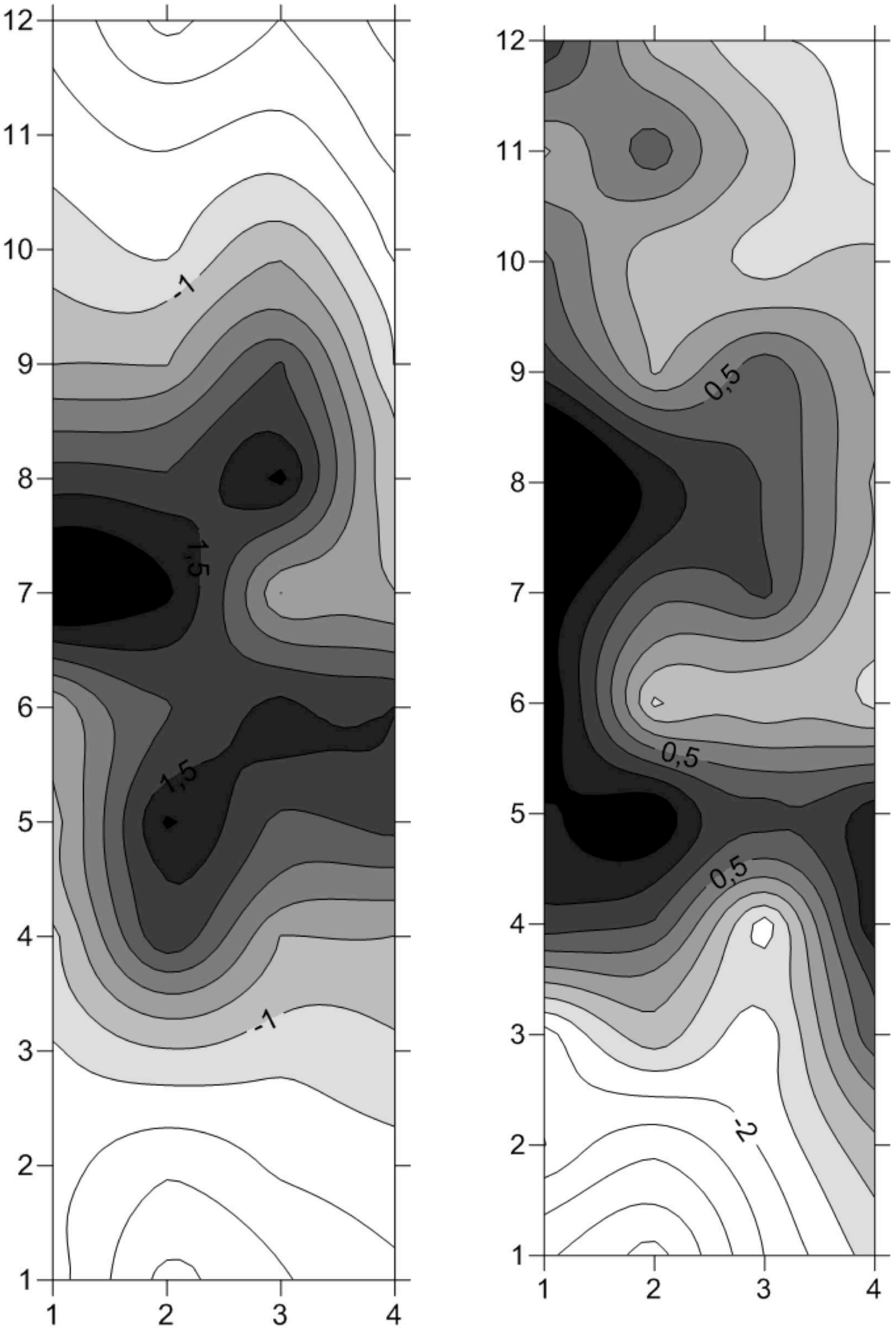


Figure 8. Sequence of contour maps of clustering index (*vi* and *vj*) for aphid populations during sampling dates 02/15/12 and 03/12/12 on strip of non-crop plants treatment, during chili pepper growing season. Lighter shading enfolds gap clusters ($vj < 1.5$); darker shading enfolds patch clusters ($vi > 1.5$). (strip non-crop plants - bottom position)

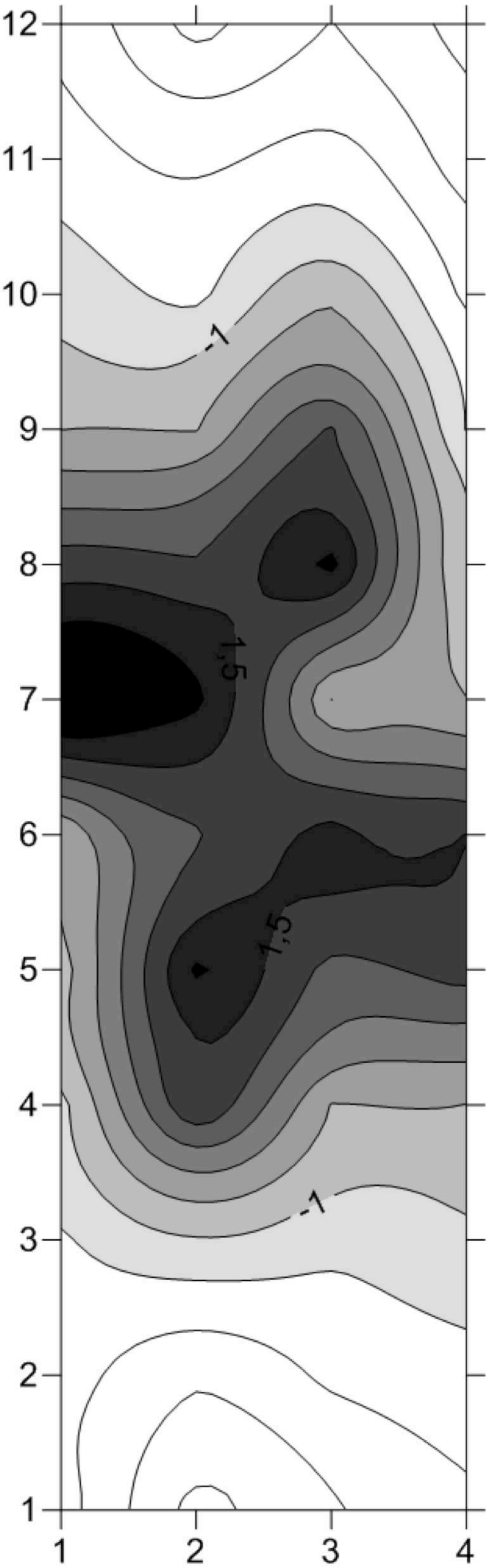


Figure 9. Sequence of contour maps of clustering index (*vi* and *vj*) for aphid populations during sampling date 05/29/12 on intercropped treatment, during chili pepper growing season. Lighter shading enfolds gap clusters (*vj* < 1.5); darker shading enfolds patch clusters (*vi* > 1.5). White areas represent boundaries between patch and gap regions where counts are distributed at random. (strip of non-crop plants - bottom position)

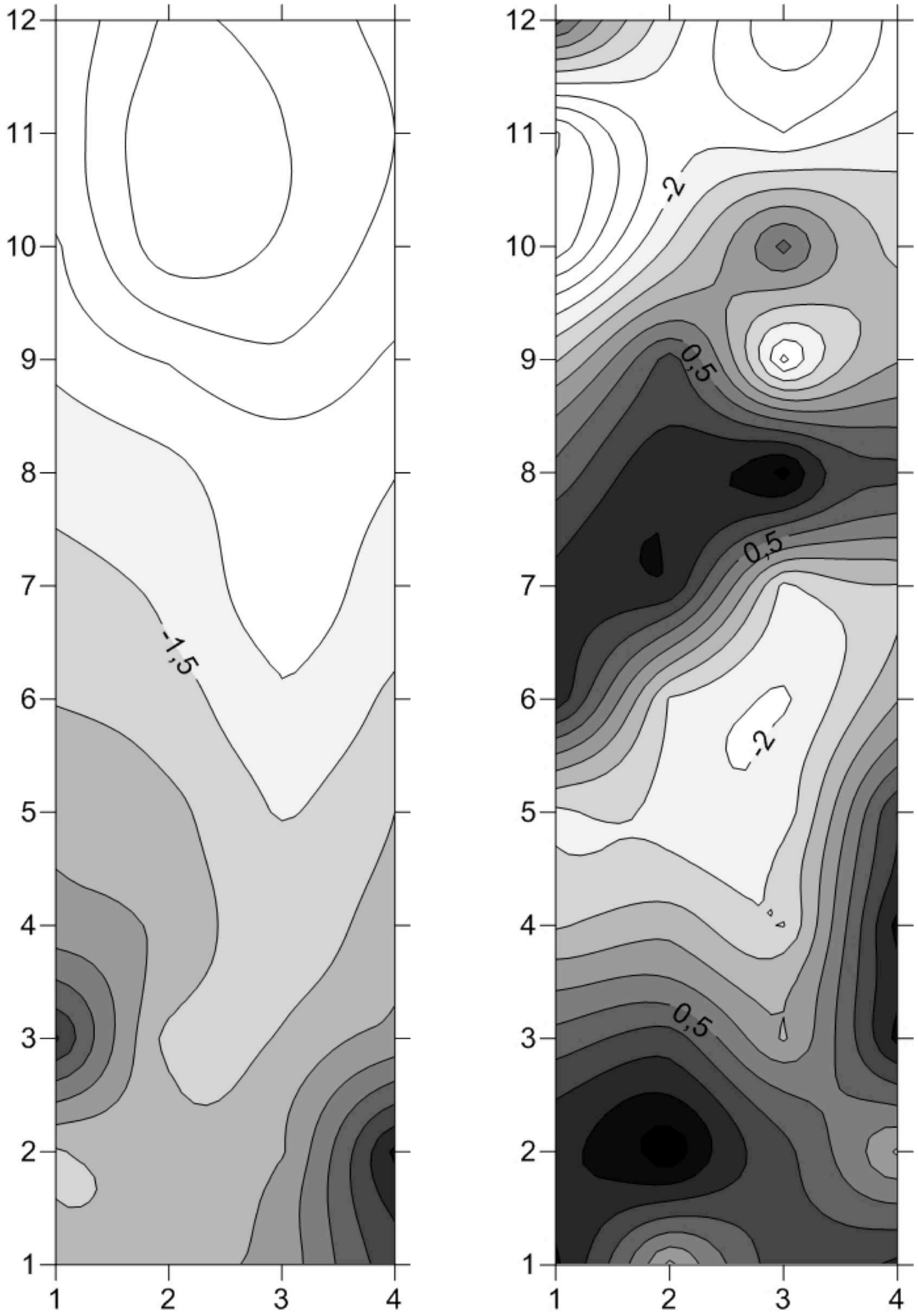


Figure 10. Sequence of contour maps of clustering index (*vi* and *vj*) for coccinelid populations during sampling dates 12/22/11 and 02/15/12 on strip non-crop plants treatment, during chili pepper growing season. Lighter shading enfolds gap clusters (*vj* < 1.5); darker shading enfolds patch clusters (*vi* > 1.5). White areas represent boundaries between patch and gap regions where counts are distributed at random. (strip of non-crop plants - bottom position).

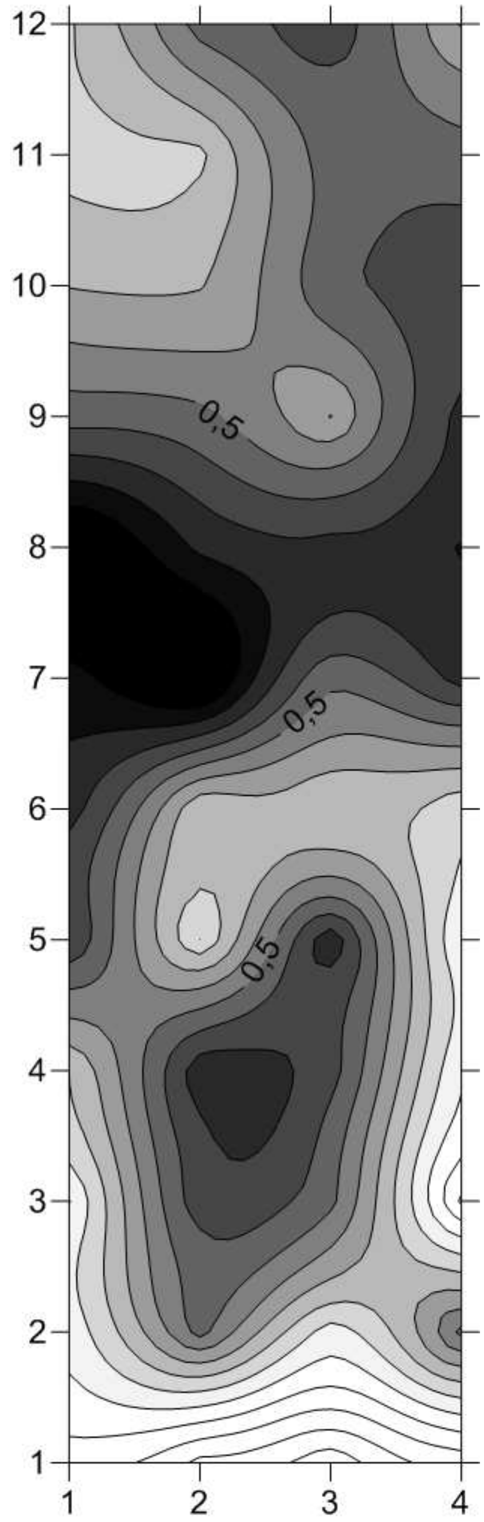
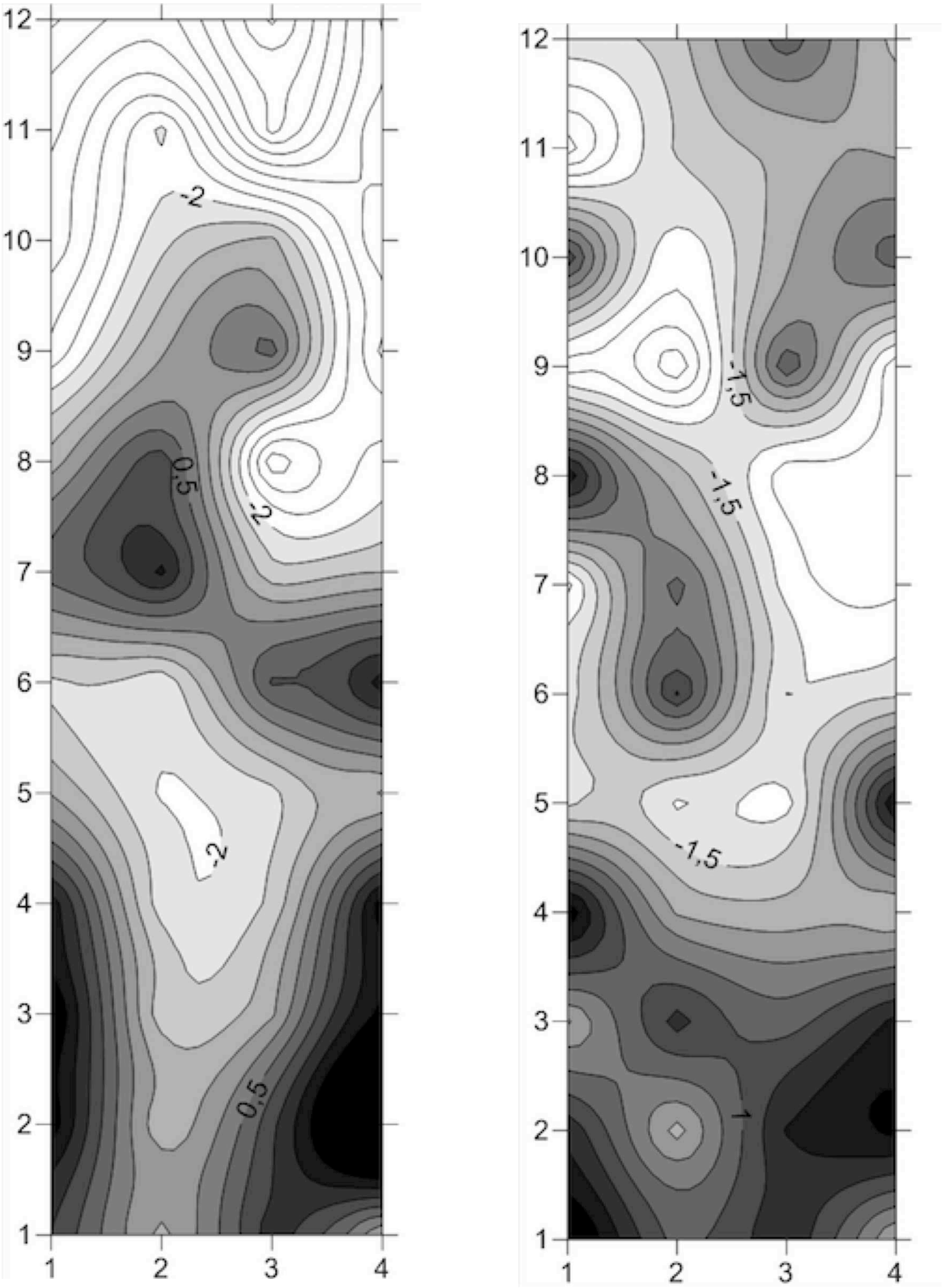


Figure 11. Sequence of contour maps of clustering index (*vi* and *vj*) for coccinelid populations during sampling date 03/12/12 on strip non-crop plants treatment, during chili pepper growing season. Lighter shading enfolds gap clusters (*vj* < 1.5); darker shading enfolds patch clusters (*vi* > 1.5). White areas represent boundaries between patch and gap



regions where counts are distributed at random. (strip of non-crop plants - bottom position)

Figure 12. Sequence of contour maps of clustering index (*vi* and *vj*) for coccinelid populations during sampling dates 02/15/12 and 03/12/12 on intercropped treatment, during chili pepper growing season. Lighter shading enfolds gap clusters (*vj* < 1.5); darker shading enfolds patch clusters (*vi* > 1.5). White areas represent boundaries between patch and gap regions where counts are distributed at random. (strip of non-crop plants - bottom position)

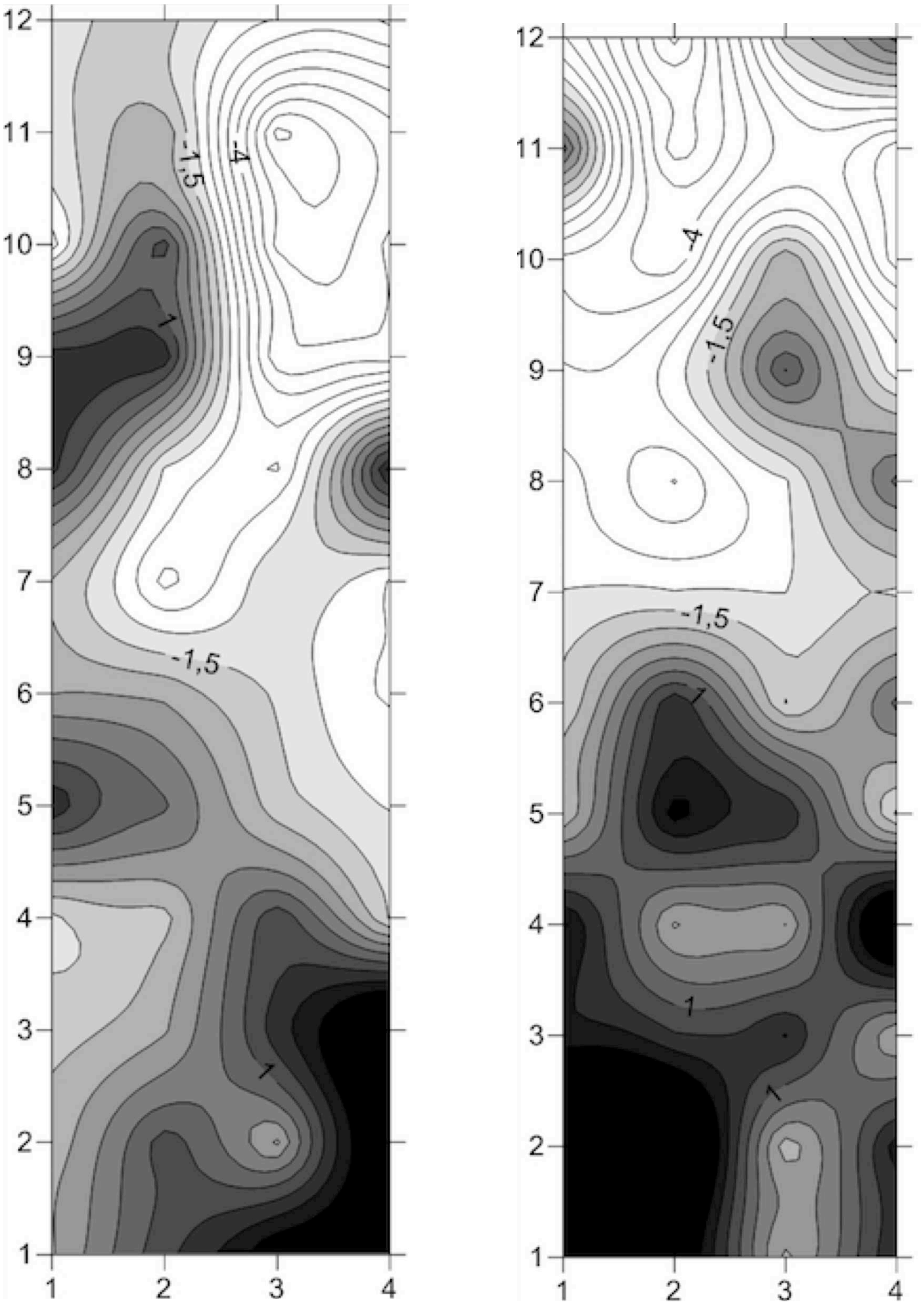


Figure 13. Sequence of contour maps of clustering index (*vi* and *vj*) for coccinelid populations during sampling dates 04/16/12 and 05/06/12 on intercropped treatment, during chili pepper growing season. Lighter shading enfolds gap clusters (*vj* < 1.5); darker shading enfolds patch clusters (*vi* > 1.5). White areas represent boundaries between patch and gap regions where counts are distributed at random. (strip of non-crop plants - bottom position)

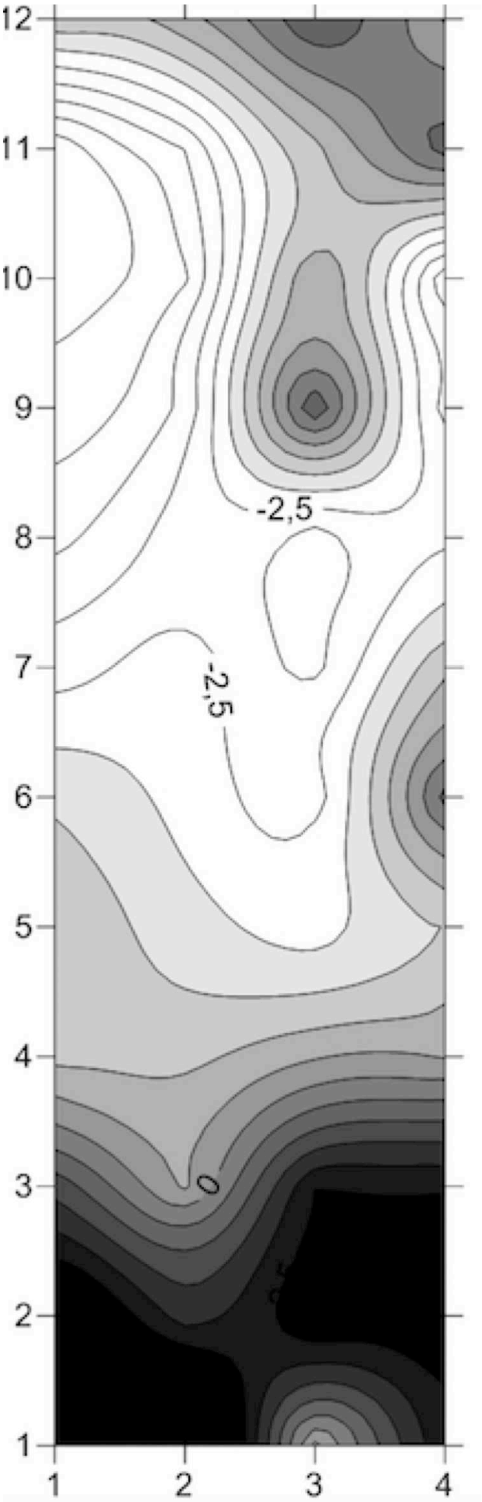


Figure 14. Sequence of contour maps of clustering index (*vi* and *vj*) for coccinelid populations during sampling date 05/29/12 on strip non-crop plants treatment, during chili pepper growing season. Lighter shading enfolds gap clusters (*vj* < 1.5); darker shading enfolds patch clusters (*vi* > 1.5). White areas represent boundaries between patch and gap regions where counts are distributed at random. (strip of non-crop plants - bottom position)

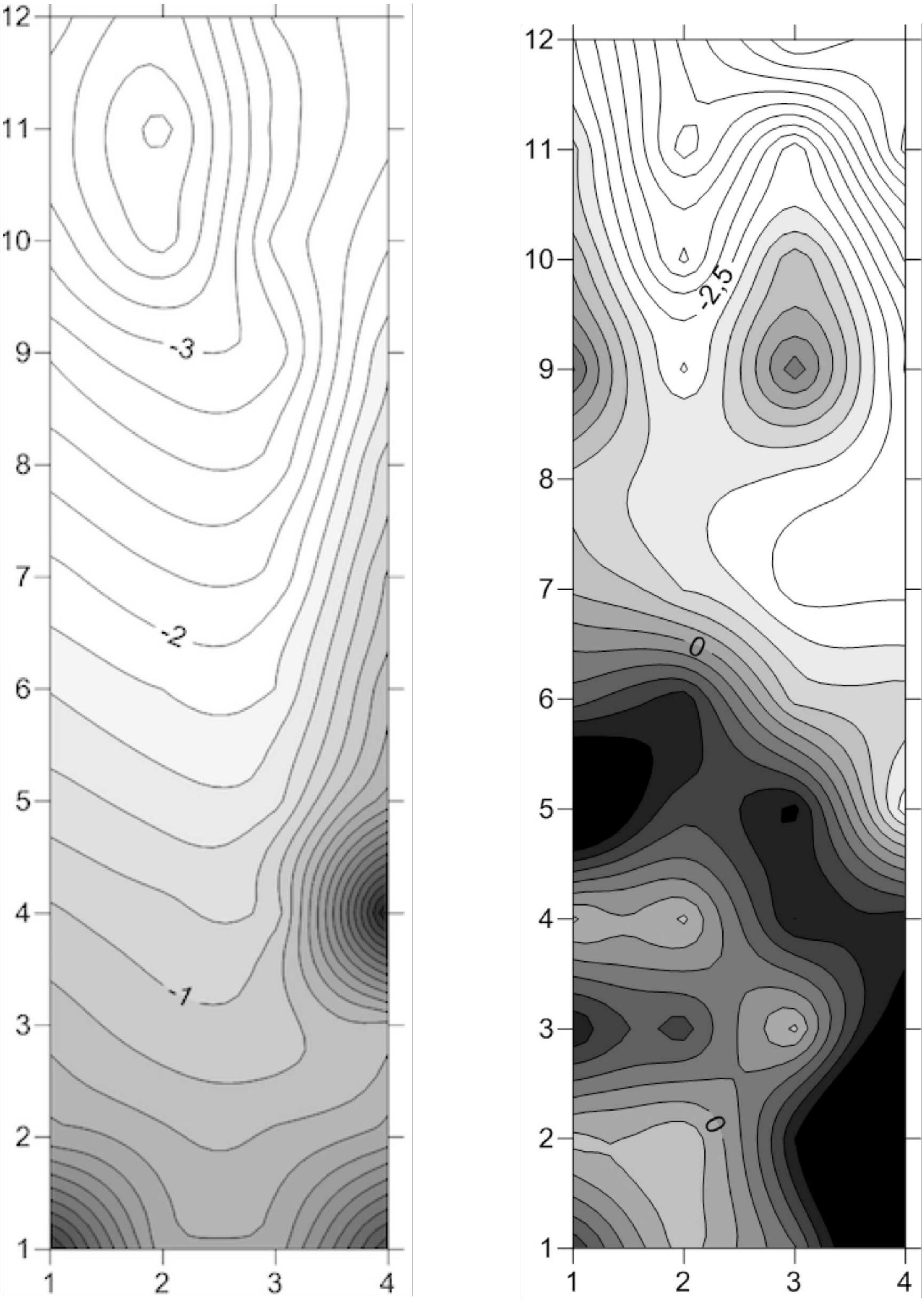


Figure 15. Sequence of contour maps of clustering index (*vi* and *vj*) for spider populations during sampling dates 01/18/12 and 02/15/12 on control, during chili pepper growing season. Lighter shading enfolds gap clusters (*vj* < 1.5); darker shading enfolds patch clusters (*vi* > 1.5). White areas represent boundaries between patch and gap regions where counts are distributed at random. (strip of non-crop plants - bottom position)

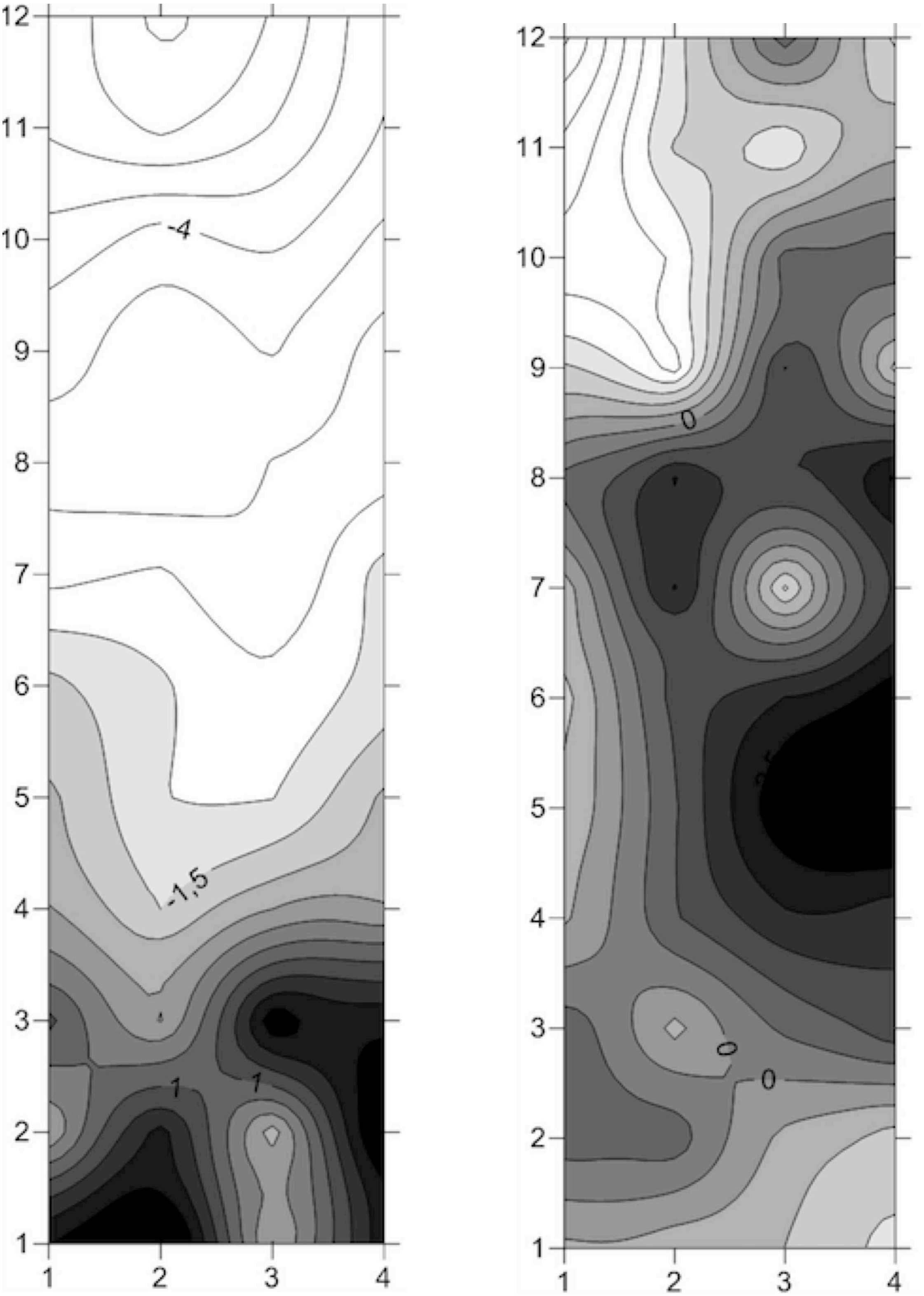


Figure 16. Sequence of contour maps of clustering index (*vi* and *vj*) for spider populations during sampling dates 12/22/11 and 05/06/12 on strip non-crop plants treatment, during chili pepper growing season. Lighter shading enfolds gap clusters (*vj* < 1.5); darker shading enfolds patch clusters (*vi* > 1.5). White areas represent boundaries between patch and gap regions where counts are distributed at random. (strip non-crop plants - bottom position)

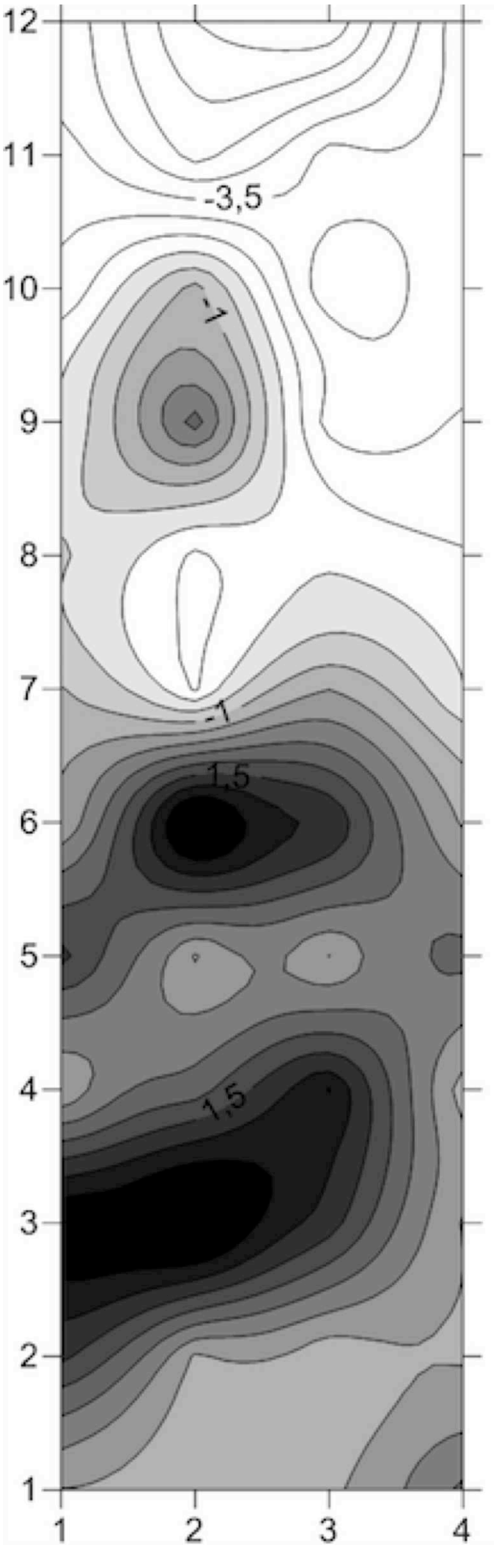


Figure 17. Sequence of contour maps of clustering index (*vi* and *vj*) for spider populations during sampling date 05/29/12 on strip non-crop plants treatment, during chili pepper growing season. Lighter shading enfolds gap clusters (*vj* < 1.5); darker shading enfolds patch clusters (*vi* > 1.5). White areas represent boundaries between patch and gap regions where counts are distributed at random. (strip non-crop plants - bottom position)

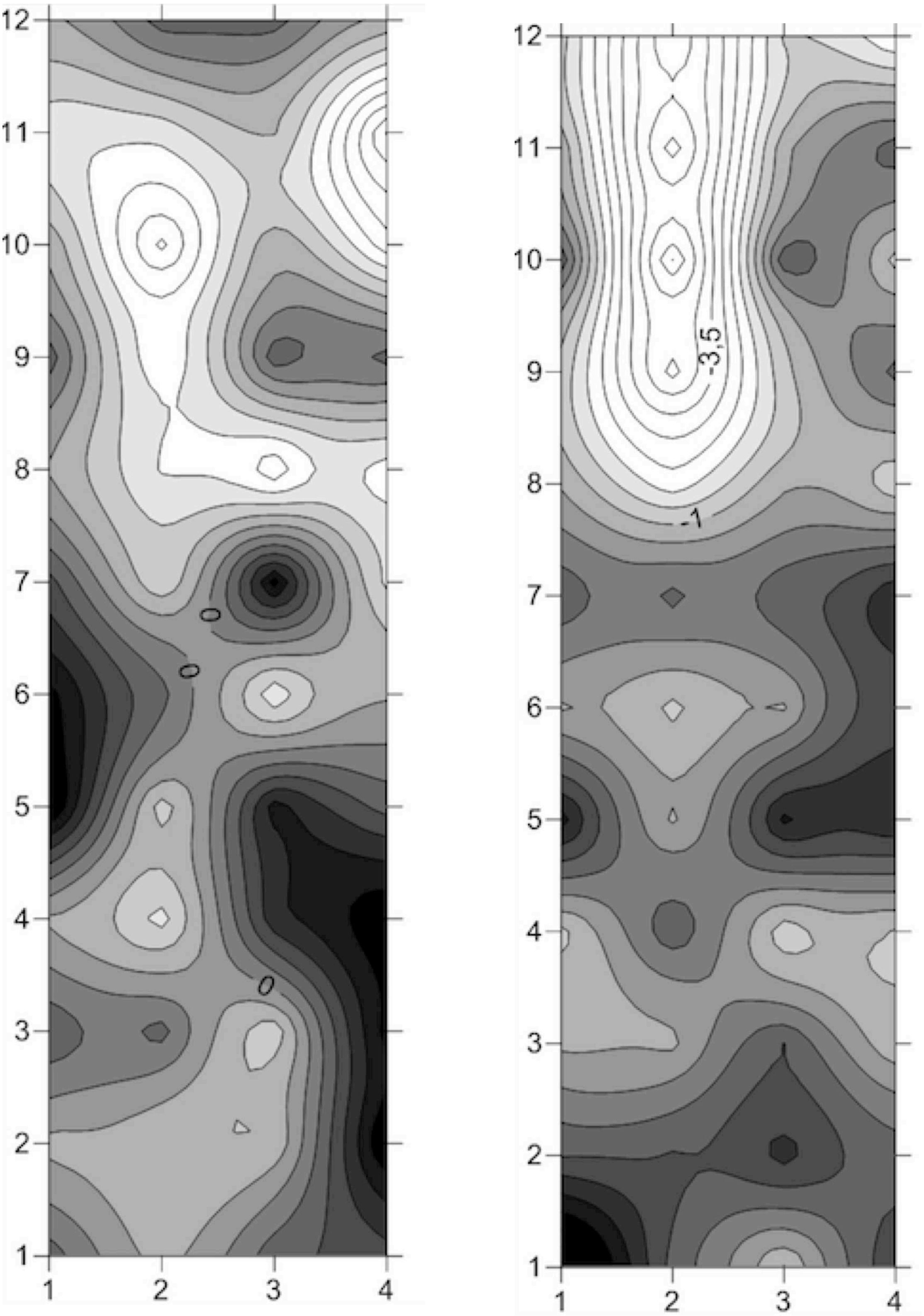


Figure 18. Sequence of contour maps of clustering index (*vi* and *vj*) for spider populations during sampling dates 02/15/12 and 04/16/12 on intercropped treatment, during chili pepper growing season. Lighter shading enfolds gap clusters (*vj* < 1.5); darker shading enfolds patch clusters (*vi* > 1.5). White areas represent boundaries between patch and gap regions where counts are distributed at random. (strip non-crop plants - bottom position)

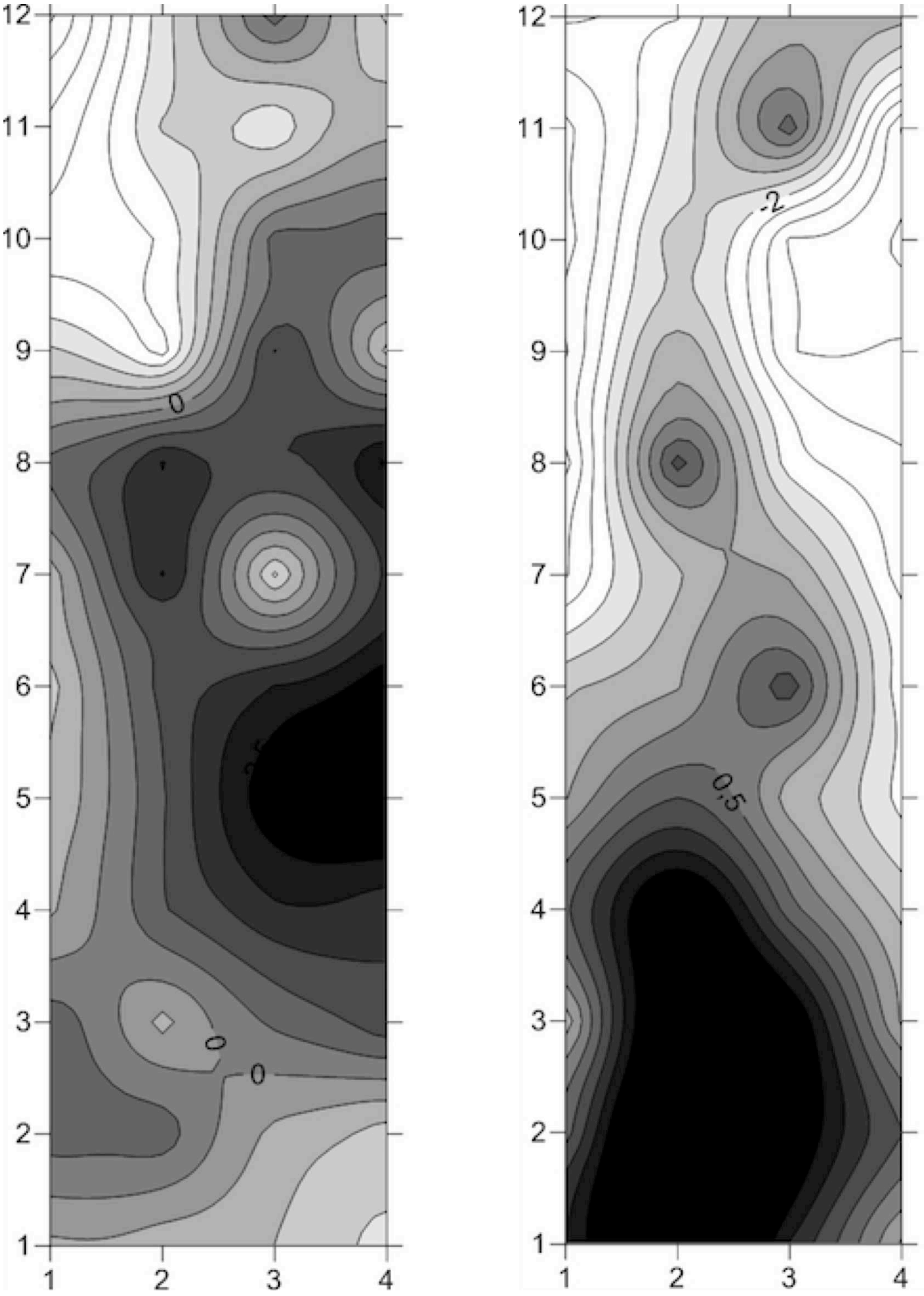


Figure 19. Sequence of contour maps of clustering index (*vi* and *vj*) for spider populations during sampling dates 05/06/12 and 05/29/12 on intercropped treatment, during chili pepper growing season. Lighter shading enfolds gap clusters (*vj* < 1.5); darker shading enfolds patch clusters (*vi* > 1.5). White areas represent boundaries between patch and gap regions where counts are distributed at random. (strip of non-crop plants - bottom position).

Chapter III

Non-crop plants influence spider communities in chili pepper agroecosystems

Abstract

Generalist arthropods predator as spider have potential to reduce herbivore populations. Spider diversity and abundance may be influenced by both the physical structure and complexity of their environment through the management of plants on agroecosystems. On chili peppers crop the management of non-crop plants may benefit different spiders group, by providing alternative food, shelter, and spatial structure to build webs. Here we examined association of non-crop plants and spider guilds with evaluation of differences in spider community on each non-crop plant species. We also compared the spider abundance and community structure in chili pepper systems with the management of non-crop plants. The non-crop plants abundance and spider families associated to each plant species were registered. We assessed also the spider functional groups found on non-crop plants and chili pepper crop. Additionally, the abundance of spiders was compared on chili pepper systems without and with non-crop plants. Our study found intrinsic association between non-crop plants and spider guild composition and abundance of spiders on chili pepper agroecosystem. The frequency of group of spider families was direct affected by presence and composition of non-crop plants. The composition of guilds was similar in natural and crop field with presence of non-crop plants. The abundance mean of spiders was also significantly higher on treatment surrounded with non-crop plants than chili pepper only. Our results suggest the strategic spider guild configuration may be manipulated by choose specific species of non-crop plants. Furthermore, even with risk of reduce crop productive, the association among crop and non-crop plants the increase of generalist predator abundance may compensate negative effects by improving the biological control of pests on agricultural systems.

Keywords: Conversation biological control, generalist predators, Araneae

1. Introduction

Generalist natural enemies play a fundamental role on biological control of pests mainly due to their behavioral and ecological characteristics (Riechert & Lockley 1984; Sunderland 1999; Symondson *et al* 2002; Stiling & Cornelissen 2005). The broad range of resources utilized by generalist predators may positively influence the building up of their populations in agroecosystems in early season, avoiding pest outbreaks (Langellotto & Denno 2004). Differently of specialist predators, generalist display a different range of foraging behavior that increases the chance to encounter potential prey (Symondson, Sunderland, & Greenstone 2002). In this context, the presence of generalist and specialist natural enemies may strengthen top-down control when they complement each other and more effectively control herbivore population (Letourneau *et al* 2009).

Spiders in annual systems are frequently the first arthropod predators to colonize new crop areas (Riechert & Lockley 1984; Öberg & Ekbom 2006; Royaute & Buddle 2012) and they exhibit a diversity of potentially complementary predation strategies (Marc, Canard, & Ysnel 1999; Hibbert & Buddle 2008). For instance, hunter spider as Salticidae family has acute vision and attack, usually resting prey (Jackson & Pollard 1996), while web spiders, as Linyphiidae, may complement pest capture when intercept insects that feel from foliage to ground increasing biological control (Sunderland, Fraser & Dixon 1986). Furthermore, the potential benefit of diverse predator communities is that the behavior of one species (e.g. actively pursuing prey) may facilitate prey capture by another species by changing the behavior of the prey (Sih *et al* 1998; Ives *et al* 2005). For agricultural systems, therefore, promoting a diverse group of spiders is likely to enhance pest biological control (Maloney *et al* 2003).

The enemy hypothesis (Root 1973) suggests that plant diversity promotes natural enemy diversity by providing multiple resources that increase attraction and maintenance of their populations in crop fields (Gurr, Wratten, & Luna 2003; Letourneau *et al* 2011). Consistent with this hypothesis, the promotion of spider colonization in agroecosystems may increase with plant diversity and habitat structural complexity (Langelloto & Denno 2004, Sunderland and Samu 2000). Habitat management to improve plant diversity occurs either within the crop fields or along field margins, or a combination (Corbertt 1998, Gurr *et al* 2003). Studies show that a variety of mechanisms may explain the attraction and maintenance effects of habitat augmentation on spider populations: (i) source to prey (Weyman & Jepson 1994); (ii) the presence of patches used as refuge against competitors or as alternative for oviposition (Finke & Denno 2002; Griffin & Yeargan 2002; Langellotto & Denno 2006); (iii) provision of complementary and supplementary food resources (alternative prey, pollen and nectar) (Lundgren 2009; Peterson, Romero, & Harwood 2010); (iv) access to favorable microclimate (Alderweireldt 1994; Chen, Chen, & You 2011); and (v) improvement of spatial structure that facilitate the web building, resulting in increase in prey capture (Robinson 1981; Maudsley 2000; Mcnett & Rypstra 2000). The association of the mechanisms of natural enemies enhancement may be important to promote the herbivore suppression, mainly in high-disturbed agroecosystems, such as chili pepper crops.

Chili pepper production is an economically important horticultural crop in several regions of World. More specifically, in Brazilian crops, the chili peppers are attacked by a variety of arthropod pest species (Venzon *et al* 2006, 2011). Growers may flack to develop an efficient pest management strategy because the chili pepper system is attacked by multiple pest species during different crop stages (Venzon *et al* 2011). Strategies to enhance beneficial arthropods may be the way to minimize the drastic reduction of chili pepper yield caused by pest attack. Moreover, finding sustainable management solutions for pest control is critical for development of agroecological systems.

A strategy widely adopted is to generate higher abundance of natural enemies by maintaining non-crop plant around or within crop fields to improve habitat structure and resource diversity (Altieri & Whitcomb 1978; Wyss 1995; Nentwig 1998; Norris & Kogan 2000; Gurr, Wratten, & Luna 2003; Norris & Kogan 2005). Despite the recognition that non-crop habitats improve abundance and diversity of natural enemies, little is known about the specific guilds associated with non-crop plants, and a scarcity of information is available to guide biological control efforts for Brazilian chili pepper production.

Our recent studies in chili pepper agroecosystems show that naturally growing non-crop on the borders of chili pepper fields has a positive effect on natural enemy abundance and survival (Amaral *et al* 2013). These authors documented the non-crop species associated with chili pepper crop, and the overall abundance of Araneae was reported. Here we examined the Araneae species collected in the prior study to determine specific associations of spider feeding guilds with non-crop plant groups. Spiders are a diverse group and are characterized by different guilds (Uetz *et al* 1999; Hofer & Brescovit 2001) and likely vary in their plant associations with non-crop habitat. We evaluated the potential for improving the recruitment of spider guilds to this system by promoting the growth of non-crop plants in and around the cultivated chili pepper field. Our experiments were designed to: (1) Characterize spider associations with non-crop plant species in Brazilian chili pepper agroecosystems, (2) Evaluate differences of spider community on each non-crop plant species, (3) Compare the spider community structure in chili pepper and non-crop plants, and (4) Examine the effects of non-crop plant management strategies on spider abundance and community structure.

2. Material & Methods

2.1. Characterization of spider communities associated with non-crop plants found in chili pepper system

The spiders were collected from non-crop plants adjacent to chili pepper fields during all crop-growing season. Five chili pepper fields located in the county of Piranga (state of Minas Gerais, Brazil, GPS coordinates 20º 45'45'' S, 43º 18'10'' W) were selected and sampled every two weeks across the primary growing season (March-

August 2010). The sampling for overall crop season was done to collect spiders in different species of non-crop plants that usually vary during time. Thus, the data were pooled over this period to form a more complete estimate of association between spiders and crop plants. Chili pepper fields were selected based on their similarity in size (~ 1 ha) and small farm agricultural practices. All fields were separated by at least 2 km. In Brazil, chili pepper agroecosystems are managed by smallholder (between 1 a 10 ha). The fields are managed using manual tools (e.g. hoe, sickle, rake etc.). Therefore, there is minimal tillage, with low disturbance of the soil, because mechanized tools and tractors and cultivation equipment are not used. There is low use of external inputs and more use of organic fertilizers and few cropping systems, crop rotations. No pesticides were applied throughout the experiment.

To analyze the specific associations of non-crop plant species and spiders families, spiders were extensively sampled from non-crop habitats. This sampling approach incorporated assessment of non-crop plant species identity and density within a field border strip and strips that transected the chili pepper field (Amaral *et al* 2013). Total abundance of non-crop plant species was characterized using 0.25 m^2 quadrats (0.5 m X 0.5 m) from 20 randomly selected sites within and surrounding each chili pepper fields. Spiders present on non-crop plants were sampled using three 100 m transects per field. Transect started within the non-crop field border, crossed perpendicularly the field, and finished in the opposite non-crop field border. Transects were perpendicular to chili pepper plant rows. To quantify spider abundance, we walked through the transect documenting each non-crop plant species and recording the number of spiders observed on each plant. Additionally, on each transect five chili pepper plants were selected to collected spiders found on foliage.

To compare the composition of the spider communities collected from the non-crop plants, similarities among the non-crop plants were analyzed by partitions dissimilarities for the sources of variation using packages *vegan* in R version 2.15.3 (R Core Team 2013). Data were pooled from all collected spider families collected in non-crop plants. The significance of similarities was tested using a multi-response permutation procedure and non-metric multidimensional scaling for within- versus among-plant dissimilarities (Oksanen 2013). We examined the effect of non-crop plant species on spider communities using Constrained Correspondence Analysis (CCA), followed by ANOVA-like permutation tests (n = 2000) to assess significance of effects. Additionally, in order to investigate the dissimilarity of spider community between non-crop and chili pepper plants Constrained Correspondence Analysis (CCA) was used. To understand the overall structure of the spider guilds in non-crop and chili pepper plants, spiders were classified in guilds according to their hunting strategy, following Uetz *et al* (1999) and Hofer & Brescovit (2001). Thus, we grouped spider families into the following five major guilds: 1) orb weaver; 2) space weavers; 3) ground weavers; 4) foliage runners; and 5) ground runners.

2.2. Effects of non-crop plant management on spider communities in chili pepper crop

Two experiments were conducted, one at Piranga county field site, and a second experiment at the Oratórios field site. The Piranga experiment was designed to examine the spiders in different non-crop plant management, and the Oratórios experiment was designed to examine the effects of non-crop habitat over the season on abundance spiders on chili pepper plants.

Piranga experiment. Spiders were collected on strips of non-crop and chili pepper plants from three experimental plots on December 2011 to May 2012 (*i.e.* period between seedling transplant and harvest). A chili pepper field was installed at experimental area located on a small farm. The experimental area was divided in three plots with 15 X 40 m each one. The chili pepper plants were spaced at 1 m within a row and between rows. Each plot received one of the following treatments: (i) control, chili pepper plants in bare soil; (ii) strip, chili pepper with non-crop plants strip outside crop area, (iii) intercropped, chili pepper non-crop plants strip on both outside and inside of plot area. To maintain control plots, the area around (at least 50 m apart) the field and the area between chili pepper rows were weeded using manual equipment. The treatments with non-crop plants strip consisted of 15 x 10 m area attached to a face of experimental plot. The other faces (at least 50 m apart) and inside chili pepper lines were kept without non-crop plants. Intercropped experimental plot contained a non-crop strip outside the plot (15 x 10 m) and non-crop plants among chili pepper lines. The non-crop plants were separated from the chili pepper rows by 0.25 m with bare soil. The other plot faces were maintained in bare soil by using mechanic tillage when necessary, at least 50 m around the experimental plot.

In all experimental plots, every 3-meters, two chili peeper plants were sampled by beating the foliage over a collection tray (96 plants/plot). All spiders were aspirated by mouth into vials with 70% ethanol and returned to the laboratory for identification. For each experimental plot, it was sampled nine times (23 December 2011, 19 January 2012, 16 February, 13 March, 24 March, 17 April, 07 May and 30 May 2012). Samples were pooled for the season to view the overall pattern of spider populations associated with different treatments. The dissimilarity of spider community between treatments was used Constrained Correspondence Analysis (CCA). Additionally, spiders were classified in guilds according to their hunting strategy (Uetz *et al* 1999; Hofer & Brescovit 2001) for understanding the overall structure of the spider guilds in response to treatments.

Oratórios site experiment. The experiment took place during a growing season from February to July 2012 at Experimental Station of EPAMIG located in Oratórios (Minas Gerais, Brazil, GPS coordinates 20^o 25’ 05” S, 42^o 48’ 08” W), state of Minas Gerais, Brazil. Chili pepper seedlings were transplanted to 10 x 10 m plots (100 per plot). Plants were spaced at one meter within a row and between rows. Here, we compared the effects of presence and absence (control) of non-crop plants on spider abundance. Control plots consisted of chili pepper plants weeded with mechanical and manual equipment to maintain bare ground between rows and a 20 m width bare ground area around the plots. The experimental plot consisted of chili plants and a 3 m non-crop plant border. Inside of chili pepper plot soil was maintained bare. Four replicates of each treatment were done in a randomized design and they were separated from each other by at least 20 m of bare ground that was maintained by periodic tilling.

Field sampling was done from early March to June. The samplings were carried out one month after transplanting. Every two weeks, 20 plants per plot were sampled beating foliage over a collection tray to ensure comprehensive sampling of the spiders. All spiders were aspirated by mouth into vials with 70% ethanol and returned to the laboratory for identification. To assess the effects of the presence of non-crop plants on spider abundance on chili pepper plants, a model was fit to mean number of spiders collected in chili pepper plants by using the GLM procedure (Poisson distribution). The R package (*rms*) was used to analyze of goodness-of-fit and dispersion of data.

3. Results

3.1. Characterization of spider communities associated with non-crop plants found in chili pepper system

The association of non-crop plants and chili pepper affected the spider community composition. A total of 40 species of non-crop plants were associated with chili pepper fields, and were dominated by 25 species, representing 75% of all non-crop present (Table 1) (adapted from Amaral *et al* 2013).

The spider community structure was significantly influenced by non-crop plant species (F Model = 2.0933, p=0.0043; Table 2), and non-crop plant species contained unique spider community (ANOVA-like permutation tests: $F_{1,11}$= 2.09, p =0.005; Figure 1). In total, we observed eight spider families distributed across the six spider feeding guilds. Spiders were most common on Asteraceae plants, but they were also observed on Lamiaceae and Poaceae plants (Table 2). Thirteen spider families were observed on chili pepper plants and non-crop plant sampling (Table 2). The more abundant families were Miturgidae, Salticidae and Oxyipidae, corresponding to 69.13% of spiders collected on chili pepper plants.

The spider community structure was significantly different when compared chili pepper and non-crop plants (ANOVA-like permutation tests: $F_{1,1}$= 2.49, p =0.005). The relative frequency of spider guilds was different in chili pepper areas as compared to non-crop plants (Fig 2). The frequency of spider guilds on chili pepper plants was 47.01 % to foliage runners, 22.89 % to space weavers, 10.45% to ambushers, 8.96% to stalkers, 5.47% to orb weaves and 5.22 % to ground runners. On non-crop plants we found 35.10 % to foliage runners, 14.57 % to space weavers, 19.87% to ambushers, 18.54% to stalkers, 10.60% to orb weaves and 1.32 % to ground runners. The foliage runners were the most common spider guild found in chili pepper plants (Fig. 2). However, incorporating non-crop plant borders and intercropped between the chili peppers increased stalker spiders to 19.04 % of the spider community when compared to control plots containing only chili pepper plants (6.21%).

3.2. Effects of non-crop plant management on spider communities in chili pepper crop

Piranga experiment. The spider community structure was not significantly different when compared the tree different experimental plots (ANOVA-like permutation tests: plants: $F_{1,2}$= 0.72, p =0.789). However, the frequencies spider guilds were different when was compared the treatments (Fig 3). The frequency of spider guilds on chili pepper plants was 51.16 % to foliage runners on control, 46.53 % on strip treatment and 38.88% on non-crop intercropped plot. Stalkers spiders represented of 19.04% of sampled individuals on intercropped plot, while control and strip of non-crop plants plot showed respectively 6.02 and 7.42%. Ambusher spiders were more common on intercropped experimental plot (15.07 %) than control (6.9%) and strip of non-crop plant plot (12.37%).

Oratórios experiment. Spiders were significantly more abundant on chili plots with non-crop plant strips than plots without non-crop strips (χ^2 =305, df = 1, P < 0.001) (Table 3, Fig. 3). Moreover, addition of non-crop plant strip enhanced spider density on chili pepper plants over the entire season (Fig. 3). The community structure of the spider families was similar between treatments, as indicated by relative abundance estimates in both treatments (Table 3).

4. Discussion

Our results showed evidence for association between different species of non-crop plants and spider families on chili pepper agroecosystem. Complementary, we found an increase of spider abundance in the presence of non-crop plants. Usually, studies have shown that spider are beneficiated by diversification of agroecosystems with non-crop plants (Wyss 1996; Rieux, Simon, & Defrance 1999; Sunderland & Samu 2000), although it is not clear the intrinsic relation between plants and arthropod. However, strategic habitat management requires knowledge of specific plants and plant species compositions that benefit natural enemies (Landis *et al* 2000). Increase of spider population may be related to numerous mechanisms that directly influence the arthropod populations. In the non-crop plants associated with chili peppers, we observed that the spiders were mostly inactive and were potentially using the plants for refuge or waiting for prey. Some specimens of Salticidae, Mituragidae and Oxypidae were observed actively feeding on herbivores (*i.e.* aphids found on *Ageratum conyzoides, Leunurus sibiricus* and *Sonchus oleraceus).* Thomisidae spiders were observed near or on these plant flowers. The intrinsic correlation between spider families and non-crop plant possibility, when we extrapolate to other crop systems, choose improve specie group of spiders predator by using more appropriate vegetation.

The frequency of group of spider guilds was direct affected by presence and composition of non-crop plants. In chili pepper plants almost 70% spiders observed were foliage runners and space weavers. When it was added non-crop plants to system, the most common spider guilds (70%) was composited of foliage runners, space weavers and ambushes spiders. The spider guilds may be influenced differently and in several ways according to both habitat and physical structure (Marc, Canard, & Ysnel 1999). For example, foliage runners and ambushers were higher in both tied and control shrubs than in clipped shrubs (Hatley & Macmahon 1980). Otherwise, orb weaver spiders were more abundant in areas with more open substrate and stalkers spiders population were affected positively by shrubs areas (Hatley & Macmahon 1980). On chili peppers, systems with non-crop plants equilibrated the frequency of guilds that may use different strategy to capture more potential prey. Plant diversity may create more balanced habitats or even communities than a chili pepper only and this impact positively on biological control. The efficiency on pest control is because natural enemies diversity and evenness increases niche complementarity and chance to capture prey (Crowder *et al* 2010). Pest biological control may be influenced positively due to higher functional diversity of spiders guilds (Nyffeler 1999). Complementary behavior as prey preference and foraging strategy successful increase pest suppression (Sunderland & Samu 2000). Web-building spiders in the strip-managed area may reduce the winged aphids that colonize crop fields (Wyss 1995). The control of aphids may be facilitated by ground-based predators generalist associated to natural enemies that foraging on leaves (Losey & Denno 1999). Chili pepper crop systems may be benefited by different spider guilds that capture aphids on complementary strategies, reducing impacts on chili pepper production.

In the Oratórios experiment the abundance mean of spiders was significantly higher when non-crop plants were associated to chili pepper plants. The presence of non-crop plants intercropped may stimulate field margin spider communities forward inside agroecosystem, mainly on micro-habitat scale (Cady 1984; Samu, Sunderland, & Szinetár 1999). However, the management of strip vegetation may cause spatial segregation between crop and non-crop plants, and affect pest control by spiders when spiders fail to move out onto the crop system (Riechert & Bishop 1990; Sunderland & Samu 2000). Although the manipulation of field edge with non-crop plants may fail to augment densities of spiders in the interior of large agricultural fields (Jmhasly & Nentwig 1995), the practice of improving plant diversity within fields reduces the distance between crop and refuge habitat (Thomas, Wratten, & Sotherton 1991). The management of non-crop plants may increase spider inside field crop improving colonization capacity. The presence of “source” habitat, using non-crop plant management, affects the amount and dispersion of spiders increasing their population size, specially to slow disperses species (Halley, Thomas, & Jepson 1996).

The non-crop plants population management may provide beneficial structural complexity for the spiders (Nentwig 1998; Samu, Sunderland, & Szinetár 1999; Schmidt *et al* 2005). There is a close positive correlation of abundance and richness of spiders combined with vegetation density (Baines *et al* 1998; Öberg 2007; Schmidt-Entling & Doebeli 2009). Balfour & Rypstra (1998) found that manipulation of non-crop plant density affected positively spider densities. The field margin management may provide permanent refuges or alternative food (Baines *et al* 1998), or substrate to building webs (Balfour & Rypstra 1998), to keep invertebrate on agroecosystems. The management of mulch and flowers has improved the densities of spider populations (Riechert & Bishop 1990). The presence of mulch may create appropriate microclimatic conditions because would provide the high humidity, reducing risk of cuticular water loss in spiders (Riechert 1999). Additionally, the management of flowers could attract pollinating insect that serve as alternative prey or even spider could use pollen as food resource (Riechert 1999; Peterson, Romero, & Harwood 2010). Although there was a risk that spiders would stay on non-crop plant and do not move to chili pepper plants, we observed that the density of spiders on these plants was higher with more plant diversity strip. Even at beginning of season, it was common found higher spider abundance on chili pepper associated to non-crop plants, maybe due to increase of alternative prey and suitable microclime. Spiders may choose colonize and concentrate on specific areas with higher prey presence (Harwood, Sunderland, & Symondson 2001).

In summary, this study showed that the association of non-crop plants, at level of plant species and at plant communities, with chili pepper plants affects the spider community composition. Although we observed spiders feeding on herbivores or waiting for prey on plant structures, it was not clear that sort of resources the vegetation may provide. Increase of spider population may be related to numerous mechanisms that directly influence the arthropod populations. Additionally, to understanding biological control process, further research is required to evaluate the temporal variation on spider community affected by non-crop presence, and the spider effects upon other arthropods predators in complex system. Ultimately, our findings highlight that studies of direct association among plants and beneficial arthropods is fundamental to building the right diversity for an efficient biological control.

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Table 1. Most abundant non-crop plants found within and around five chili pepper fields sampled in Piranga (2010), State of Minas Gerais, Brazil (adapted from *Amaral et al* 2013).

Scientific name	Common name	Family
Ageratum conyzoides	tropic ageratum	Asteraceae
Amaranthus sp.	amaranth, low	Amaranthaceae
Baccharis sp.	baccharis, eastern	Asteraceae
Bidens pilosa	beggarticks, hairy	Asteraceae
Blainvillea sp.	-	Asteraceae
Brachiaria decumbens	panicum, sprawling	Poaceae
Buddleja stachyoides	-	Scrophulariaceae
Chaptalia nutans	-	Asteraceae
Chloris sp.	windmillgrass	Poaceae
Commelina sp.	dayflower	Commelinaceae
Cyperus esculentus	nutsedge, yellow	Cyperaceae
Digitaria sp.	crabgrass	Poaceae
Emilia fosgergii	cupid's-shaving-brush	Asteraceae
Erechtites valerianifolius	burnweed	Asteraceae
Euphorbia heterophylla	poinsettia, wild	Euphorbiaceae
Galinsoga sp.	galinsoga	Asteraceae
Gnaphalium purpureum	cudweed, purple	Asteraceae
Hypochaeris radicata	catsear, common	Asteraceae
Leonotis nepetifolia	lionsear	Lamiaceae
Leonurus sibiricus	motherwort, siberian	Lamiaceae
Melampodium divaricatum	-	Asteraceae
Oxalis sp.	woodsorrel	Oxlidaceae
Senna obtusifolia	sicklepod	Fabaceae-Caesalpinioideae
Solanum americanum	nightshade, American black	Solanaceae
Sonchus oleraceus	sowthistle, annual	Asteraceae

Table 2. Characterization of spider families associated with specific non-crop plant species in chili pepper agroecosystem sampled on Piranga, Brazil (MG) over the growing season of 2010.

	Spider Families*								
Non crop plants	Mi	Ox	Ar	Tm	Sa	Te	Th	Pi	Observed spiders
Ageratum conyzoides	0	4	1	4	12	1	13	3	38
Leonurus sibiricus	15	1	1	5	6	1	1	2	32
Sonchus oleraceus	5	2	1	7	0	2	0	0	17
Melampodium divaricatum	0	4	3	1	1	0	4	3	16
Bidens pilosa	0	1	1	5	3	0	1	4	15
Blainvillea sp.	6	1	0	0	0	1	0	0	8
Senna obtusifolia	6	0	0	2	0	0	0	0	8
Buddleja stachyoides	2	1	1	0	1	0	2	0	7
Amaranthus spp	0	2	0	1	2	0	1	0	6
Baccharis sp.	0	2	1	1	0	1	0	0	5
Euphorbia heterophylla	1	0	0	0	2	0	0	1	4
Digitaria sp.	1	0		1	1	0	0	0	3
Chloris sp.	0	0	0	0	0	1	0	0	1
Observed spiders	36	18	09	27	28	7	22	3	

*Mi= Miturgidae; Ox= Oxypidae; Ar= Araneidae; Sa= Salticidae; Pi= Pisauridae; Te= Tetragnathidae; Th= Theridiidae; Tm= Tomisidae.

Table 3. Abundance and frequency of spiders collected on agroecosystems without border of non-crop plants and chili pepper experimental plots containing non-crop plants, sampled on Oratórios, Brazil (MG).

Spider families	**Chili pepper**	**% Frequency**	**Chili pepper with non-crop plants**	**% Frequency**
Miturgidae	69	26.23	165	28.49
Araneidae	39	14.82	92	15.89
Oxyopidae	30	11.41	69	11.92
Tomisidae	30	11.41	55	9.49
Theridiidae	20	7.60	47	8.12
Corinidae	11	4.18	13	2.24
Tetragnatidae	10	3.80	16	2.76
Mimetidae	6	2.28	5	0.86
Pisauridae	4	1.52	15	2.59
Scytodidae	2	0.76	4	0.69
TOTAL	**263**	**100**	**579**	**100**

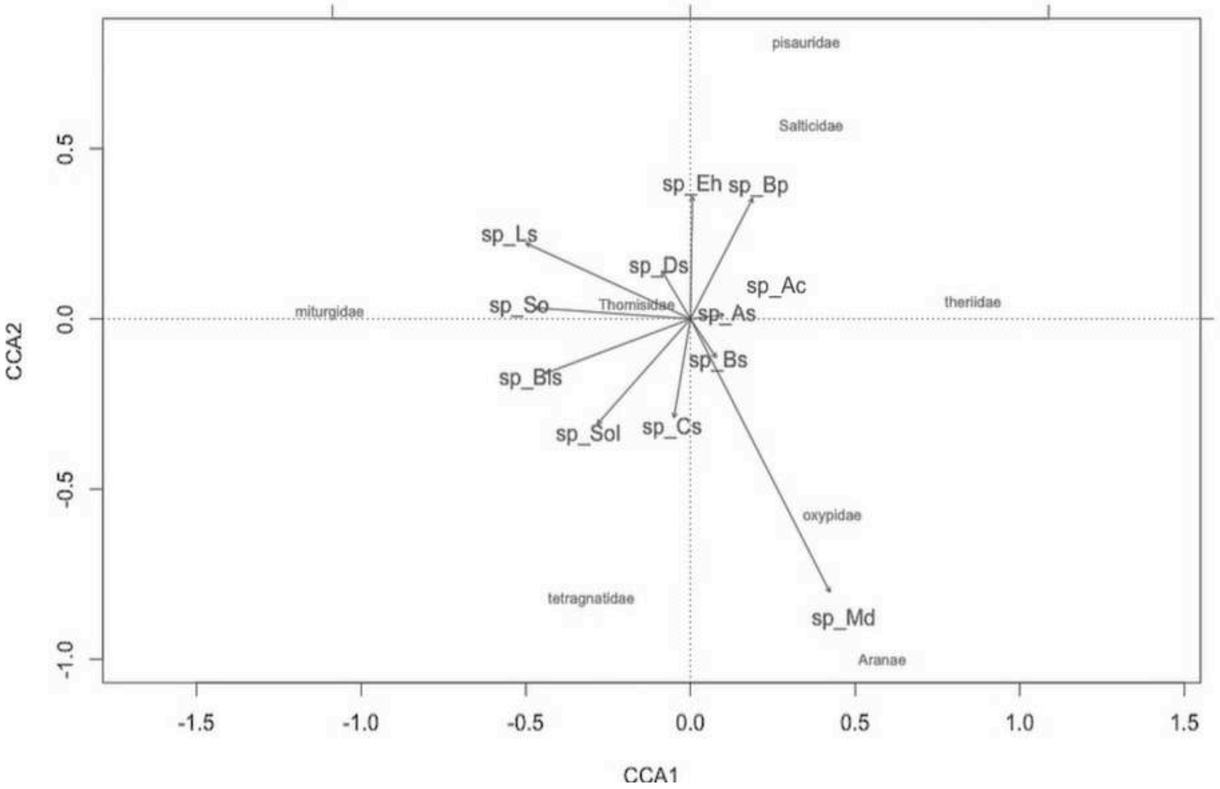

Figure 1. Canonical correspondence analysis biplot of spider community variation dependent on non-crop plant species. Ac= *A.* conyzoides, As = *Amaranthus* spp., Bp=*B. pilosa*, Bls= *Blainvillea* sp., Bs = *B. stachyoides*, Cs = *Chloris* sp., Ds = *Digitaria* sp., ES = *E. heterophylla*, Md= *M. divaricatum*, So = *S. obtusifolia*, Sol = *S. oleraceus.*

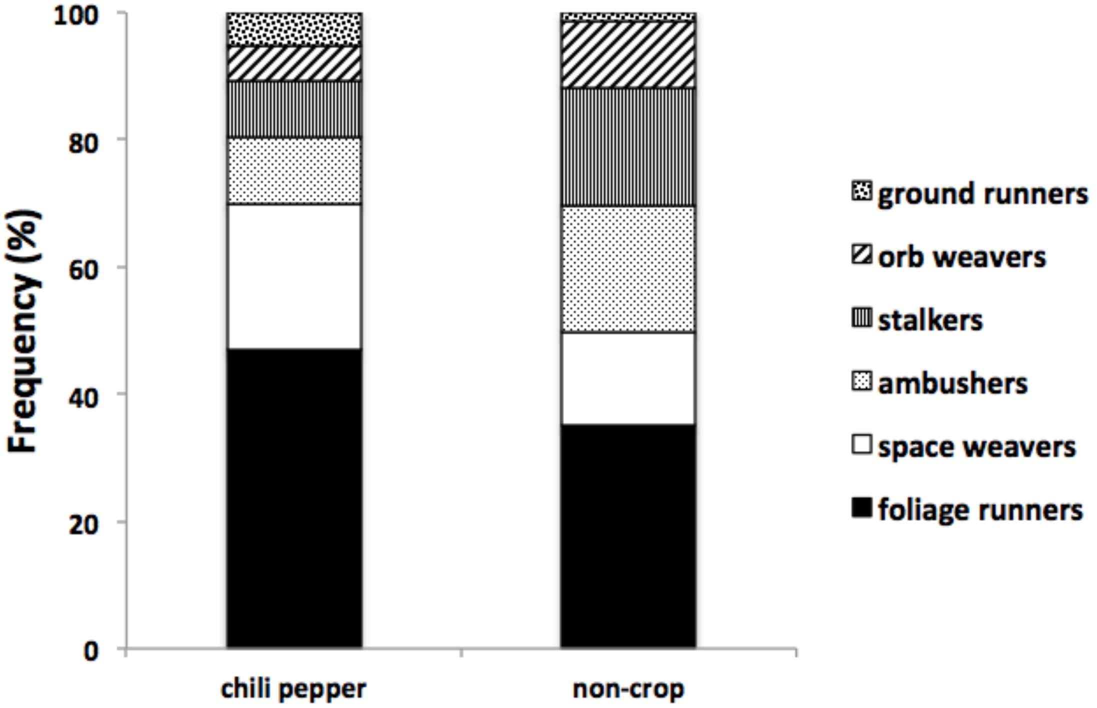

Figure 2. Spiders feeding guilds associated directly with bare soil chili pepper field and chili pepper field with non-crop plant border.

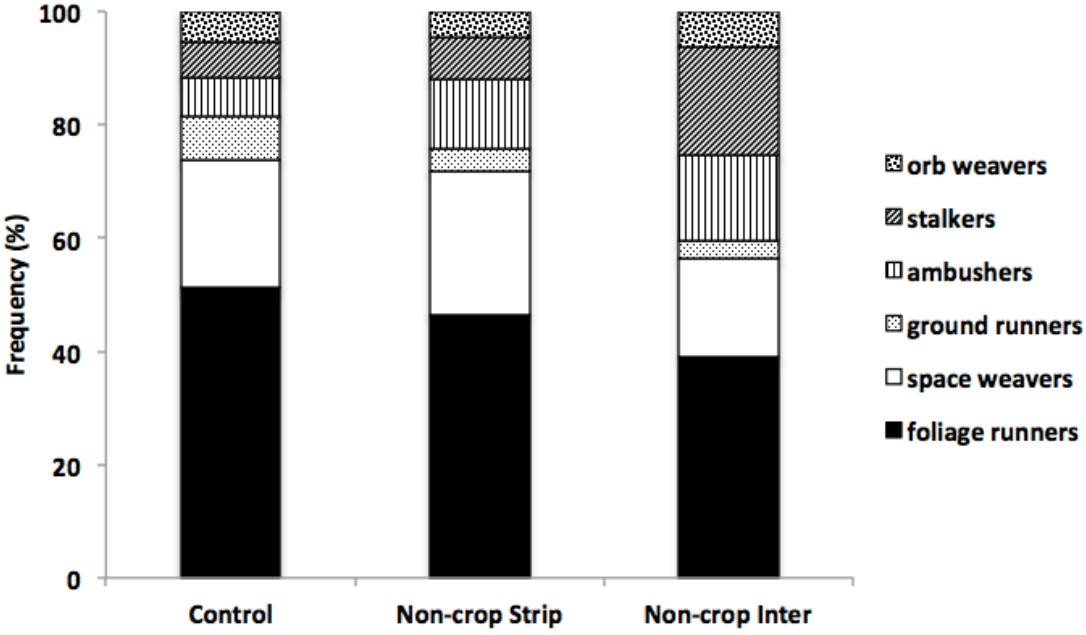

Figure 3. Comparison of spider feeding guilds under three different non-crop management approaches: control (non-crop plants removed), non-crop strip (non-crop plants allowed to grow in border strip adjacent to chili pepper rows), and non-crop inter (non-crop plants allowed to grow border strip adjacent and between the chili pepper rows).

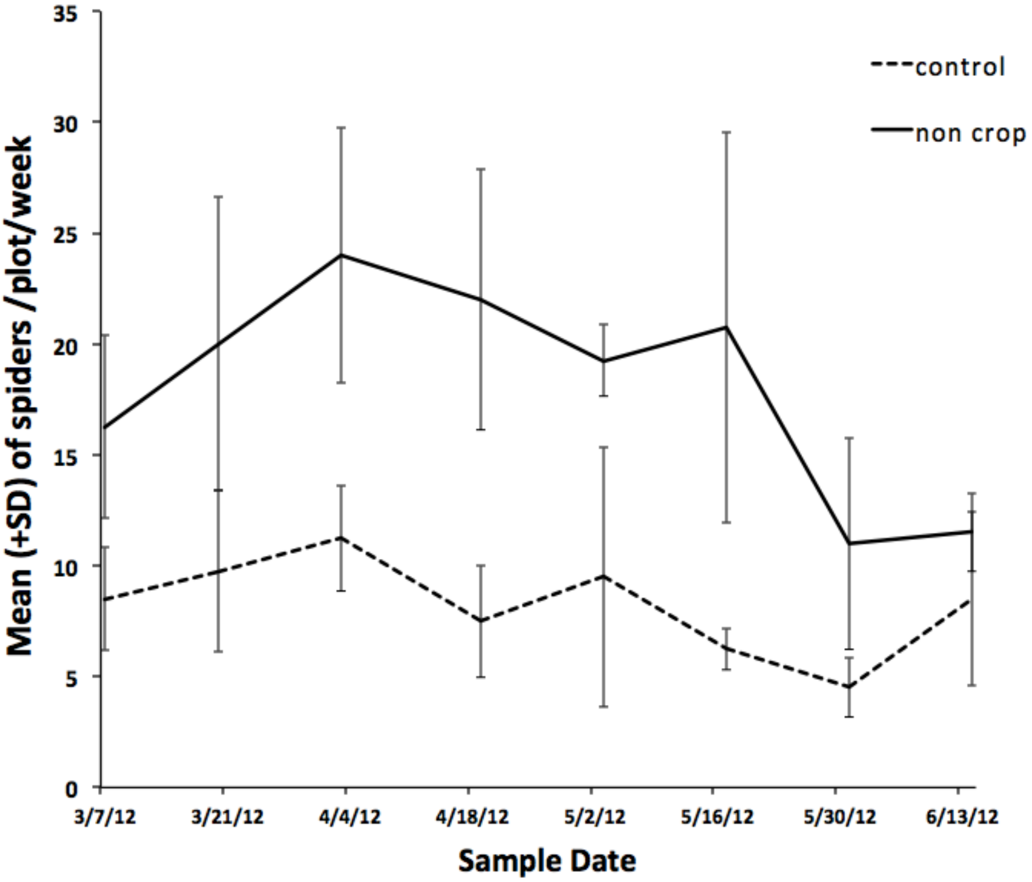

Figure 4. Mean abundance of spiders on bare soil chili pepper field and chili pepper field with non-crop plant border (Oratórios, Brazil, MG).

Chapter IV

Coccinellid interactions mediated by spatial plant heterogeneity

Abstract

Understanding the effects of environmental heterogeneity on agroecosystems is important for improving ecosystem services such as biological control and maintaining sustainable production systems. Promoting system diversity via non-crop plants could have numerous effects on the system driven by changes in spatial configuration and access food resources. In addition, arthropod predators pass through multiple life-stages that may benefit differentially from improved spatial structure. In this paper, we examined the effects of small-scale spatial structure on life-stage specific interactions between a native coccinellid *Hippodamia convergens* and exotic *Harmonia axyridis* species that overlap in their spatial distributions in many crop systems. Squash plants (*Cucurbita pepo* L) and non-crop mugwort (*Artemesia vulgaris*) plants with aphids present or absent were used as a model of spatial heterogeneity in micro and mesocosmos experiments. In response to factorial treatment combinations, we evaluated adult and oviposition behavior, egg intraguild predation, larval survival, and larval predator-prey and predator-predator interactions. The foraging and oviposition behavior of *H. convergens* was altered significantly on presence of spatial heterogeneity. Presence of non-crop plant reduced intraguild predation and competition between *H. convergens* and *H. axyridis.* The management of spatial heterogeneity may provide mechanism of spatial guild partition that mechanism to avoid negative interactions among coccinelids. Thus, the introduction or maintenance of attractive non-crop plants enhances the possibility of coexistence of multiple natural enemies and therefore improves top-down control of pests.

Key words: arthropod predators, foraging behavior, *Harmonia axyridis,* conservation biological control.

1. Introduction

Diverse communities of arthropods have been considered as more stable due to providing insurance against environmental fluctuations that diminish important species interactions (Murdoch 1975; Ives & Cardinale 2004). The insect community structure may be affected by interactions among organisms and environmental characteristics can reshape the these interactions (Hunter & Price, 1992, Haddad *et al* 2001, Hirzel *et al* 2007). For instance, habitat complexity, known as abundance of individual structural components (McCoy & Bell 1991), has been shown to influence predator-prey and predator-predator interactions (Root 1973; Langellotto & Denno 2004). At small spatial scales, habitat complexity can mediate agonistic interactions between predators, and at larger spatial scales contributes to observed increases in population densities of predatory arthropods and other natural enemies (Landis *et al* 2000; Langellotto & Denno 2004).

Generally, the habitat heterogeneity at small or large scales is primarily a function of the diversity of physical elements present in an area such as rocks, sticks, litter and plant species (McCoy & Bell 1991). A practice that has been widely adopted for habitat management in agroecosystems is the conservation of non-crop vegetation strips to promote colonization of beneficial arthropod populations (Altieri & Whitcomb 1978; Wyss 1995; Nentwig 1998; Gurr, Wratten & Luna 2003; Norris & Kogan 2005). In agroecosystems the species richness and abundance of predators is strongly affected by both landscape heterogeneity and farming practice (Bianchi, Schellhorn & van der Werf 2009). In addition, modifications to leaf litter presence, vegetation structure and plant diversity (e.g., associated to policultive, mulching technics, weedy cropping systems) affect the diversity of beneficial arthropods (Uetz 1991; Denno, Lewis & Gratton 2005) and biological control services provided (Dornelas *et al* 2009).

Multiple mechanisms are proposed to explain the effects of complex-structured habitats on the composition of natural enemies populations: i) higher abundance of prey (ii) alternative resource (pollen and nectar) iii) microclimate, iv) refuge against cannibalism and intraguild predation (Cottrell & Yeargan 1998; Landis, Wratten & Gurr 2000; Finke & Denno 2006; Robinson *et al* 2008). Although there is evidence that the improvement of spatial heterogeneity may reduce intraguild predation or cannibalism on diverse group as spiders, mites and heteropterans (Denno *et al* 2005, Janssen *et al* 2007), few studies explored the effects on coccinellids (Lucas, Labrecque & Coderre 2004). It is likely that non-crop habitats provide pollen and nectar as alternative non-prey food resources (Pemberton &Vandenberg 1993, Triltsch 1999, Lungreen 2009, Amaral *et al* 2013). In addition, non-crop plants may alter coccinelids anti-predator behavior or create refuge against the attack from other arthropods. Furthermore, cannibalism and intraguild predation occur at high levels during immature stages of coccinelids (Dixon 2000), and habitat heterogeneity has the potential to attenuate these interactions to improve biological control.

Recently, intraguild predation is observed to explain the negative impact of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) on native aphidophagous communities in invaded areas (Alyokhin & Sewell 2004; Pell *et al* 2008; Kindlmann, Ameixa & Dixon 2011). The invasion of *H. axyridis* has resulted in decline of native lady beetle populations by egg and larval predation (Gardiner, O'Neal & Landis 2011) (Fig. 1). Encouragingly, studies conducted on *H. axyridis* provide some evidence that increased habitat heterogeneity may enhance the potential for the coexistence of the exotic *H. axyridis* and native aphidophagous predators in invaded areas (Osawa 2011). Adult and larvae coccinelids may co-occur using different plant parts, and the arthropods may avoid direct interaction when the habitat became more structure and complex (Lucas & Broudeur 1999, Hoogendoorn & Heimpel 2004). Thus, the spatial structure may provide alternative oviposition site, improve anti-predator behavior and alter foraging efficiency (Janssen *et al* 2006; Lucas 2012)

Here we examined the effects of habitat heterogeneity (using non-crop plant) on life-stage specific interactions between a native coccinelid and the exotic, *H. axyridis* that overlap in their spatial distributions. Initially, we evaluated whether spatial heterogeneity mediated by non-crop plants reduces negative interactions between coccinelids. Squash plants infested by *A. gossypii* and non-crop plants *Artemisa vulgaris* were manipulated to alter spatial heterogeneity. The native coccinelid *H. convergens* was used as intraguild prey for the exotic *H. axyridis.* We evaluated the hypothesis that habitat heterogeneity influences coccinellid competition or predation (cannibalism or intraguild) by mediating interactions at multiple stages during the life history of these predators. The spatial heterogeneity may reduce adverse interactions between coccinelids on several life stages, by providing changes on environment and affecting the arthropods behavior. Specifically we explore the effects of habitat heterogeneity on: 1) adult foraging behavior, 2) oviposition behavior, 3) egg predation rates by an intraguild predator, 4) larval survival, and 5) larval predator-prey and predator-predator interactions.

2. Material & Methods

2.1. Field observations and study system

Field observations were undertaken in a cucurbit agroecosystem (*Cucurbita pepo* L.) at the University of Kentucky Horticulture Research Farm (South Farm) near Lexington, KY, USA (37°58'39" N, 84°32'03' W, elevation ~ 317 m). The most common non-crop plant in the border around the squash row was the mugwort *Artemesia vulgaris* (Asteraceae). In September of 2012, three-week-old, greenhouse-grown transplants were set into raised beds with 2 meters among plants with a non-crop weed border of 5 m. After two weeks, we observed aphid infestation and coccinelid presence. Over a three-week period we observed the aphid *Aphis gossypii* Glover (Hemiptera: Aphididae) attacking mainly new leaves of squash plants. We also observed aphids *Macrosiphoniella artemisiae* Boyer de Fonscolombe (Heteroptera: Aphididae) colonizing the mugwort border. Two coccinelids species were observed on both the squash plants and the mugwort border: *H. axyridis* and *Hippodamia convergens* Guérin-Méneville (Coleoptera: Coccinelidae). All coccinellid life stages were observed actively feeding on both aphid species, and adults were ovipositing on squash and on the mugwort.

2.2. Insect and plant material

In all experiments we used *H. convergens*, a common native coccinellid throughout the U.S. (Flint & Dreistadt 2005), as a model of intraguild prey. The *H. axyridis* was considered as intraguild predator because this species is considered an exotic insect that causes decline on native ladybird population (Pell *et al.* 2008; Sloggett 2012). Initial rearing of insects used in the experiments was started with field-collected insects from University of Kentucky Horticulture Research Farm in September 2012. Laboratory colonies of *H. axyridis* and *H. convergens* were maintained under in an environmental chamber at 22 ± 2° C and 16:8 (L:D) photoperiod, and to maintain humidity and available water sources, each dish received small cotton balls soaked with water. Larvae and adult coccinellids were fed daily *ad libitium* with the pea aphid *Acyrthosiphon pisum* (Sternorrhyncha: Aphididae) that was reared on fava beans *Vicia faba* plants (Variety: Windsor, Johnny's Select Seeds, Waterville, Maine); and with *A. gossypii* that was reared on squash plants, *Cucurbita pepo* (Variety: Yellow straight neck squash; W. Altee Burpee, Warminster, PA). Larvae coccinellids were kept individuality in aerated plastic dishes (10 cm diameter X 5 cm height) until pupation, and newly emerged adults were sexed and paired with the opposite sex from a different egg brood to allow for reproduction. Following oviposition adults were transferred to new Petri dish and the eggs cluster was kept isolated from either parent. Newly emerged larvae were individualized to avoid cannibalism and they were fed with *A. gossypii*.

Plant cultivation and the experiments were conducted in an environment-controlled greenhouse under natural incoming lighting and ventilation system to maintain the temperature at 23 ± 05 °C, 60 ± 5% RH and a 16L:8D with 16:8 h daily light:dark cycles. The squash plants seeds were cultivated in 128-cell trays as the host plants for rearing *A. gossypii* and used in experiments. To cultivate mugwort (*A. vulgaris*), seeds were collected from the UK Horticulture Research Farm and planted in similar trays. Two weeks after germination the seedlings were transferred to 10 cm-diameter plastic pots with organic substrate. Plants were placed in insect rearing cage, Bug dorms, mesh cages (MegaView Science Co., Ltd. Taiwan) measuring 60X60X60 cm to contain and separate mugwort plants infested or not with aphid *M. artemisiae.* No fertilizers or pesticides were applied to any plants at any time during the experiment.

2.3. Adult foraging behavior

In response to habitat complexity and intraguild predator treatments, we monitored the behavior of adult female of *H. convergens.* Behavior was observed on squash and non-crop plants within experimental microcosms. Each microcosm consisted of a plastic cylinder (20 cm diameter, 50 cm tall) covered with mesh screen cloth, and to avoid insect emigration and immigration, the cylinder was pushed down into soil approximately 2 cm and taped to sidewall of pot. Each microcosm was assigned to a treatment from a 2 x 2 factorial treatment design: 1) squash plant (s); 2) squash plant + one *H. axyridis* female (sH); 3) squash plant + mugwort plant (sN); and 4) squash plant + mugwort plant + one *H. axyridis* (sNH). The squash plants were standardized to be approximately 10 cm high, with two fully developed leaves. The non-crop plant, mugwort, was standardized to approximately 25 cm tall with no more than eight developed leaves. To provide a standard amount of food, approximately 10 aphids were transferred to each plant. On treatments with both plants, squash and non-crop plants were transplanted to the same pot and covered by the mesh vented plastic cylinder.

To initiate trials containing the intraguild predator, *H. axyridis*, we first introduced this beetle into the microcosm and allowed for a 20 min dispersal period, and then we carefully introduced *H. convergens*. We measured every 2 hours the response of *H. convergens* to treatment combinations by observing the position (i.e. bottom, middle, top) and behavior (i.e. eating, foraging, resting). The eating behavior was considered when the coccinelid was feeding on aphids or cleaning its mouthparts. Foraging behavior was registered when the insect was walking randomly on either plant or on plastic cylinder surface. Beetles observed without any movement were considered as stopping. The response variable was the frequency of position or behavior related to presence of heterospecific and spatial heterogeneity. Each treatment was replicated 10 times. All statistical analyses were computed using R 2.15.3 software (R Development Core Team

2013). Contingency tables were used to estimate position and behavior frequency of *H. convergens* in treatment with and without spatial heterogeneity (Quinn & Keough 2002). The experimental units (with or without spatial diversity) were considered as predictor variable and position (bottom, middle, top) and behaviors (foraging, eating, stop) were considered as the response variable. G^2-test distribution was performed to evaluate interaction between variable. To avoid problems of distribution associated with small sample sizes, we used William's correction (Logan 2010), running the package 'biology'1.0.

2.4. Oviposition behavior

In order to assess the influence of heterospecific species and spatial heterogeneity on the frequency and location of oviposition, we conducted an experiment in the same type of microcosms described above (i.e. see *Adult foraging behavior experiment*). The experiment consisted of *H. convergens* adult females exposed to intraguild predator treatments (presence and absence of intraguild predator cues from *H. axyridis*). All microcosms consisted of squash plants and mugwort plants transplanted together in the same pot and covered with the plastic cylinder (20 cm diameter, 50 cm tall).

To initiate trials with intraguild predator cues, three females of *H. axyridis* were released inside a microcosm for a 48-hour period. *Harmonia axyridis* were then removed, and one adult female of *H. convergens* was placed inside each microcosm. The position and number of eggs deposited was registered every 2 hours during light period. The oviposition location on plants (top, middle, bottom) was used as a qualitative measure. To separate the position, we divided the arena on three parts with 10 cm each one. Each treatment was replicated 10 times. We used a contingency table (G^2-test distribution, William's correction) to evaluate the effects of intraguild predator cues on the position of deposited eggs. To determine the effect of spatial heterogeneity on amount of deposited eggs we compared the means, using non-parametric Welch test.

2.5. Egg intraguild predation

To investigate the effect of spatial heterogeneity and complementary food resources on *H. convergens* egg predation, we used a 2 x 2 factorial design of presence or absence of non-crop plants and presence or absence of aphid as food source. Eggs were collected prior to initiation of the experiment by isolating female *H. convergens* into plastic vials (6 cm diameter) with aphids and water *ad libitum* (25° C; LD 16:8 h). Females were allowed for eat and deposit eggs over a 24 hr period. To standardize the egg clusters introduced into microcosms, we choose egg clusters with at least 12 eggs. Cluster with less than 12 eggs were discarded. If egg clusters contained more than 12 eggs, we removed them using a small paintbrush. Each cluster was fixed to the squash plant at 10 cm above soil surface using green pvc-adhesive tape. Plants were covered by a plastic cylinder (20 cm diameter, 50 cm tall), using the same methodology described on *Adult foraging behavior* experiment.

Each arena containing a plant with egg cluster was exposed to one of the following treatments: a) one squash plant, b) two squash plants, c) two squash plants infested with aphids, d) one squash and one mugwort plant; e) one squash and one mugwort plant, both infested with aphids. Each squash plant was infested with 50 *A. gossypii* (adults and nymphs), and each mugwort plant with 30 (adults and nymphs) *M. artemisiae*. One *H. axyridis,* starved for 24 hr, was released into each cylinder. Predation of *H. axyridis* on *H. convergens* eggs was evaluated after 24 and 48 hr from predator release. Each treatment was replicated 15 times. To analyze the mean of number of predated eggs we used GLM models, with Poisson distribution. To stabilize variances, absolute data were square root transformed prior to analysis.

2.6. Short-term larval survival rates on plant leaves

We conducted an experiment in Petri dishes (10 cm in diameter, 1.5 cm in height) to evaluate the effect on habitat heterogeneity on larvae intraguild predation. Intraguild predation levels were measured in response to increasing plant heterogeneity containing different combinations of plant leaves. The Petri dishes were prepared with moist filter paper on the inside base and following treatments were applied: 1) no leaves (control); 2) one squash leaf (s); 3) two squash leaves (2s); 4) two mugwort leaves (2m); and 5) one squash leaf +one mugwort leaf (s+m). Squash and mugwort leaves used measured 5 - 7 cm. To initiate trials, a second instar larvae of *H. convergens* (intraguild prey), and third instar *H. axyridis*, (intraguild predator), were placed individually into Petri dishes and starved for 24 h with water before release. We chose to pair larvae in different instar because larvae in same instar rarely prey upon on each other; and the intraguild predation occurs when there difference in size between larvae (Snyder *et al* 2004). Usually, smaller individuals are attacked and killed by large ones (Agarwala and Dixon 1992, Yasuda *et al* 2001). Petri dishes were then placed in an environmental chamber at 23 ± 05 °C, 60 ± 5% RH and a 16L:8 D photoperiod. The survival of larvae of *H. convergens* was registered each hour during 7 hours. Each treatment was replicated 20 times. Survival curves were estimated by Kaplan–Meier analysis (Kaplan & Meier, 1958), with equations adjusted to a non-linear model identity. A log-rank test was applied to compare survival rates among all treatments.

2.7. Long-term larval cannibalism and intraguild predation

To test the effects of spatial heterogeneity on the frequency of cannibalism and intraguild predation, we conducted a factorial experiment (two plant managements crossed with two predator manipulations) in the same greenhouse. Treatments were presence and absence of non-crop mugwort plant (*A. vulgaris*) crossed with presence of larger conspecific larvae or intraguild predator. Squash plants (with 10 cm tall) were individually caged by placing them into 30 cm diameter X 60 cm tall plastic tubes so that insects used could not emigrate from plants. All squash plants were infested with 30 *A. gossipy* (nymphs and adults). The mugwort plants (25 - 30 cm tall) used were collected from the field and maintained in pots in the greenhouse until the beginning of experiments. For cannibalism treatment, we used one day-emerged third instar *H. convergens* larva; while the intraguild predation treatment was used one day-emerged third instar *H. axyridis* larva. Both predator types were starved for 24 h prior to initiating the experiment. In all treatments, 2 hours after introduction of predators, five *H. convergens* second instar larvae (intraguild prey) were carefully placed on plants within cages. After 48 h, the predators were removed and we counted he aphid, and the number intraguild prey alive. Each treatment combination was replicated 7 times. To calculate effects of spatial heterogeneity on aphid predation and on cannibalism and intraguild predation, we used GLM model (Poison distribution). The variable response (mean of aphid consumed and mean of larvae predated) was included as a fixed effect in two-way ANOVA interactions between interaction (intraguild predation and cannibalism) and spatial heterogeneity (with or without non-crop plant). The significance of each term was assessed using χ^2 test, based on an estimated mean deviance parameter.

3. Results

3.1. Adult foraging behavior

The presence of additional habitat provided by mugwort and the intraguild predator, *H. axyridis* influenced space-use of the intraguild prey, *H. convergens* females ($G^2 = 26.59$, X-squared df = 6, $P<0.001$; Fig. 2A). Intraguild were frequently observed in the middle region of the microcosm. When only squash plants were available and an intraguild predator, *Harmonia axyridis*, intraguild prey avoided the bottom on the soil and showed greater preference for the middle region of the squash plant ($G^2 = 6.37$, X-squared df = 2, $P=0.041$).

In addition to spatial position responses to habitat and an intraguild predator, behavioral state of the intraguild prey was also significantly altered (Fig. 2B). The frequency of behaviors exhibited by *H. convergens* significantly differed when a non-crop plant was added ($G^2 = 19.68$, X-squared df = 2, $P<0.001$) by reducing the time spent resting as compared to when *H. convergens* were exposed to only a squash plant (Fig. 2B), and when *H. axyridis* were present ($G^2 = 41.57$, X-squared df = 2, $P<0.001$). In the presence of *H. axyridis*, the addition of non-crop plant increased the frequency of eating behavior (i.e. consuming aphids) of *H. convergens* ($G^2 = 8.09$, X-squared df = 2, $P=0.017$; Fig. 2B).

3.2. Oviposition behavior

The egg clusters were deposited either on plants or on the wall of the plastic cylinder container. We observed the location of oviposition relative to the base of the plant, middle or top and counted the number of eggs produced. The frequency of oviposition in different areas in the microcosm was significantly affected by intraguild predator cues (G^2 = 49.58, X-squared df = 6, P<0.001) and *H. convergens* oviposited more on top position of plants (Fig 3A). The number of eggs produced was not influenced by intraguild predator cues (t=0.353, df=16.43, p=0.637; Fig 3B).

3.3. Egg intraguild predation

The mean number of predated eggs was significantly influenced by habitat treatments over 24 hr exposure period to an intraguild predator (χ^2 = 17.29, d.f. = 4, P =0.002; Fig. 4). Following 24 hr, treatments containing only squash or squash with aphids food source were not significantly different (χ^2 = 0.73, d.f. = 1, P =0.38). The treatments containing one squash plant or two plants was not significantly differed from each other (χ^2 = 0.29, d.f. = 1, P =0.59; Fig. 4). However, egg predation was significantly reduced when a squash plant was paired with a non-crop plant or non-crop plant with aphids (χ^2 = 4.73, d.f. = 1, P =0.02). The treatment with squash and non-crop plant was not statistically different from treatment with two squash plants with aphid (χ^2 = 1.75, d.f. = 1, P =0.18).

A similar egg predation pattern was observed following the 48 hr period (χ^2 = 19.43, d.f. = 4, P < 0.001; Fig 4). Egg predation was not significantly different when in treatments containing squash or squash and aphids (Fig. 4). When squash and non-crop plants were combined, this significantly lowered egg predation as compared to treatments with only squash plants (Fig. 3). Importantly, even after 48 hours and no renewal of prey, combining two habitat types or two habitat types and aphid food significantly reduced egg predation (Fig. 4).

3.4. Short-term larval survival rates on plant leaves

The intraguild prey, *H. convergens* larvae, *s*urvival was significantly influenced by habitat treatments (log rank statistic = 24.2, df = 4, $P < 0.001$; Fig. 5). Larvae survival was higher in the presence of leaves than without leaves (log rank statistic = 17.8, df = 4, $P < 0.001$), and the highest survival was observed when a squash plant was combined with a non-crop plant (log rank statistic = 8.1, df = 1, $P < 0.003$; Fig. 5). The amount of leaves present did not appear to influence survival as treatments with 1 squash leaf, 2 squash leaves and 2 non-crop leaves showed similar larval survival levels (log rank statistic = 1.8, df = 2, P= 0.183).

3.5. Long-term larval cannibalism and intraguild predation

The survival of *H. convergens* larvae was significantly influenced by spatial heterogeneity and type of interaction (cannibalism or intraguild predation ($\chi^2 = 21.86$, d.f. = 3, P = 0.0026; Fig. 6A). The number of *H. convergens* larvae alive at the end of the 24 hr period was higher when a non-crop plant was added to the system for the cannibalism treatment ($\chi^2 = 12.36$ d.f. = 1, P = 0.0011). However, intraguild predation on *H. convergens* larvae did not differ in presence or absence of non-crop plant ($\chi^2 = 7.21$ d.f. = 1, P = 0.729; Fig. 6A). Although cannibalism was impacted by habitat, these interactions did not impact the consumption of aphids ($\chi^2 = 1263$ d.f. = 3, P = 0.597; Figure 6B).

4. Discussion

Our study showed that the spatial heterogeneity may benefit predator coexistence, by acting on reproductive choices, contacts on competitor or intraguild prey-predator individuals and on foraging behavior (Fig 07). This study provides evidence that spatial heterogeneity of non-crop plants mediates life-stage dependent intraguild interactions. The spatial heterogeneity ‘created’ a spatial guild partition (Lucas 2012) that reduces negative impacts on susceptible coccinelids life stages (Fig 07). Foraging responses to complex habitat containing a non-crop plant and a squash plant, showed preference by *H.*

convergens for the middle area containing both plant types and predators more actively foraged in this area. The presence of an intraguild predator shifted oviposition behavior of *H. convergens* from the bottom of the habitat to near the top. Egg predation was lowered by the presence of habitat and prey availability, suggesting an interaction between resource availability and habitat complexity in determining egg predation. Furthermore, habitat complexity significantly improved larval survival in the presence of an intraguild predator or to cannibalism of larger conspecific. Combined our results indicate a high degree of behavioral plasticity of coccinelids in response to variable foraging sites. Because patch quality for predators is dynamically changing over time and space (Dixon 2000), systems with greater spatial heterogeneity may signal foraging coccinelids of increased chances to secure food and reduce risk.

The within-plant distribution of coccinelids is potentially species-specific and related to temporal patterns and resource availability (Musser & Shelton 2003; Hoogendoorn & Heimpel 2004; Hodek, Honek & van Emden 2012). In our experiment, an intraguild predator and the presence of spatial heterogeneity altered their distribution. These results *H. convergens* showed preference for these areas containing more mugwort leaves when *H. axyridis* was present. Additionally, when exposed at the same time to plant and heterospecific, *H. convergens* adults remained less time resting and increase the foraging behavior. In addition in the presence of non-crop plant or *H. axyridis,* the intraguild prey, *H. convergens,* stayed more time eating and foraging. Few studies have shown behavior modification occurring on plant structural complexity (Legrand & Barbosa 2003; Hodek & Evans 2012). However, although invasive species as *H. axyridis* have been considered competitor species due spent more time on searching resources than local coccinelids species (Labrie, Lucas & Coderre 2006), the spatial heterogeneity may increase the foraging behavior of native species, which should result in better capacity to compete. Studies have shown that coccinellid respond to habitat heterogeneity on crop and non-crop plants at large scales (Elliott *et al* 1998; 2002), and here we show that micro-scale differences in habitat also alter coccinelid space use.

We found that *H. convergens* shifted oviposition behavior in response to spatial heterogeneity. Coccinellids have evolved optimal oviposition behavior towards site selection that favors offspring development times (Mangel 1987; Hemptinne *et al.* 1993). Oviposition site quality is also related prey availability (Evans & Dixon 1986; Kindlmann & Dixon 1993; Omkar & Mishra 2005), and risk (Schellhorn & Andow 1999; Seagraves & Yeargan 2009). Our results show that females preferentially chose the top position of non-crop plant leaves to oviposit, and the showed preference for mugwort plants. The mugwort leaf morphology, which shows complex architecture when compared with squash plants, may provide better shelter for coccinelids eggs. For example, when *Coleomegilla maculata* females were exposed to nine different weedy plants, they preferred *Abutilon theophrasti* to other plants, probably because of the complexity of leaf surface containing glandular trichomes on the stem and petioles (Griffin & Yeargan 2002).

Intraguild predation and specifically egg predation is a common source of coccinelid mortality (Burgio, Santi & Maini 2002; Lucas 2005; Seagraves 2009). Additionally, the successful dominance of exotic coccinellids is usually related to capacity of these insects to prey on native species (Pell *et al* 2008; Ware, Yguel & Majerus 2009; Sloggett 2012). Our results show that the presence of additional plant complexity and prey availability benefited reproductive output of *H. convergens* by reducing intra and interspecific egg predation. After 24 hours or 48 hours, the addition of non-crop plant habitat and trophic resources reduced egg predation. Interesting, providing more squash plant habitat and aphids did not lower egg predation, and the lowest levels of egg predation were observed in the mixed plant and aphid treatments. By manipulating the availability of habitat and prey, we were able to show that providing non-crop plants enhances the potential for coexistence of invasive and native coccinelids even in confined areas where none of the interacting species can escape.

H. convergens larval survival decreased rapidly over a 8 hour period and was positively affected by presence of non-crop plants. In this very small-scaled experiment, petri dishes with different habitat and combinations of larvae, the presence of leaves from two different plants (squash and mugwort) increased *H. convergens* survival in the presence of the intraguild predator *H. axyridis*. The spatial heterogeneity reduced intraguild predation between larvae by creating refuge to intraguild prey and, therefore, reducing larvae encounters (Janssen *et al* 2007). In the longer term and larger scale intraguild and cannibalism experiment, the number of *H. convergens* larvae alive was significantly higher with non-crop plant in the presence of a larger intraspecific, but intraguild predation was not impacted. The experimental conditions of low prey availability may have generated greater intraguild predation risk. Initially, both *H. convergens* and *H. axyridis* larvae migrated toward the area containing aphids that infested squash plant. In low prey abundance intraguild predators often switch between feeding exclusively on one prey, and in the presence of a potential competitor may attack other species to increase feeding on the preferred prey (Mylius *et al* 2001). Cannibalism between *H. convergens* larvae was reduced when a non-crop plant was added to the system. Conspecific larvae have higher change to escape to predation than heterospecific predators species due to morphological differences as size and difference on aggressiveness (Yasuda *et al* 2001). However, our study shows that cannibalism is a similar risk to intraguild predation in simple environments, and additional habitat lowers levels of cannibalism.

In conclusion, this study shows that microscale spatial heterogeneity modifies predators-predator interactions. Complex-structured habitats diminished intraguild predation and, consequently, improved survival and reproduction of an intraguild prey, the native coccinelid *H. convergens*. Although the vegetational diversity manipulation have been used to provided alternative food resource to coccinelids (Landis, Wratten & Gurr 2000; Lundgren 2009), our study shows habitat complexity and food source availability also influences behavior and the strength of species interactions, by promoting spatial guild partition (Lucas 2012). On this point of view, the management of plant diversity may act as a “scaffold” that helps to improve the fitness of invidious and coexistence among species. Therefore, habitat enhancements that improve habitat heterogeneity likely play an important role in conservation and coexistence of coccinelid species in agroecosystems.

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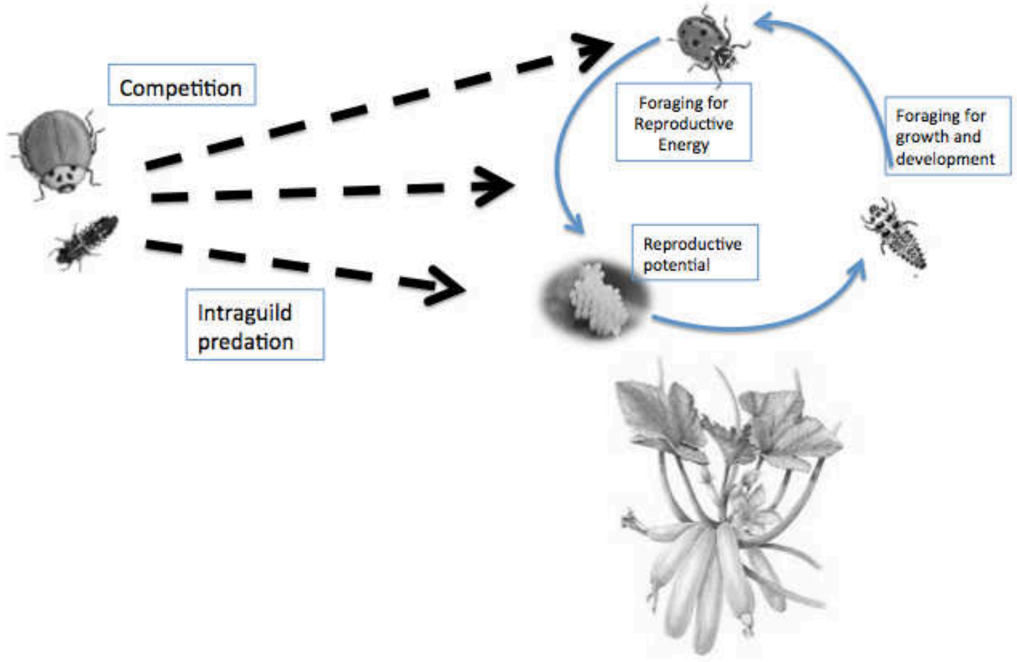

Figure 1. Negative impact of co-occorrence of multiple species of coccinelids.

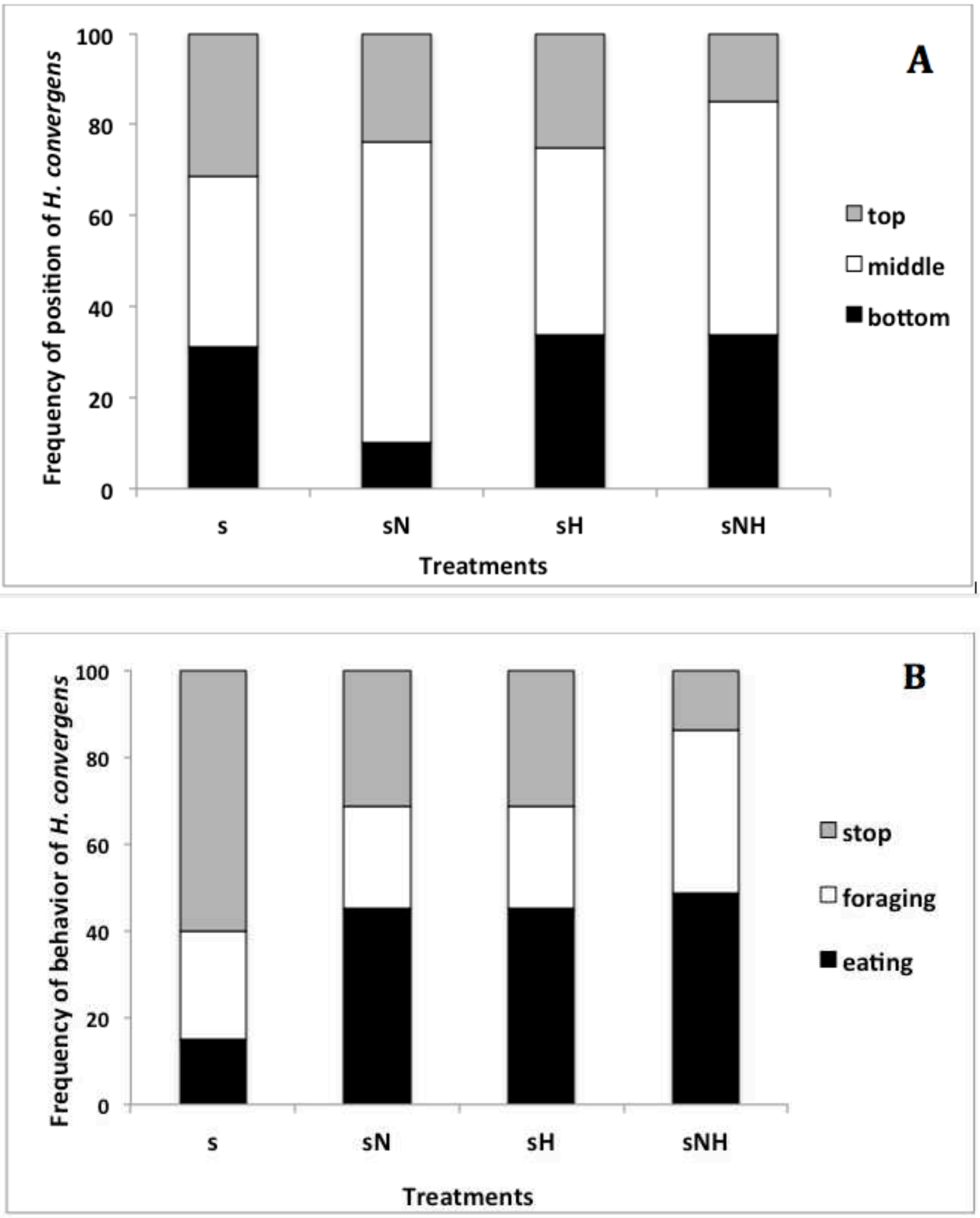

Figure 2. Bars represent the frequency of behaviors exhibited by adult females of *H. convergens* in response to combinations of habitat (S = squash, or N = non crop plant), and the presence of the heterospecific adult female *H. axyridis* (H). (A) Represents the relative position that *H. convergens* was observed (over all experiment period of time). (B) Represents the adult foraging behaviors observed in relation to habitat and presence of *H. axyridis* adult.

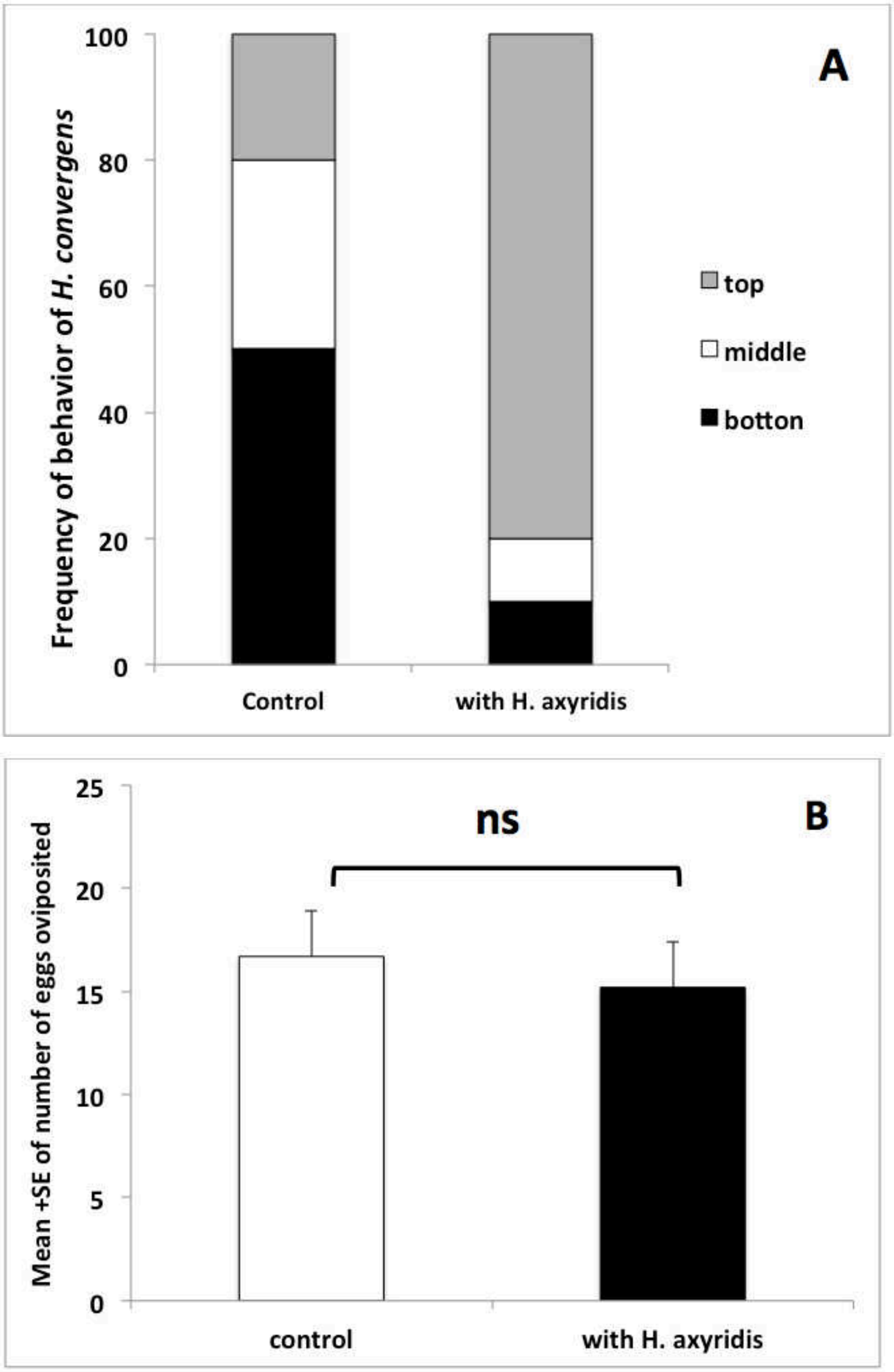

Figure 3. Frequency of position of egg clusters (A) and mean (± SE) number of eggs (B) deposited on plants without (control) and with intraguild predator cues.

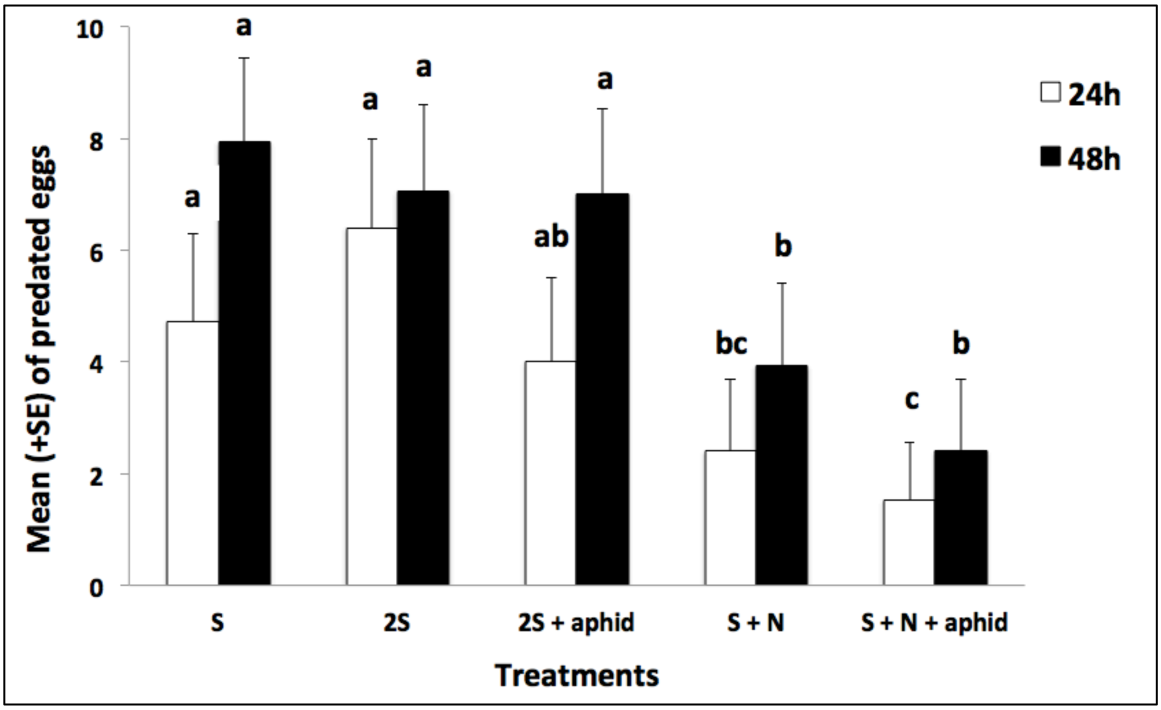

Figure 4. Proportion of intact eggs on different treatment: S (only squash plant), 2S (two squash plant), 2S + aphid (two squash plants with aphids), S+N (squash and non-crop plants) and S+N+aphid (aphid added on both plants). Bars with different letters are statistically different from each other ($P < 0.05$) (comparisons within each time period only).

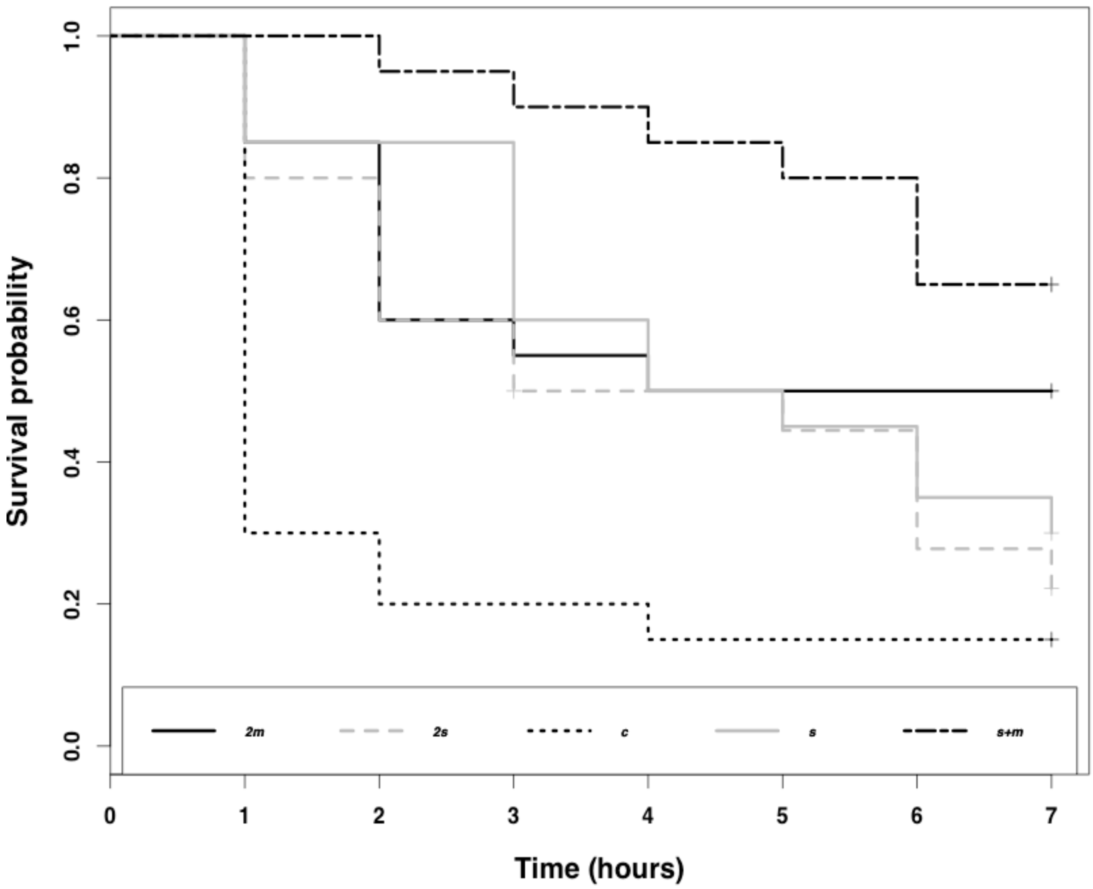

Figure 5. Kaplan–Meier estimates of survivorship function of 2nd instar *Hippodamia convergens* larvae survival in the presence of intraguild predator 3rd instar *Harmonia axyridis* in relation *to* spatial heterogeneity. Different shaded lines represent survival curves for *H. convergens* larvae in Petri dishes exposed to different habitat treatments: Median survival time was calculated as 1 hour without leaves (control), 4,5 hours to one squash leaf (s), 4 hours to two squash leaves (2s) or two mugwort leaves (2m). On treatment with one squash leaf +one mugwort leaf (s+m) the survival probability remains above 50% for the entire period.

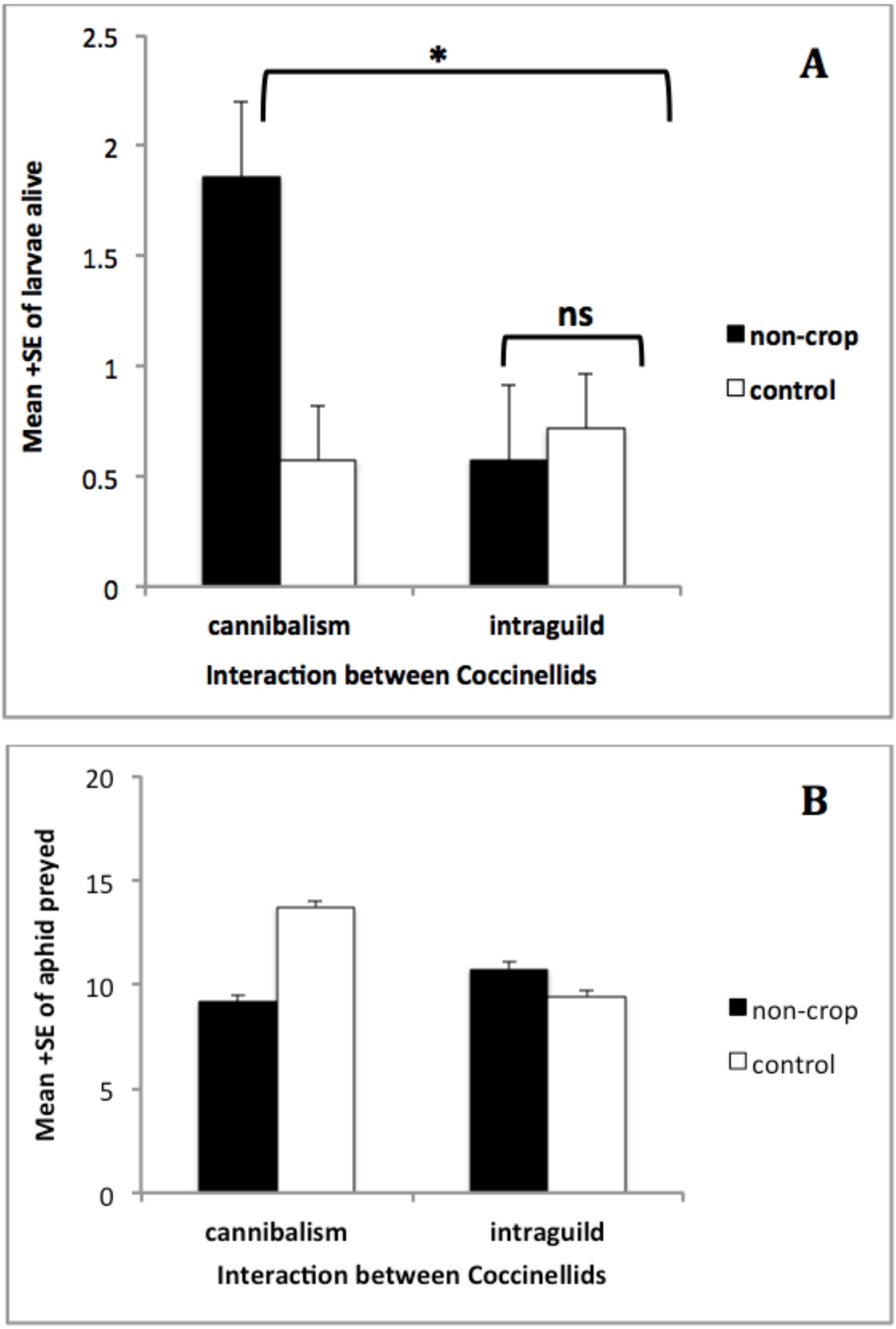

Figure 6. Mean number (±SEM) of larvae alive (A) and mean of aphid preyed (B) in two different interaction (cannibalism and intraguild predation) with and without non-crop plant.

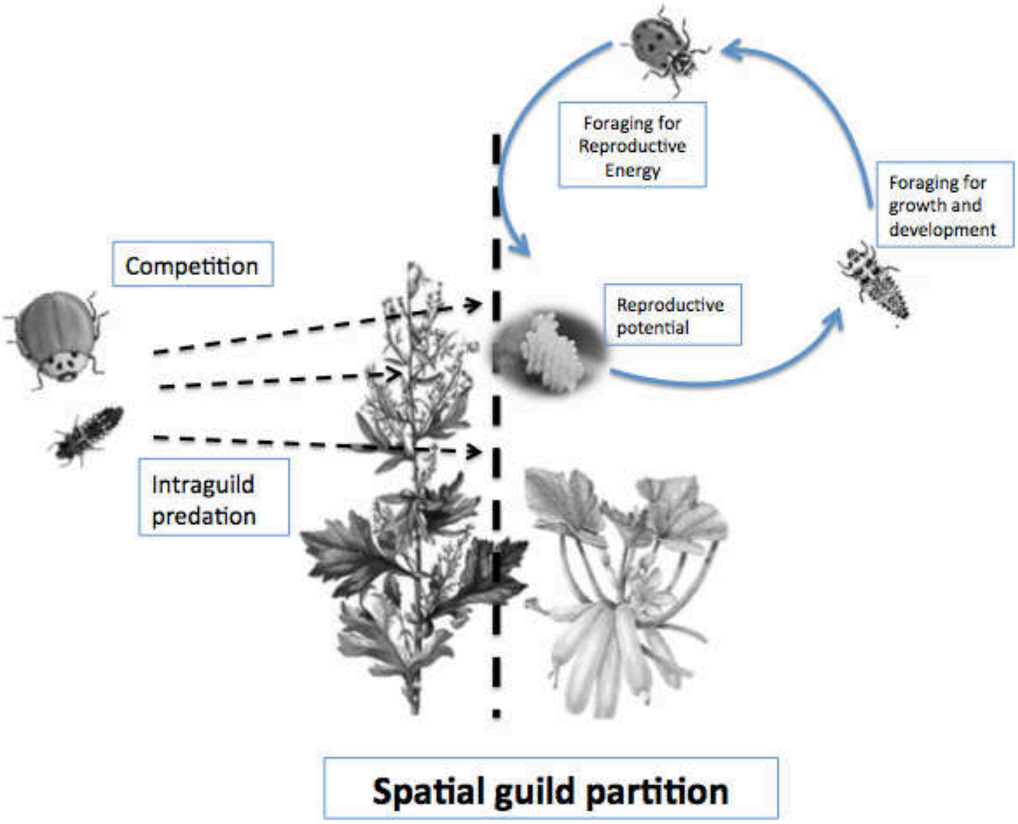

Figure 7. Increasing of spatial heterogeneity creating spatial guild partition and reducing impacts on native coccinelids.

Conclusões

O principal objetivo desta tese foi avaliar a influencia do manejo de plantas espontâneas no aumento da diversidade de inimigos naturais e a eficiência no controle biológico de afídeos. Além disso, foram descritos mecanismos, relacionados às plantas espontâneas, que explicam efeitos positivos sobre artrópodes predadores. Portanto, os resultados dessa tese apresentam e reforçam alguns princípios e padrões da influência da diversidade vegetal sobre inimigos naturais:

i. Plantas espontâneas e artrópodes predadores interagem de forma diferenciada, dependendo da espécies envolvidas e do tipo de recurso fornecido (presas alternativas, local de refúgio, alimento alternativo, local de oviposição). Para coccinelídeos, a presença de presas alternativas aumenta a abundância de organismos encontrados, enquanto que para sirfídeos a presença de inflorescência nas plantas espontâneas contribui para a atração de adultos. Para outros artrópodes predadores, como crisopídeos e aranhas, o tipo de recurso fornecido pelas plantas espontâneas estudadas não afetou diferentemente os organismos.

ii. Dentro de cada grupo de artrópodes predadores, o manejo de plantas espontâneas pode influenciar diferentemente cada espécie. Adultos e larvas da *Cycloneda sanguinea* (Coleoptera: Coccinelidae) apresentam aumento na sobrevivência quando expostas a inflorescências de mentrasto e picão, enquanto larvas e adultos de *Harmonia axyridis* não são diretamente influenciadas pela pelos recursos presentes nas inflorescências.

iii. De maneira geral, em cultivos de pimenta-malagueta onde as plantas espontâneas estão presentes ocorre aumento significativo na abundância da maioria dos inimigos naturais, bem como a redução na infestação de afídeos. Dessa forma, além de promover acréscimo da população de insetos benéficos, em especial artrópodes predadores, as plantas espontâneas podem auxiliar na promoção do controle biológico conservativo. Além da preservação da biodiversidade no sistema de produção, o manejo de plantas espontâneas também reduz o trabalho com práticas culturais, podendo, assim, reduzir custos de produção.

iv. A agregação de inimigos naturais em plantios de pimenta é influenciada pela proximidade com faixas de vegetação de plantas espontâneas. Portanto, além do aumento da abundância dos artrópodes predadores estudados, as plantas espontânea influenciam a distribuição espacial destes organismos. Principalmente, coccinelídeos e aranhas que apresentam uma distribuição com agregação significativa próxima das faixas com plantas espontâneas. Adicionalmente, quando se associa a presença de faixas de planta espontânea dentro e fora da área de cultivo da pimenta se verifica um aumento da área com a presença agregação tanto joaninhas quanto aranhas. Isso tem reflexos diretos na concepção de estratégias de manejo de diversidade com plantas espontâneas, devendo ser considerado a distância da fonte de diversidade vegetacional, bem como as características de movimentação e forrageamento dos inimigos naturais importantes para diferentes culturas e pragas-chave.

v. Mais especificamente, considerando diversos grupos funcionais de organismos, as plantas espontâneas podem influenciar a composição da comunidade de inimigos naturais, sobretudo em aranhas. Cada espécie de planta espontânea estudada nos cultivos de pimenta é capaz de abrigar composição distinta de famílias de aranhas. Dessa forma, o controle biológico pode ser positivamente influenciado pela diversidade de estratégias empregadas por diferentes guildas de aranhas. Em cultivo de pimenta, o manejo de plantas espontâneas afeta a frequência de guildas de aranhas (*p.e.* construtores de teia, caçadoras ativos, tocaia, etc.). Mais do que afetar, de maneira geral, a abundância de inimigos naturais, plantas espontâneas podem influenciar grupos estratégicos de artrópodes benéficos, aumentando diversidade de organismos favoráveis e tornando mais eficiente o controle de pragas-chave nas culturas.

vi. A heterogeneidade espacial advinda da manipulação de plantas espontâneas pode alterar as interações entre inimigos naturais, reduzindo os efeitos negativos da presença de múltiplas espécies. A presença de planta espontânea altera o comportamento de oviposição e forrageamento de coccinelídeos, além de reduzir a predação intraguilda. Portanto, além dos mecanismo que explicam o aumento de populações de inimigos naturais, como fornecimento de alimento alternativo, a heterogeneidade espacial, associada a presença de plantas espontâneas, pode também influenciar interações multitróficas, criando áreas de refúgio e modificando comportamento dos organismos alvo. Portanto, o manejo de plantas espontâneas, como fonte de heterogeneidade espacial, pode criar particionamento de nicho, reduzindo interferências entre organismos. Adicionalmente, isso poder ser prova de que em sistemas naturais a importância de efeitos negativos da interação de artrópodes predadores pode ser minimizada pela diversidade de plantas.

Anexo

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

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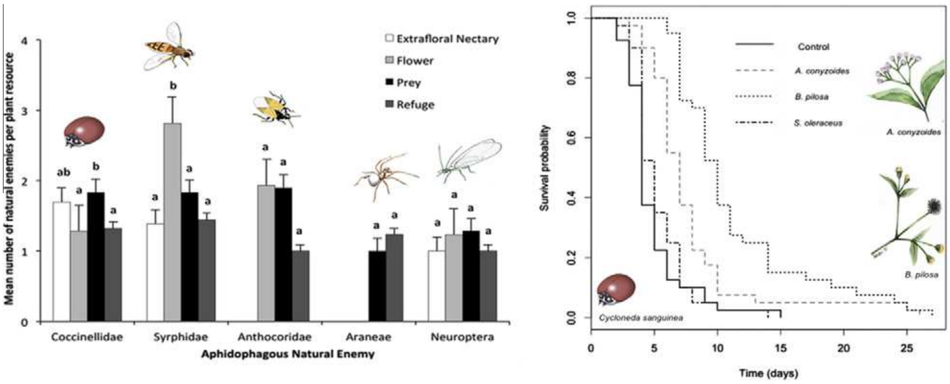
HIGHLIGHTS

- 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; Liljesthröm 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 Tscharntke, 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 Yeargan, 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 significant 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, Ryukyus [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 m^2 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 ± 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).

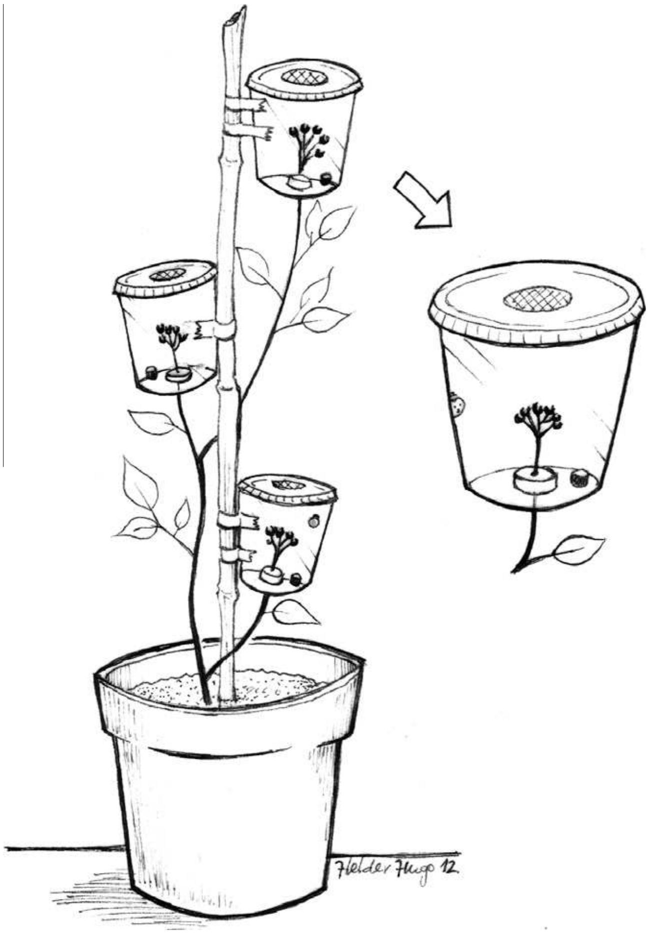

Fig. 1. Experimental design of laboratory experiments to quantify the effect of weeds on survival of Coccinellidae.

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

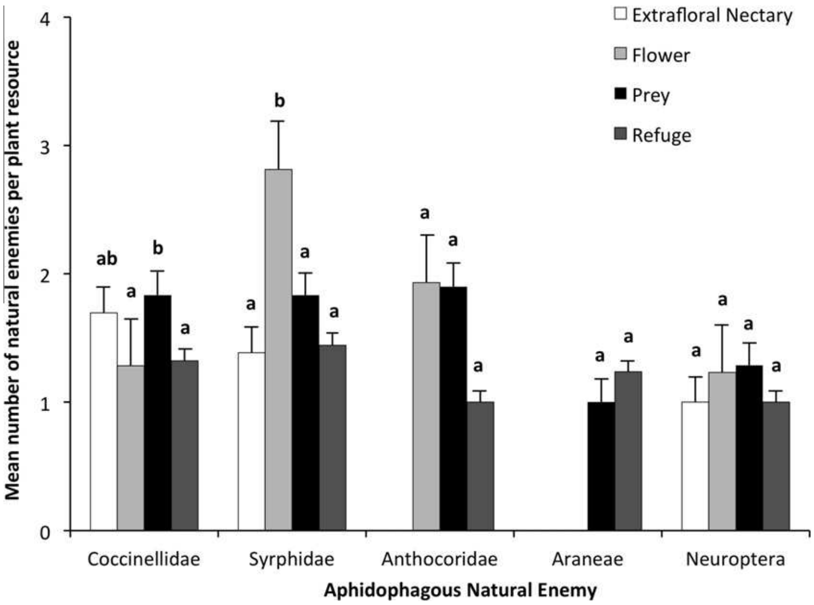

Fig. 2. Mean (+SE) number of natural enemies per plant recorded on different resources provided by weeds in chili pepper fields in Piranga, Minas Gerais, Brazil. Bars with different letters are statistically different from each other ($P < 0.05$) (comparisons within each insect taxa).

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

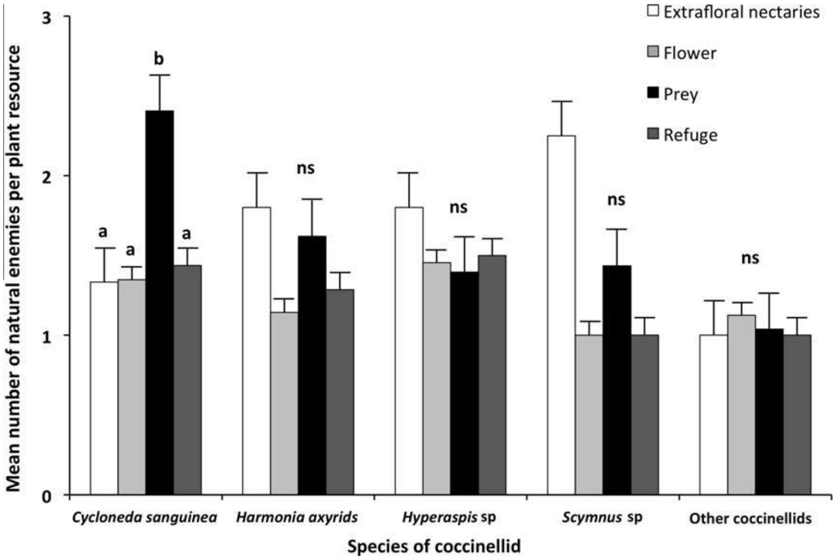

Fig. 3. Mean (+SE) numbers of coccinellid species per plant recorded on different resources provided by weeds in chili pepper fields in Piranga, Minas Gerais, Brazil. Bars with different letters are statistically different from each other ($P < 0.05$) (comparisons within each species).

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. sanguinea* 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

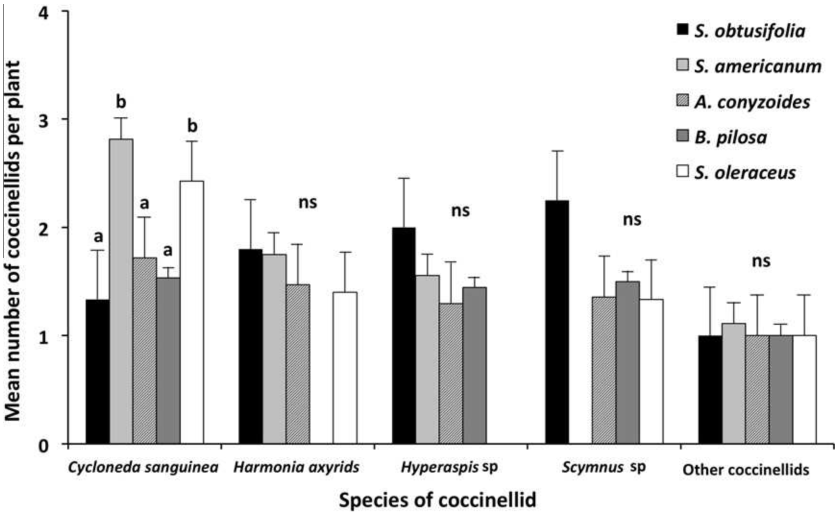

Fig. 4. Mean (+SE) numbers of coccinellid species per plant recorded on different weed species in chili pepper fields in Piranga, Minas Gerais, Brazil. Bars with different letters are statistically different from each other ($P < 0.05$) (comparisons within each species).

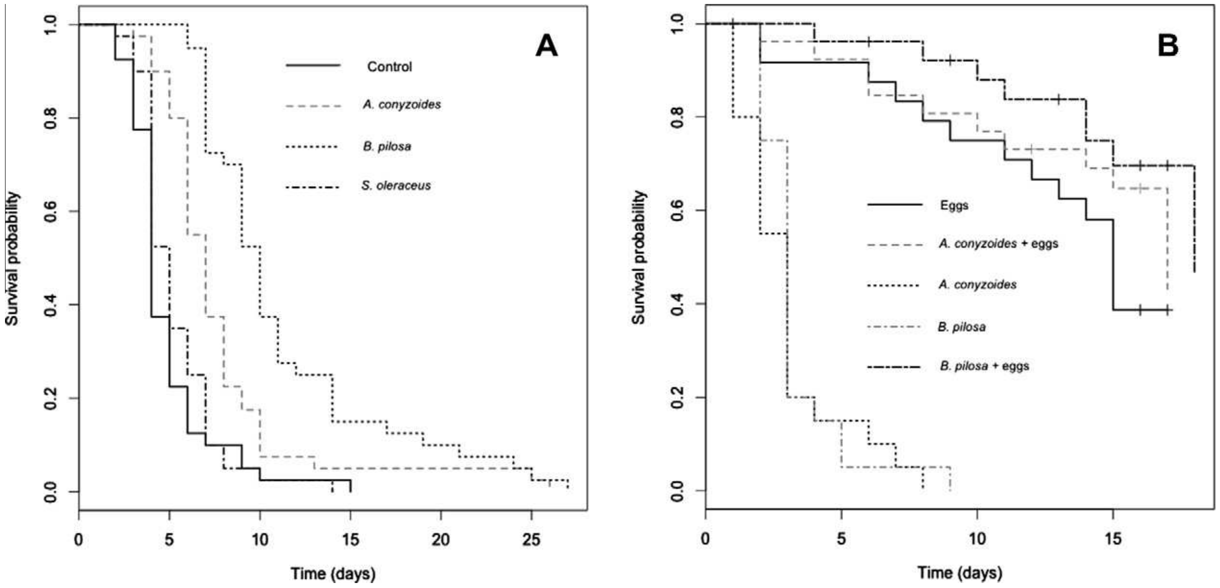

Fig. 5. (A) Kaplan–Meier estimates of survivorship function of *Cycloneda sanguinea* adults on flowers of three weeds and a control treatment. Median survival time was calculated as 10 days for coccinellids on *Bidens pilosa*, 7 days on *Ageratum conyzoides*, 5 days on *Sonchus oleraceus* and 4 days 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).

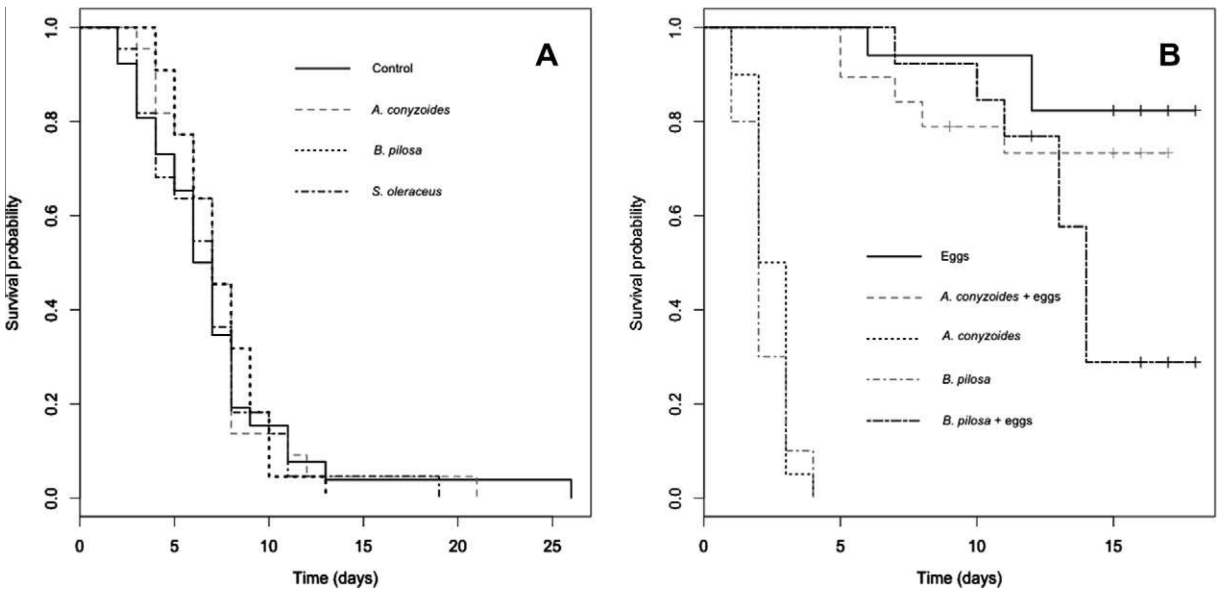

Fig. 6. (A) Kaplan–Meier estimates of survivorship function of *Harmonia axyridis* adults on flowers of three weeds and a control treatment. Median survival time was calculated as 7 days for coccinellids on *Bidens pilosa*, 7 days on *Ageratum conyzoides*, 7 days on *Sonchus oleraceus* and 6.5 days for 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 aphidophagous 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., Pemberton 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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