

# Spider foraging strategies dominate pest suppression in organic tea plantations

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**Abstract** Organic management of crops generally leads to greater predator richness. However conservation of natural enemy species richness does not consistently strengthen herbivore suppression. Here we explored relationships between abundance and diversity of predatory spiders with two distinct foraging strategies and their prey, leafhopper pests. In three organic tea plantations, we investigated abundance of these spiders, and population dynamics of an important tea green leafhopper pest, *Empoasca*

*vitis* (Homoptera: Cicadellidae). We found that abundance and diversity of actively hunting spiders were significantly negatively correlated with leafhopper pest populations, but sit-and-wait spiders were not. The latter may have been limited by intraguild predation or other trophic interactions. Furthermore, there was no significant correlation between total spider and leafhopper numbers. Our study thus suggests that predator foraging strategy might be a key functional trait that can help to explain variation in pest suppression in agricultural systems.

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## Introduction

Biological pest control is a valuable ecosystem service, but intensification of farming, including use of herbicides and pesticides, can drastically decrease the diversity of natural enemy communities (Macfadyen et al. 2009). As an alternative to such agricultural practices, organic farming aims to promote and enhance biodiversity while maintaining an adequate level of agricultural productivity. Previous studies have shown that biodiversity is enhanced by organic management practices, for example, beetles (Rusch et al. 2013), vascular plants and birds (Flohr

et al. 2011). For predatory arthropods in particular, greater biodiversity on farms is clearly desirable from a conservation perspective, but its consequences for pest suppression are less clear (Snyder et al. 2005).

Effects of general predator richness enhanced herbivore suppression relative to a single predator species by meta-analysis (Griffin et al. 2013). However, in many cases, a diverse assemblage of natural enemies can weaken, or have no effect on biological pest control, rather than consistently suppressing herbivores (Straub et al. 2008; Letourneau et al. 2009; Paredes et al. 2015). Finke and Denno (2004) found that enhancing predator diversity could dampen effects on pest populations due to intraguild interactions among predators. Another study found that increasing predator species richness did not affect aphid biological control, because there was no strong complementarity or interference among predator species (Straub and Snyder 2006).

A focus on functional traits, such as foraging modes, can improve predictions of predator diversity effects on pest suppression. Foraging modes of predators, whether actively foraging or sit-and-wait, may determine their ability to suppress herbivore densities by changing probability of encountering prey (Schmitz 2009). An early study predicted that sedentary prey were more likely to be captured by widely foraging predators, while sit-and-wait predators were more likely to encounter and consume mobile prey (Huey and Pianka 1981). These two different foraging strategies of predator have different direct effects on herbivores, with cascading effects on plant species (Schmitz and Suttle 2001; Schmitz 2008, 2009). Therefore, predator foraging strategy could be a key functional trait explaining variation in effectiveness of biological control (Schmitz 2008; Schmitz and Barton 2014).

Spiders have been regarded as generalist predators and biological-control agents (Riechert and Lockley 1984). However, spiders have variable effects on prey depending on their foraging strategies (Schmitz 2008). Actively hunting spiders decreased density of grasshoppers by capturing and consuming them, while sit-and-wait spiders modified grasshopper foraging activity in a manner that reduced predation risk (Schmitz 2008).

The false-eye leafhopper, *Empoasca vitis* (Homoptera: Cicadellidae), is a major insect pest affecting tea production throughout China (Ye et al. 2010). Both

adults and nymphs are highly mobile and cause damage by sucking on the tender leaves and shoots that are usually picked for high-quality tea products. This damage causes curling of young leaves with parched edges or spots and reduces tea quality and yield (Ye et al. 2010). Peak *E. vitis* populations occurring during summer (from June to July) are often extremely devastating (Hu et al. 2005). In recent decades, this pest has been controlled mainly with pesticides in conventional tea plantations. A major challenge for organic tea plantation is to suppress this leafhopper throughout tea-cultivation areas of China (Hu et al. 2005). Spiders dominate the natural enemy communities in tea plantations, and play an important role in regulating *E. vitis* (Ye et al. 2010). How leafhopper populations are affected by spider abundance and diversity, representing different foraging strategies, remains unclear.

Here we designed a study in organic tea plantations in Pu'er city, an important tea-plantation area in China, to address the following questions: (1) How do spider abundance and diversity affect populations of this tea green leafhopper? (2) Do different spider-foraging strategies, actively hunting (AH) and sit-and-wait spiders (SW), have different effects on tea green leafhoppers? Following Schmitz (2008), we hypothesised that AH spiders with widely roaming strategy would be more effective on *E. vitis* suppression than SW spiders, because SW spiders cause largely evasive behavioral response in their prey (non-lethal effect), and AH spiders may reduce prey density (lethal effect).

## Materials and methods

### Study site

This study was conducted in Pu'er (23°55'N, 101°12'E), southern Yunnan province, in southwestern China. This region has a warm humid subtropical climate with mean annual temperature of 18.3 °C, ranging from 12.5 °C (January) to 22.3 °C (June). Annual precipitation averages are about 1600 mm, from which 70 % occurs during the June to October rainy season. Elevation ranges from 376 to 3306 meters.

Pu'er is a major tea producing region in China and tea plantations have important roles in regional socio-

economics. We selected three organic tea plantations at different altitudes to analyze spiders and this important pest, leafhopper *E. vitis*. Tea plantation 1: Nan Dao He tea plantation (22°37'N, 100°59'E), altitude 1000 meters. Plantation size is 110 ha and interplanted with fruit trees, coffee and *Bothrocaryum controversum*; Tea plantation 2: Da Cao Di tea plantation (23°59'N, 100°49'E), altitude 1200 meters. Plantation size is 47 ha and interplanted with coniferous trees and bamboos; Tea plantation 3: Da Jian Shan tea plantation (22°49'N, 100°57'E), altitude 1700 m. Plantation size is 43 ha and interplanted with large tea trees. These tea plantations are at least 30 km apart. Surrounding landscapes of the three tea plantations are patchy forests of 0.5–1.5 ha. Each sampling site is at least 50 m from the forest to minimize edge effects. These organic tea plantations rely on techniques such as green manure, compost and biological pest management with no use of pesticides, herbicides or other chemicals.

#### Sampling design and sample collection

We established two sites (100 × 100 m) in tea plantation 2 and three sites (100 × 100 m) in tea plantations 1 and 3 to collect leafhoppers and spiders. In each plantation, the survey sites were 1 km apart. In each site, abundance of leafhoppers was assessed at the beginning of February, April, June and November 2013. Leafhoppers were sampled using two different methods: (1) yellow sticky traps and (2) sweep netting. Fifty double-sided yellow sticky traps and ten sweep-net samples were conducted in each survey site.

The yellow sticky traps (25 × 15 cm) were installed at the top of the tea plant and the distance between traps was at least 10 m. All traps were left in place for 24 h on each sample date at each site, collected, and transported to the laboratory in a cooler for counting. Each sticky trap was treated as a replicate (Gardiner et al. 2009a, b). Sweep-net sampling was conducted by sweeping a net (50 cm diameter) through the tea row along a 20 m transect, and swinging the net in a 180° arc at the top of tea plants. Net contents were transferred to plastic bags containing 70 % ethanol and taken to the laboratory. Each transect was considered a replicate. Net samples were taken between 10h00 and 18h00 only on sunny days.

We monitored abundance and diversity of spiders in June 2013, because peak leafhopper populations in

June have the largest effects on tea plantation (Hu et al. 2005). Beating trays were used to assess tea-dwelling spider communities. Twenty beating tray samples were collected from each survey site. To sample spiders, the cloth-covered beating tray (44 × 44 cm) was held beneath tea plants, and the tea plants were struck sharply ten times with a stick. Two tea plants, sampled randomly, were included in each sample. Spiders were collected from the trays with an aspirator, and preserved in 70 % ethanol. Beating tray samples were taken between 10h00 and 18h00 on sunny days. All spider samples were returned to the laboratory and examined under a dissecting microscope for identification. For the subtropical spiders we collected, individuals are difficult to assign to known species or even genera. Therefore we identified spiders as morphospecies. The spider morphospecies were distinguished according to external morphological characteristics, such as eye size, count and arrangement, body morphology, body size, walking legs, spinnerets, chelicerae, etc. All the identifications were done in a consistent way for all samples by one person. We divided spiders into two different functional guilds: actively hunting spider (AH) and sit-and-wait spider (SW) according to Murphy and Murphy (2000). Voucher specimen of the collected leafhoppers and spiders were deposited at the Xishuangbanna tropical botanical garden, Chinese Academy of Sciences, Xishuangbanna, China. The sticky traps, nets and beating tray samples were set up in different tea rows in each site, taking care not to disturb other samples.

#### Statistical analysis

The data from the spider survey consisted of the total number of individuals and the diversity measured by the Shannon–Wiener Index ( $H'$ ) (Shannon 1948). First, we performed one-way ANOVA to assess abundance and diversity of spider differences among tea plantations. The leafhopper survey consisted of the total number per sample. Two-way ANOVA were performed to test for effects of sampling time and tea plantation on the abundance of leafhoppers. To account for multiple comparisons, we used Tukey's HSD post-hoc to test for differences among tea plantations and sampling time. Log-transformation was employed when the data did not meet the assumptions of normality. We assessed spider community composition, employing the metaMDS

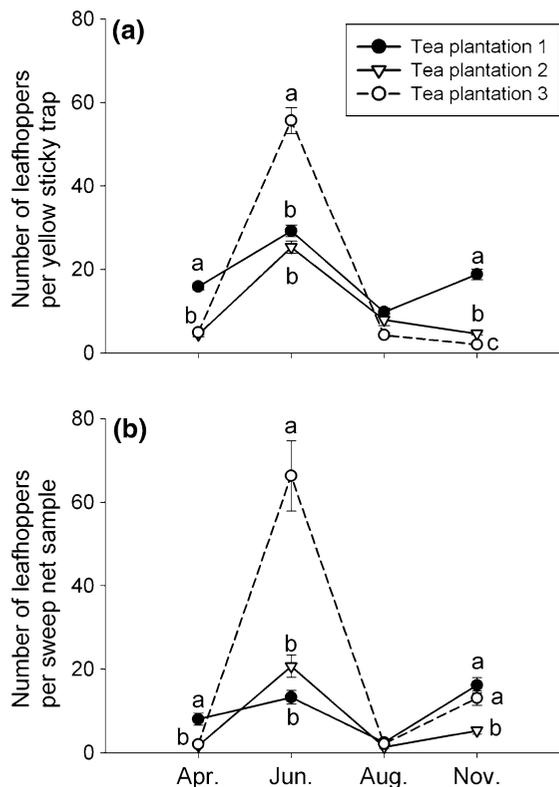
function in R 2.10.1 (R Development Core Team 2014), across the three organic tea plantations using non-metric multi-dimensional scaling (NMDS). NMDS is commonly used in arthropod community analysis (Hillstrom and Lindroth 2008). Bray–Curtis distances of the original data were used in NMDS. A two-dimensional solution was selected because it consistently maintained a low stress ( $<0.2$ ) across multiple runs (Faith et al. 1987). One-way analysis of similarity (ANOSIM) with 4999 permutations was conducted to test differences in spider assemblage composition among tea plantations. Ordinations were conducted at morphospecies level.

A general linear mixed model was used to analyze relationships between leafhopper and spider abundance and diversity in June, and sampling sites within tea plantation as a random factor. To avoid pseudoreplication, we used the mean number of leafhoppers and spiders of eight sites as replicate for linear regression. All these statistical analysis were conducted using SPSS statistical program (version 20.0).

## Results

### Population dynamics of leafhopper

For the leafhopper sticky trap and sweep net methods, population dynamics of the leafhopper were similar (Fig. 1). Population dynamics from sticky trap samples were highly correlated with leafhoppers from sweep net sample ( $R = 0.64$ ,  $P < 0.0001$ ). Months and tea plantations had significant effects on the population dynamics of leafhopper ( $F = 60.32$ ,  $df = 3, 286$ ,  $P < 0.0001$ ;  $F = 20.81$ ,  $df = 2, 286$ ,  $P < 0.0001$ , respectively). The abundance of leafhoppers peaked in June at all three tea plantations, and the abundance of leafhoppers in June at tea plantation 3 was higher than it at tea plantations 1 and 2 (Tukey's HSD post-hoc, all  $P < 0.001$ ). There were no differences between tea plantation 1 and 2 (Tukey's HSD post-hoc,  $P = 0.36$  yellow sticky trap method;  $P = 0.09$  sweep net method) (Fig. 1 and supplementary material Table S1). The abundance of leafhoppers in June at tea plantation 3 was significant higher than other months (Tukey's HSD post-hoc, all  $P < 0.001$ ), and the same pattern held for tea plantation 1 (Fig. 1 and supplementary material Table S1).



**Fig. 1** The population dynamics of leafhoppers from yellow sticky trap samples (a) and sweep net samples (b) among three tea plantations. Bars represent SE. To account for multiple comparisons, we used Tukey's HSD post-hoc to test for differences among tea plantations. Different letters indicate a significant difference among three tea plantations at the same month ( $P < 0.05$ )

### Spider abundance and diversity across the three organic tea plantations

A total of 1633 individuals from 46 morphospecies of spiders were collected which included 1028 individuals from 28 morphospecies of SW spiders, and 605 individuals from 18 morphospecies of AH spiders (for more detail see supplementary material Table S2). Tea plantations had significant effects on the spider abundance and diversity (AH spiders:  $F = 5.67$ ,  $df = 2, 155$ ,  $P = 0.004$ ;  $F = 9.81$ ,  $df = 2, 155$ ,  $P < 0.001$ ; SW spiders:  $F = 2.14$ ,  $df = 2, 155$ ,  $P = 0.12$ ;  $F = 0.97$ ,  $df = 2, 155$ ,  $P = 0.38$ , respectively). The number of AH spiders was lower at tea plantation 3 than tea plantation 1 or 2 (Tukey's HSD post-hoc,  $P = 0.026$ ,  $P = 0.029$ , respectively) (supplementary material Table S3). Compared with tea plantation 3, tea plantation 2 had significantly higher

AH spider diversity (Tukey's HSD post-hoc,  $P = 0.01$ ) (supplementary material Table S3), but there were insignificant differences in AH spider diversity between tea plantation 1 and 2 (Tukey's HSD post-hoc,  $P = 0.09$ ) (supplementary material Table S3). For SW spider abundance and diversity, there were no significant differences among the three tea plantations (supplementary material Table S3).

The non-metric multi-dimensional scaling (NMDS) ordination showed that AH and SW spider assemblage compositions differed among the three tea plantations (Global  $R = 0.57$ ,  $P < 0.001$ ). For AH, although there were not strong differences among the three tea plantations, there is evidence that spider assemblage composition in tea plantation 2 was different from the tea plantations 1 and 3 (one-way ANOSIM: Global  $R = 0.49$ ,  $P = 0.009$ ; Global  $R = 0.52$ ,  $P = 0.001$ , respectively) (Fig. 2a). We found the same trend for sit-and-wait spiders in these three tea plantations, and tea plantation 2 differed from the tea plantations 1 and 3 (one-way ANOSIM: Global  $R = 0.57$ ,  $P < 0.001$ ; Global  $R = 0.61$ ,  $P < 0.001$ , respectively) (Fig. 2b).

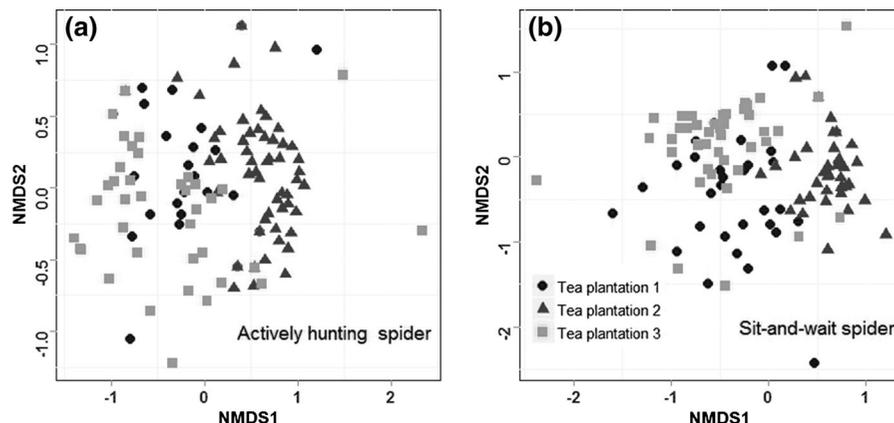
#### Correlation between spider abundance and diversity and leafhopper abundance

For leafhoppers from sweep net samples, linear regressions showed that AH spider abundance and diversity were negatively correlated with leafhopper

abundance ( $R^2 = 0.31$ ,  $P = 0.05$ ,  $y = -0.03x + 4.82$ ;  $R^2 = 0.53$ ,  $P = 0.039$ ,  $y = -0.006x + 0.87$ , respectively) (Fig. 3a, b), SW spider abundance was positively correlated with leafhopper abundance ( $R^2 = 0.35$ ,  $P = 0.04$ ,  $y = 0.06x + 3.02$ ), and no significant correlation was observed between SW spider diversity and leafhopper abundance (Fig. 3c, d). A similar correlation between spider parameters and leafhopper abundance was found in sticky trap samples, but numbers of AH and SW spiders were not significantly correlated with leafhopper abundance ( $R^2 = 0.18$ ,  $P = 0.31$ ,  $y = -0.03x + 4.97$ ;  $R^2 = 0.45$ ,  $P = 0.06$ ,  $y = 0.095x + 1.68$ , respectively) (Fig. 4a, c). No significant correlation was observed between total spider parameters and leafhopper abundance (data not shown).

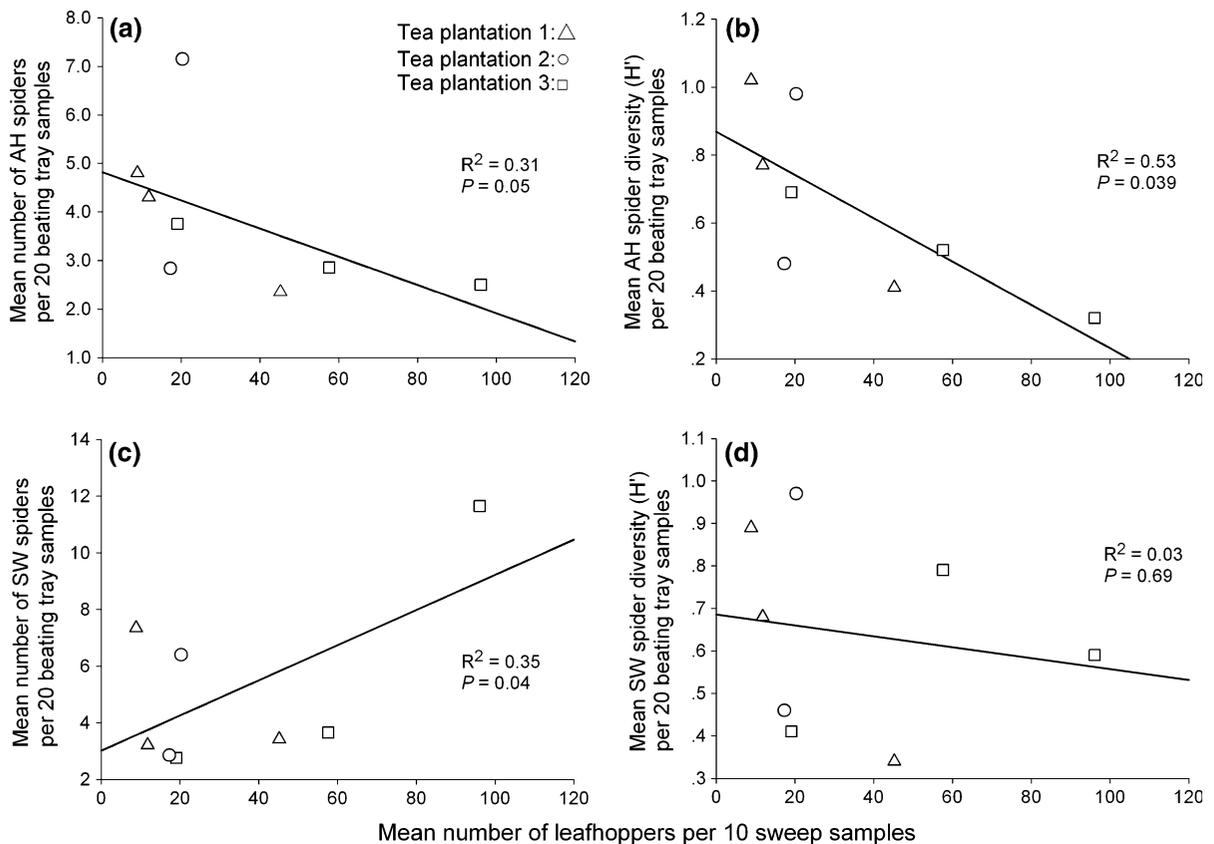
#### Discussion

In this study, we investigated relationships between assemblages of spiders with two foraging strategies and abundance of tea green leafhopper, *E. vitis*, in organic tea plantations. While AH spider abundance and diversity were significantly negatively correlated with *E. vitis* populations, those of SW spiders were not. The associations of different foraging strategies of spiders with leafhopper abundance allow us to determine which spider strategy contributes more to pest



**Fig. 2** Non-metric multidimensional scaling (NMDS) ordinations of actively hunting spider (a) and sit-and-wait spider (b) assemblage compositions in three tea plantations. The plot displays the data of spider communities per beating tray sample

at three tea plantations. *Filled circle* represent tea plantation 1; *filled triangle* represent tea plantation 2; *filled rectangle* represent tea plantation 3



**Fig. 3** Relationship between spider variables, including mean number (a) and diversity (b) of actively hunting spiders (AH), and mean number (c) and diversity (d) of sit-and-wait spiders

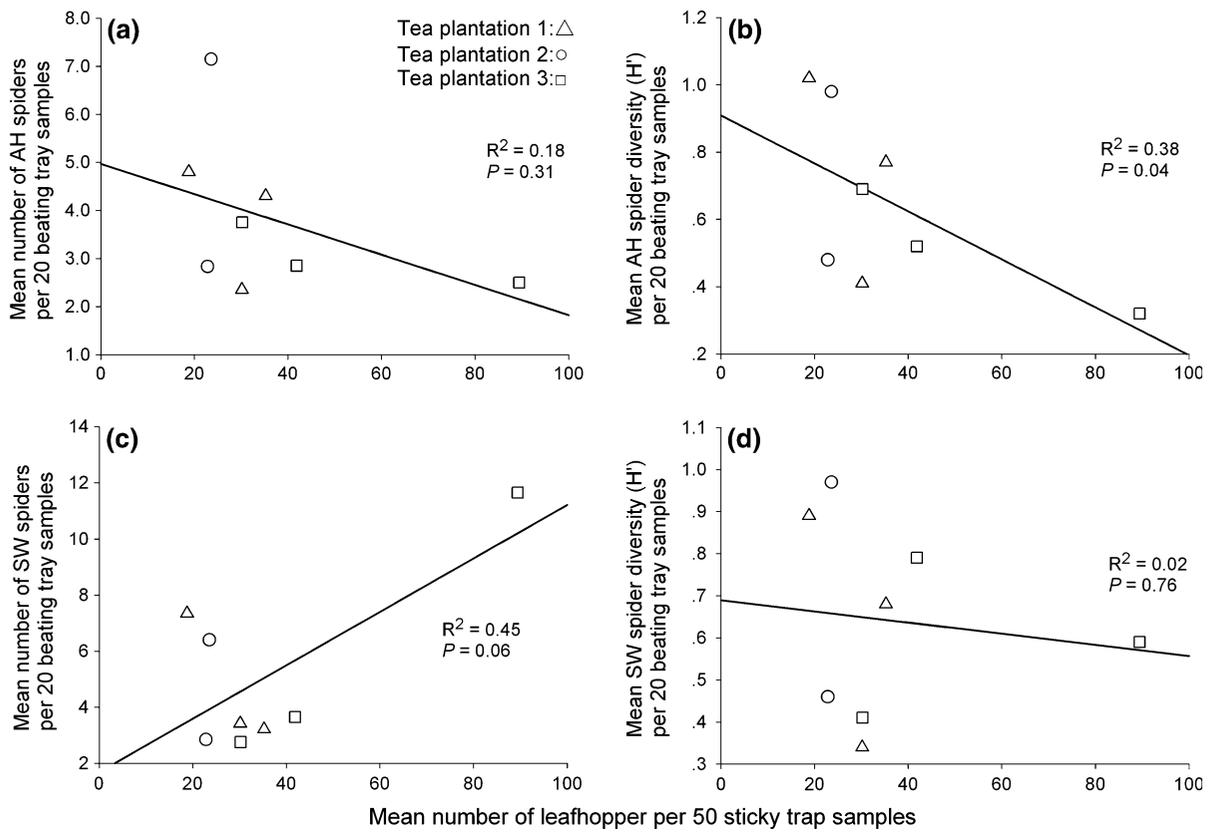
(SW), and leafhopper, *E. vitis*, abundance in sweep net samples. Ten sweep net samples and 20 beating tray samples were taken in each survey site in each of three tea plantations

suppression in these tea plantations. In this study, AH spiders were more effective on *E. vitis* suppression with potential cascading effects on tea quality and yield than were SW spiders.

Predators can affect prey through lethal effects (or density effects), where prey is directly consumed, or through non-lethal effects (or trait effects), where behavioral compensation to predation risk occurs (Cresswell et al. 2010). Previous studies have found that SW spiders cause habitat shifts by prey without significant density effects, and AH spiders have strong density effects on prey populations but cause little or no habitat shift (Schmitz and Suttle 2001; Schmitz 2008, 2009). Empirical studies have shown that SW predators cause largely evasive behavioral responses because prey species respond strongly to persistent, point-source cues of predator presence. This may explain why AH spiders appear to be more strongly correlated with leafhopper abundance than are SW

spiders. Widely roaming AH predators may reduce prey density, but they present highly variable predation risk cues and are thus unlikely to cause chronic behavioral responses in their prey (Schmitz 2008, 2009). For example, the leafhopper *E. vitis* is known to exhibit adaptive anti-predator behaviors of switching hosts and dispersing because of high predation pressure (Novotny 1994).

In contrast, SW spider abundance was positively related to *E. vitis* abundance from sweep net samples. One potential explanation is that the abundant tea leafhoppers are an important resource for SW reproduction and population growth. Some SW spiders in these tea plantations mate and reproduce in May or June, especially the dominant morphospecies (sp. 10, supplementary material Table S2, S. Liu personal observation). Thus the tea leafhopper, *E. vitis*, can be a dominant prey for these SW spider juveniles. Another possible explanation is that alternative prey may



**Fig. 4** Relationship between spider variables, including mean number (a) and diversity (b) of actively hunting spiders (AH), and mean number (c) and diversity (d) of sit-and-wait spiders (SW), and leafhopper, *E. vitis*, abundance in beating tray

samples. Fifty double-sided yellow sticky traps and 20 beating tray samples were taken in each survey site in each of three tea plantations

attract spiders, or positively affect their reproductive success (Östman 2004). For example, Östman (2004) found a positive correlation between generalist predator and alternative prey abundance.

Spider community composition differs among tea plantations and may play a role in leafhopper suppression. Studies of multiple-predator systems reveal a possibility that interference among predators (such as synergism, antagonism, or additivity) is caused by variation in species composition and hunting strategies, which might lead to niche complementarity or functional redundancy among predator species (Letourneau et al. 2009; Griffin et al. 2013). While multiple-predators may differ considerably in their influence on pest suppression and ecosystem processes as a result of these species composition effects (Petchey and Gaston 2002; Straub 2006), predator species identity is an important factor in prey suppression (Chalcraft and Resatarits

2003; Straub and Snyder 2006). Furthermore, spiders with hunting strategies other than sit-and-wait or actively hunting, such as sensing web weavers and ground spiders, could also impact interference among spiders (Cardoso et al. 2011).

Pest suppression in agroecosystems is also influenced by other factors, such as anthropogenic disturbance (tillage, harvesting etc.) and age, structure and composition of surrounding landscapes (Gardiner et al. 2009a, b; Rand et al. 2012). Our study tea plantations all practice organic management and their surrounding landscapes are patchy forests. The major difference among these three tea plantations is altitude. Because insects are ectothermic, it is generally expected that insect herbivory rates decrease with elevation (Rasmann et al. 2014). Farmers thus prefer to grow crops at higher elevations to limit negative effects of herbivores and pathogens (Poveda et al.

2012). Altitude gradients are known to affect species composition and biodiversity (Hodkinson 2005), and this may explain why these three plantations have different spider communities by morphospecies level. However, tea plantation 3 was at the highest elevation, and leafhopper populations peaked in June at all three tea plantations, implying altitudes within this range did not affect population dynamics of leafhoppers.

In conclusion, our study revealed that actively hunting spiders had stronger negative correlations with *E. vitis* abundance than sit-and-wait spiders in organic tea plantation. We suggest that a continued focus on natural enemy functional traits will increase our ability to identify appropriate diversity to improve the biological control practices.

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- Shengjie Liu** conducted this research as part of his PhD thesis on biological control effects of spiders on tea green leafhopper pest.
- Zhipeng Li** explores the ecology and taxonomy of spiders and arthropods.
- Yi Sui** explores the ecology and taxonomy of spiders and arthropods.
- Douglas A. Schaefer** is emeritus associate professor. His primary research area is soil ecology.
- Peter O. Alele** explores the ecology and taxonomy of spiders and arthropods.
- Jin Chen** is professor in Xishuangbanna Tropical Botanical Garden. Collaborative research touches on a number of topics in ecology, such as biological control, plant-animal interactions, seed dispersal and climate change.
- Xiaodong Yang** is professor in Xishuangbanna Tropical Botanical Garden. His work focuses on the integrated pest management and biological control of agricultural pests.