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AGROECOSYSTEMS

Effects of different tea plantation management systems on arthropod assemblages and network structure

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Abstract. Tea plantations are intensive monocultures and vulnerable to various pests due to a low diversity of natural enemies. In ancient tea plantations, the trees have grown for hundreds of years in mixed stands with many native trees, resulting in a landscape deemed as a "forest tea plantation." However, no empirical studies have explicitly examined the effects of forest tea plantations on arthropod communities. Here, we addressed the difference of arthropod assemblages and ecological networks between the forest tea plantations and monoculture tea plantations, specifically focusing on the natural enemies and insect herbivores. Our results showed that the diversity of all arthropods, insect herbivore, and their natural enemies was higher in forest tea plantations compared to the monoculture tea plantations. In contrast, monoculture tea plantations had a higher abundance of all arthropods and insect herbivores due to a sharp increase in the abundance of the pest leafhopper, *Empoasca vitis*. Furthermore, forest tea plantation had higher co-occurrences among natural enemies and insect herbivores than a randomized network, which suggests that natural enemies may co-occur with some specific herbivore species. These results allow us to predict that forest tea plantations enhance insect herbivore control by increasing diversity of natural enemies and network structure between natural enemies and herbivores. Our study suggests that the ecological network approach opens up new possibilities for improving our prediction and understanding of pest suppression in agroecosystems.

Key words: agroecosystem; arthropod assemblage; biocontrol; ecological network; spatial variation; tea plantation.

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Introduction

Globally, tea plantations dramatically increased from 1.37 million ha to over 4.08 million ha from 1961 to 2017 (ITC 2017). China, the largest tea-producing country, accounts for over 54% (2.22 million ha) of the world's tea plantation area (ITC 2017). Most tea plantations are intensive monocultures and vulnerable to various pests due to a low diversity of natural enemies (Ye et al. 2014). Pest outbreaks result in serious yield losses in monoculture tea plantations; therefore, a major challenge in pest biological control is to promote and increase the abundance and diversity of predator communities (Ye et al. 2014).

Habitat management, a new biological pest control practice, has been widely applied in agroecosystems because it is an environment-friendly pest management approach (Li et al. 2019). Habitat management in tea plantations could indirectly control insect pests by increasing the abundance and diversity of natural enemies (Gurr et al. 2017). For example, Zhang et al. (2017) showed that intercrops of *Cassia tora* in monoculture tea plantations significantly reduced the tea green leafhopper pest (*Empoasca onukii*) due to a marked increase of natural enemies such as coccinellids and spiders. Chen et al. (2019) found that intercropping ground covers such as *Chamaecrista rotundifolia* in monoculture tea plantations increased the abundance of arthropod predators by providing favorable microhabitats for nests and shelter.

The enhanced diversity of natural enemies is a common consequence of intercropping in monoculture tea plantations (Gurr et al. 2017). However, previous studies focus mostly on simple indices of natural enemies, such as abundance or diversity (Tylianakis and Binzer 2014, Welch and Harwood 2014). In ecosystems, species are embedded in complex ecological networks and have interactions with multiple other species; analyzing these networks provides a better understanding of ecosystem functions including pest control (Tylianakis and Binzer 2014, Welch and Harwood 2014). Ecological networks capture direct or indirect interactions among species, which could be useful for evaluating the efficacy of pest control (Ings et al. 2009). Generally, increasing the complexity structure of ecological networks should lead to strong interaction strength between predator and prey (Ings et al. 2009). This implies that structurally complex ecological networks should have enhanced pest suppression relative to simplified networks. However, little is known about how the structure of ecological networks mediates pest control in tea plantations.

Forest tea plantations, also referred to as ancient tea plantations, have a long tradition history in Menghai, Yunnan Province, southwest of China, and likely dates back to the Tang Dynasty (800 yr ago; Qi et al. 2013). Different from the monoculture tea plantations which are dwarf shrubs (about 1 m high), the ancient tea trees (about 4 m high) have grown for hundreds of years in mixed stands with many native trees, resulting in a landscape deemed "forest tea plantation" (Fig. 1). The forest tea plantations and monoculture tea plantations are the dominant tea plantation types in Menghai, but about 36% of forest tea plantations were converted to monoculture tea plantations from 1990 to 2010 to increase tea production (Hung 2013). Although forest tea plantations likely support more diverse arthropod assemblages, no empirical studies have explicitly assessed the natural enemies and insect herbivore communities in forest tea plantations. Here, we compared the arthropod assemblages in monoculture tea plantations and forest tea plantations and attempted to address the following questions: (1) What is the difference in arthropod assemblages between monoculture tea plantations and forest tea plantations, specifically the natural enemies and inset herbivores? (2) What are the differences in natural enemy and insect herbivore ecological networks between monoculture tea plantations and forest tea plantations?

Methods

Study site

Our study was conducted in Menghai (1650 m in elevation, 21°54′ N, 100°08′ E), located in Xishuangbanna, southwestern China. Menghai has a subtropical warm humid climate with annual average precipitation of 1640 mm/yr and temperature of 21°C. Menghai is one of the main tea-producing areas in China, and tea has been the major cash crop in Menghai, which has a strong influence on regional socio-economics (Hung 2013). We selected a monoculture tea plantation and a forest tea plantation that were one km apart to investigate arthropod assemblages. The forest tea plantation is about 600 hm^2 and is dominated by 200-yr-old tea trees (Fig. 1). The diameter at breast height (DBH) and height of tea trees are about 37 cm and 3–5 m, respectively. The native plant species within the plantation are mainly *Alangium kurzii* Craib, *Homalium ceylanicum* Benth, *Ostodes katharinae* Pax, *Macaranga indica* Wight, *Glochidion wrightii* Benth, and *Balakata baccata* Roxb. The monoculture tea plantation size is about 500 hm^2 and has 30-yr-old tea trees (Fig. 1) with a DBH of about 8 cm and are about 1 m tall. Forest tea

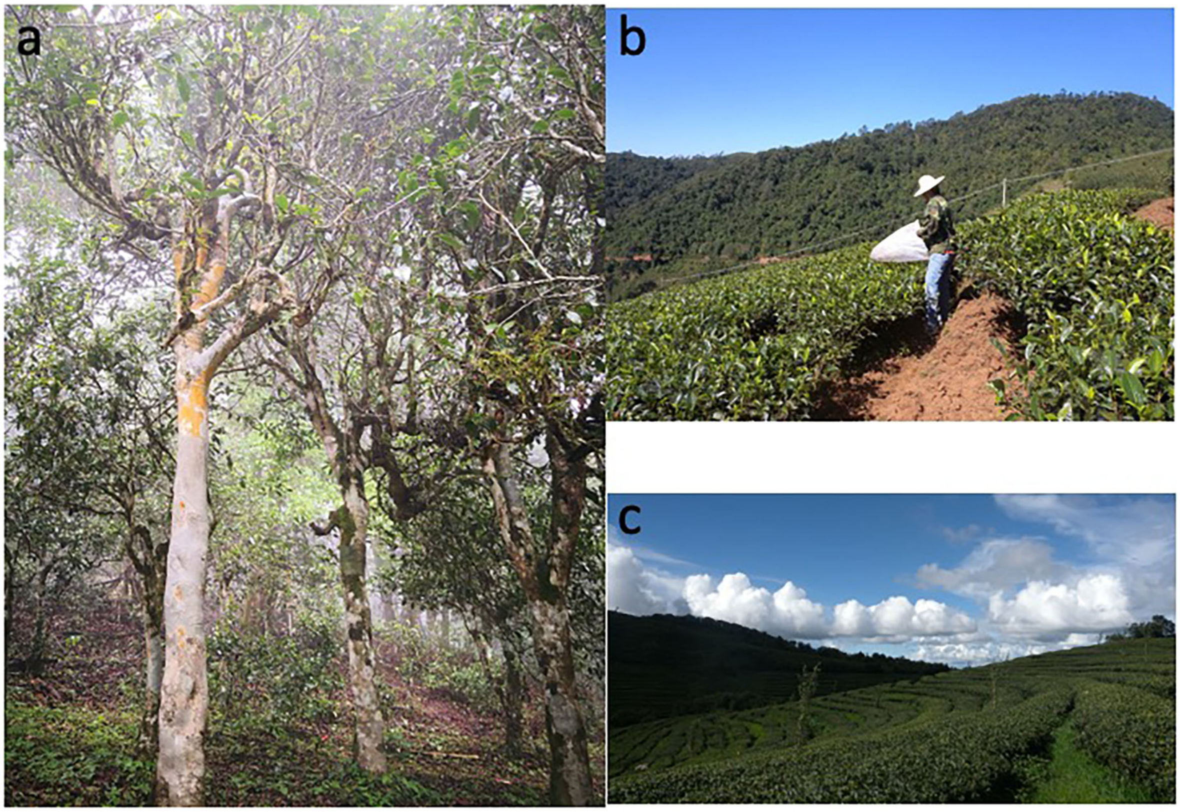

Fig. 1. Forest tea plantation (a) and monoculture tea plantation (b, c) in our study site, Menghai (21°54′ N, 100°08′ E), located in Xishuangbanna, southwestern China. Photo credit: Shengjie Liu.

plantations have variety of plant life forms, such as trees, shrubs, vines, and herbs, while monoculture tea plantations are dominated by tea shrubs with some herb species such as *Conyza canadensis* Linn and *Orychophragmus corniculata*. These two tea plantations use similar biological pest control without pesticides or other chemicals.

Sampling design and arthropod collection

In July 2019, we established a single plot (102 × 102 m) in each plantation at least 100 m from the perimeter to avoid edge effects. The plots were divided into 36 contiguous 17 × 17 m sections, and we used sweep netting and beating tray methods to sample arthropod assemblages in each section. Crawling arthropods were collected through the beating tray and flying insects by sweep netting (Yi et al. 2012). Sweep netting was conducted by sweeping a net (30 cm radius) through the tea row or canopy for 15 min in each section. We randomly selected five tea trees for beating tray sampling and combined them into one sample in each section. Each section was considered a replicate, and in total, we had 36 replicates for each sampling method. Because the two sampling methods targeted different arthropods, we combined the data from the different sampling methods to represent the full arthropod assemblage and used these data to perform subsequent analyses. Samples were taken between 8:00 and 18:00 on sunny days. The arthropod samples were preserved in 80% ethanol and identified under microscope.

We identified arthropods to species or morphospecies, according to external morphological characteristics, such as wings, genitalia, body morphology, legs, and chelicerae. Then, we classified the arthropods into different trophic guilds: insect herbivore, natural enemy including predators and parasitoids, and neutral arthropod including pollinators and decomposers.

Specimen vouchers were deposited at the Xishuangbanna Tropical Botanical Garden in the authors' personal collection.

Data analyses

The sweep netting and beating tray sampling collected 28% and 72% of total arthropods in the monoculture tea plantation, and 53% and 47% in the forest tea plantation, respectively. To analyze our arthropod samples, we first used generalized linear models (GLMs) to test whether abundance and Shannon-Wiener Index (H') of arthropods collected within each section varied between forest tea plantations and monoculture tea plantations. We performed GLMs with a Gaussian distribution and identity link for H' data and Poisson distribution with a log link for abundance data. GLMs were performed using the stats package in the R software (Cheek et al. 1990). The spatial variability of arthropod abundance and H' diversity across the 36 contiguous sections was visualized using a heatmap in the lattice package in R (Sarkar 2007).

We used non-metric multidimensional scaling (NMDS) with Bray-Curtis distances to assess the differences in species community composition between forest tea plantations and monoculture tea plantations across the difference trophic guilds. We selected the first two-dimensional solution because it consistently maintained a low stress (<0.2) across multiple runs. Non-metric multidimensional scaling was performed using the vegan package in R (Oksanen et al. 2019).

A co-occurrence network for each tea plantation was generated to explore interaction between natural enemies and insect herbivores. For inference of the ecological network, we calculated all possible pairwise Spearman's rank correlations (r) between natural enemies and insect herbivore species across the plot. We considered the correlation between two species to be statistically robust if Spearman's correlation coefficient r was >0.8 and the $P < 0.01$ (Junker and Schreiber 2008). Subsequently, we calculated the parameters of ecological network topology, which include effect size (the number of edge), average degree (the average number of links connecting one node to any other nodes), average path length (the average shortest path between all nodes), modularity index (interlinked subsets of species), and clustering coefficient (proportion of nodes that can be reached through the other neighboring nodes; Newman 2003). Network analyses were performed using the psych (Revelle 2017) and igraph (Han et al. 2010) packages in the R software. Network visualization was generated using Gephi (http://gephi.github.io/; Bastian et al. 2009). We used Erdos-Renyi random network model to test whether the observed network metrics are different from random network. We generated 999 Erdos-Renyi random network, each random network with the same nodes and edges to the observed network (Erdős and Rényi 1959). We then computed network metrics for each random network and generated a distribution of each metrics. P value was calculated as the frequencies of the random network metrics smaller or bigger than the observed network metrics (Matloff 2016).

Results

Effects of different tea plantations on arthropod community

A total of 4274 individuals from 175 species or morphospecies were recorded at the monoculture tea plantation, and 1906 individuals from 272 species or morphospecies were recorded at the forest tea plantation (Appendix S1: Table S1). Overall, 92 arthropod species were observed in both tea plantations: 53 shared species were herbivores, 31 were natural enemies, and eight were classified as neutral arthropods (Appendix S1: Table S1). The most abundant species in the forest and monoculture tea plantations were *Aspidobyctiscus lacunipennis* (10.23%) and *Empoasca vitis* (57.07%), respectively (see more detail in Appendix S1: Table S1).

For subsequent analyses, we divided arthropod species into natural enemies, insect herbivores, and neutral arthropods, and we found that forest tea plantation had higher diversity (H') of all arthropods ($F = 86.19$, $P < 0.001$), natural enemies ($F = 19.81$, $P < 0.001$), and insect herbivores ($F = 77.34$, $P < 0.001$), but not neutral arthropods ($F = 2.22$, $P = 0.14$; Fig. 2; Appendix S1: Table S2). The abundance of all arthropods and herbivores was significantly higher in monoculture tea plantations than forest tea plantations ($P < 0.001$), but forest tea plantations had a higher abundance of natural enemies

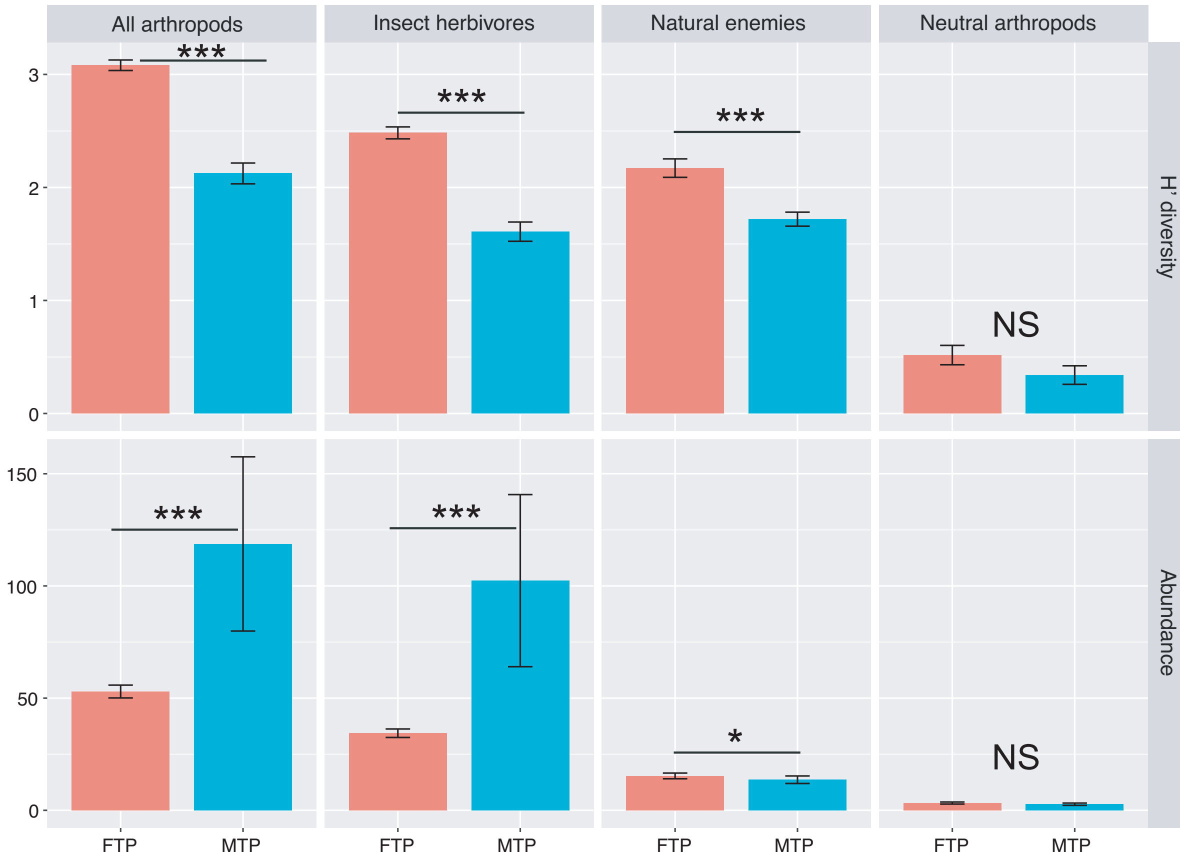

Fig. 2. Abundance and H' diversity of arthropod including all arthropod, natural enemy, insect herbivore, and neutral arthropod in forest tea plantations (FTP) and monoculture tea plantation (MTP). $^{*}P < 0.05$, $^{***}P < 0.001$, NS = not significant ($P > 0.05$).

than monoculture tea plantations ($P < 0.05$; Fig. 2; Appendix S1: Table S2).

The NMDS analyses showed that the assemblage compositions of all arthropods ($r = 0.75$, $P < 0.001$), natural enemies ($r = 0.55$, $P = 0.01$), and herbivores ($r = 0.67$, $P < 0.001$) differed between the two tea plantations (Fig. 3). In contrast, there was no difference between the two tea plantations for neutral arthropods ($r = 0.02$, $P = 0.76$; Fig. 3).

Effects of different tea plantations on spatial variation and ecological network of arthropods

We mapped the spatial distribution of the abundance and diversity of different arthropod guilds within the plots in two different tea plantations (Fig. 4). The coefficient of variation (CV = [standard deviation/mean value] × 100%) was used to interpret the spatial-varying characteristics. For H' diversity and abundance of all arthropods, the spatial distribution in the monoculture tea plantation (CV = 385%, CV = 51%) was relatively uniform compared to the forest tea plantation (CV = 1103%, CV = 309%; Fig. 4a, b, g, h). Similarly, the spatial variation of herbivore abundance and diversity was significantly different between the two tea plantation types (forest tea plantation, abundance CV = 302%, diversity CV = 783%; monoculture tea plantation, abundance CV = 44%, diversity CV = 315%; Fig. 4e, f, k, l). In contrast, for the natural enemy abundance and diversity, the two tea plantation types had similar spatial variation (forest tea plantation, abundance CV = 201%, diversity

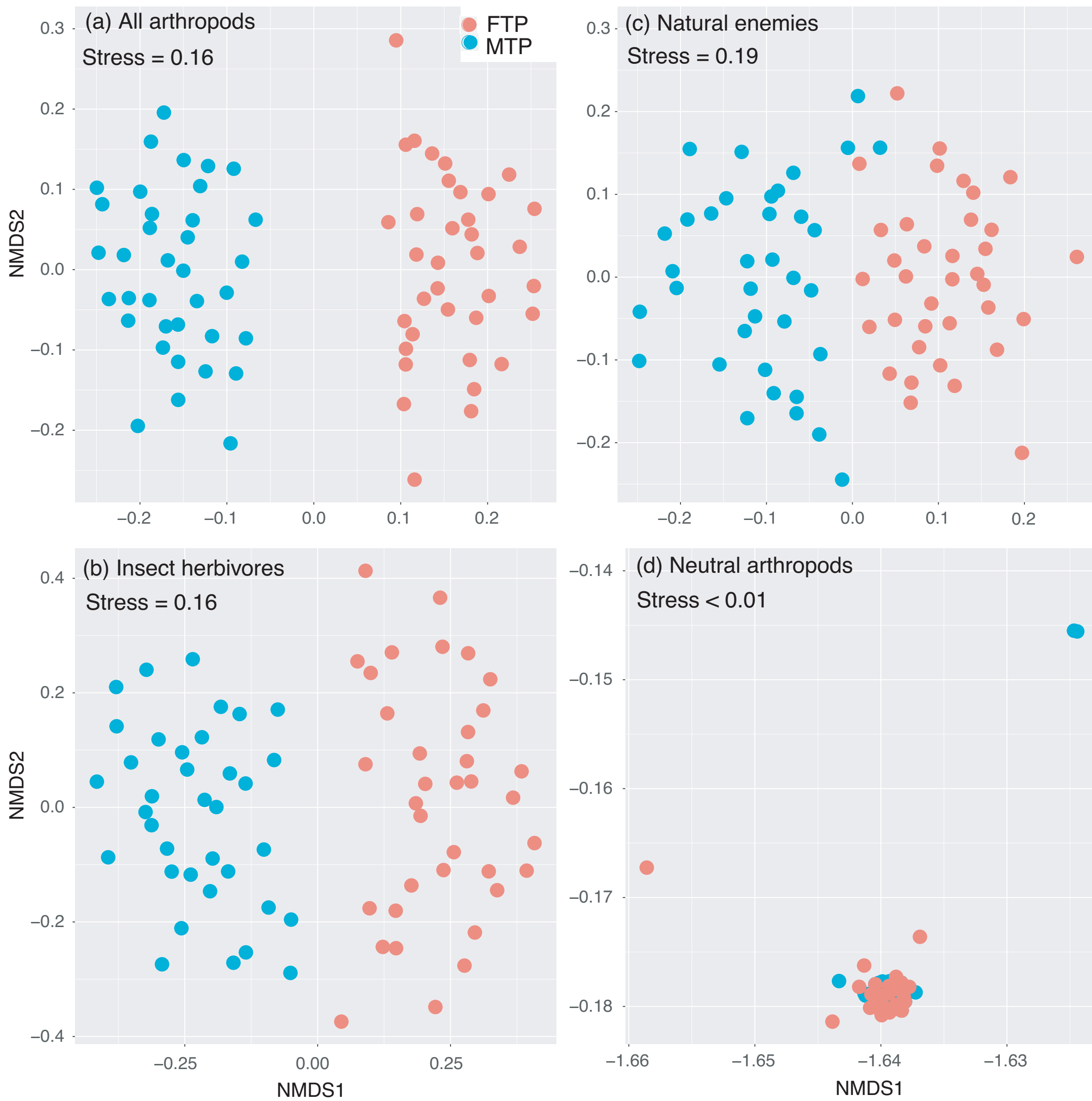

Fig. 3. The non-metric multidimensional scaling ordinations (NMDS) of species assemblage composition of all arthropods (a), insect herbivores (b), natural enemies (c), and neutral arthropods (d) in the forest tea plantation (FTP) plot sections and monoculture tea plantation (MTP) plot sections. Stress indicates the goodness of fit statistic for points and the value below 0.2 is considered fair.

CV = 443%; monoculture tea plantation, abundance CV = 136%, diversity CV = 462%; Fig. 4c, d, i, j).

Some topological features widely used in ecological network analysis were calculated to describe the pattern of co-occurrence between natural enemies and insect herbivores. We found that the forest tea plantation had a higher effect size (515) than the monoculture tea plantation (313) due to higher arthropod diversity (Fig. 5; Appendix S1: Table S3). Compared to the null model, forest tea plantations had significantly higher topological properties of the ecological networks (Fig. 5; Appendix S1: Table S3), which

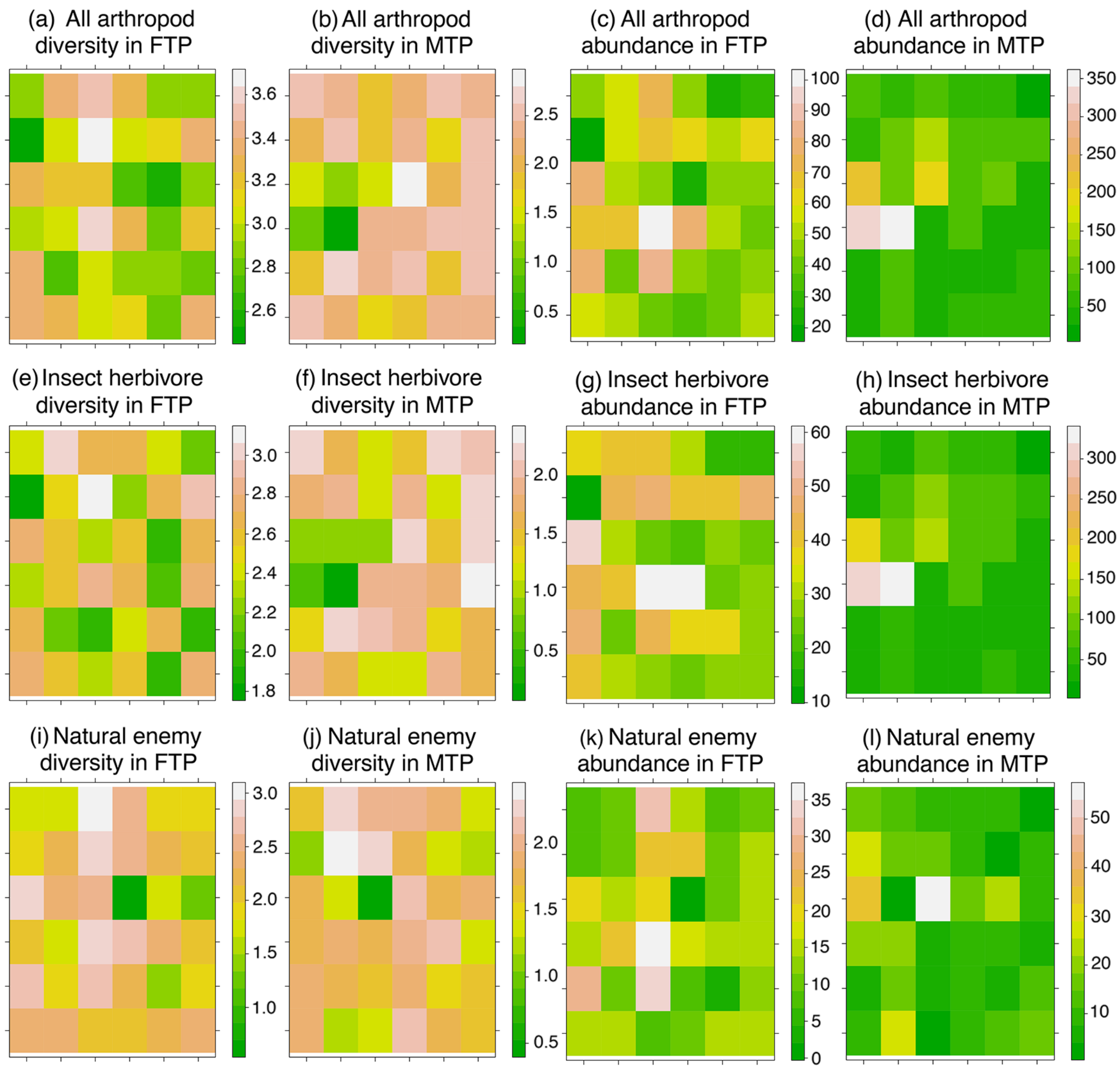

Fig. 4. Heatmap mapping the spatial pattern of all arthropod diversity (a, b) and abundance (c, d), insect herbivore diversity (e, f) and abundance (g, h), natural enemy diversity (i, j) and abundance (k, l) within a plot (102 × 102 m) in the forest tea plantations (FTP) and the monoculture tea plantation (MTP).

indicated that forest tea plantation had higher co-occurrences among natural enemies and insect herbivores than a randomized network. The smaller modularity index indicated the network had more subnetworks (or modules); thus, forest tea plantation had less subnetworks than randomized network (Fig. 5; Appendix S1: Table S3), which suggests that natural enemies may not randomly co-occur with herbivore species, they may co-occur with some specific herbivore species. However, average degree and average path length in the monoculture tea plantation were significantly lower than the randomized network (Fig. 5; Appendix S1: Table S3).

Discussion

In our study, we investigated the arthropod assemblages, especially natural enemies and insect herbivores, in two tea plantations with

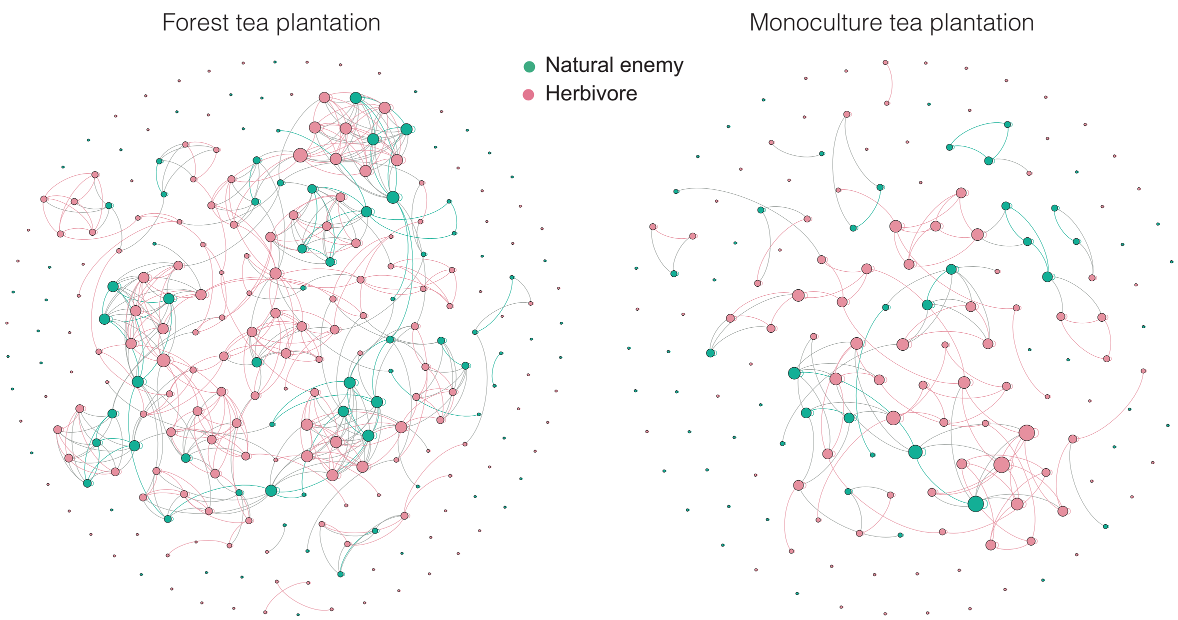

Fig. 5. The network analysis showing the co-occurrence patterns between natural enemy and insect herbivore in forest tea plantations and monoculture tea plantation. Each dot represents a arthropod species, and the size of each dot is proportional to the abundance. A connection between dots represents a strong and significant correlation ($r > 0.8$, $P < 0.01$).

different management systems. Our results show that compared to the monoculture tea plantations, forest tea plantations had a higher diversity and abundance of natural enemies, a more complex network structure, and a lower abundance of insect herbivores. Our results are consistent with the prediction that forest tea plantations enhance herbivore control by increasing natural enemy diversity and network structure between natural enemies and herbivores.

Arthropod assemblages in two different tea plantations

We found forest tea plantations harbored a greater diversity of all arthropods, natural enemies, and insect herbivores than monoculture tea plantations. Previous work demonstrated that vegetation communities of the forest tea plantations are similar to natural forests including herbs, shrubs, vines, and epiphytes, while the monoculture tea plantations are dominated by herbs without trees (Qi et al. 2013). Vegetation complexity including structural complexity and plant species diversity may increase the arthropod diversity by creating environmental heterogeneity and resource availability (Li et al. 2019). Our result is consistent with previous finding that diverse plants in plantations could provide natural enemies with additional prey species, and plantations can be moderated by various plant species, which can provide microhabitats that enhance predator and parasitoid survival during winter (Gurr et al. 2017).

In our study, the higher abundance of all arthropods and herbivores in the monoculture tea plantation is mostly caused by a sharp increase of *E. vitis*, a major insect pest affecting tea production throughout China that causes major outbreaks during summers that are often extremely devastating (Liu et al. 2015). *Empoasca vitis* accounts for 57% of arthropod individuals in the monoculture tea plantations, but it accounts for only 0.73% in the forest tea plantation. The dramatic increase of this dominant species may cause a loss in diversity of herbivores in monoculture tea plantations by decreasing resource and niche availability for other herbivore species.

Spatial variation and ecological network of arthropod in two different tea plantations

Our results show that the spatial distribution of arthropods and insect herbivores in the monoculture tea plantation was relatively uniform compared to the forest tea plantation. The differences are probably due to micro-environment differences (Gurr et al. 2017). Homogeneous monoculture tea plantations have less structural complexity and resource variation than do forest tea plantations, as well as less varied microhabitats and microclimates, which lead to diversity homogenization due to the relatively uniform environmental conditions (Laliberte et al. 2014). Unexpectedly, the two tea plantations had similar spatial variation of natural enemy abundance and diversity. The possible explanation is that natural enemies including predators and parasitoids have higher mobility and search range for prey and thus lead to similar spatial distribution pattern.

Generally, biological control efficiency increases with the diversity of natural enemies (Griffin et al. 2013). However, a diverse assemblage of natural enemies may weaken pest suppression due to antagonistic interactions among natural enemies (Liu et al. 2015). Therefore, the evaluating stability of biological control for multi-species natural enemy communities requires ecological network approach. An ecological network approach may improve our understanding of the relationships between natural enemy assemblages and insect herbivores (Tylianakis and Binzer 2014, Welch and Harwood 2014). In our study, we found that the topology of natural enemy–insect herbivore co-occurrence networks in the forest tea plantations is more complex than that in the monoculture tea plantations. This implied that forest tea plantation had stable network structure and strong co-occurrence between natural enemy–insect herbivore, which was a more efficient system for pest suppression (Ollivier et al. 2020). The ecological network in the monoculture tea plantations was relatively simple, which may indicate the natural enemy and insect herbivore community is probably unstable and dynamic and may explain the outbreak of the leafhopper *E. vitis*. Furthermore, the differences in network structure might be a result of multiple factors, such as plant communities, predator identity, parasitoids, insect herbivores, and environmental variables (Gardarin et al. 2018).

Our study, to the best of our knowledge, is the first that formally evaluates arthropod assemblages in forest and monoculture tea plantations. In summary, our study revealed that the forest tea plantation had a higher diversity of arthropod and more complex network structure than the monoculture tea plantation. Moreover, our study suggests that the ecological network approach opens up new possibilities for improving our prediction and understanding of pest suppression in agroecosystem, with cascading effects on crop yield.

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Data Availability

Data are available from Dryad: https://doi.org/10.5061/dryad.m63xsj41n

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3677/full