Research Article

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Intercropped *Flemingia macrophylla* successfully traps tea aphid (*Toxoptera aurantia*) and alters associated networks to enhance tea quality

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Abstract

BACKGROUND: The tea aphid, *Toxoptera aurantia* is a destructive pest causing severe damage to the quality and yield of tea, *Camellia sinensis*. Relying on chemical insecticides to control this pest causes adverse ecological and economic consequences. Trap plants are an eco-friendly alternative strategy to mitigate pest damage on focal plants by attracting target insects and natural enemies. Yet, the utilization of trap plants in tea plantations remains limited. Besides, the effects of the trap plant on the tea aphid–ant–predator community and tea quality and yield are unknown.

RESULTS: Intercropped *Flemingia macrophylla* successfully trapped tea aphids and enhanced the complexity of aphid–ant–predator networks over three consecutive years compared to monoculture management. Moreover, *F. macrophylla* significantly increased the abundance of natural predators by 3100% and species richness by 57%. The increasing predators suppressed the aphid population and hampered its spillover to neighbouring tea plants. Consequently, *F. macrophylla* improved tea quality by an 8% increase in soluble sugar and a 26% reduction in polyphenols to amino acids ratio.

CONCLUSION: The study illustrated that *F. macrophylla* is a suitable trap crop for tea aphid control in tea plantations. This legume increases species nodes and strengthens multiple connections in aphid-associated communities through its cascade effects, improving tea quality. These findings shed light on the potential application of trap plants in tea plantations as an efficient integrated pest management (IPM) strategy.

Keywords: intercropping; trap plant; tea aphid; network; tea quality

1 INTRODUCTION

Trap plants are potential intercropping candidates that attract target insects from focal crops as an effective component of integrated pest management (IPM) strategies.[1,2] The trap plants have successfully managed certain destructive pests, such as stem-borers[3,4] and fruit flies.[5] Moreover, genotypic cultivars of wheat can be used as trap plants to reduce aphid infestation on focal wheat plants.[6] Furthermore, when combined with other IPM practices such as pesticides or yellow sticky traps, the trap plants efficiently suppress *Diaphorina citri*,[7] whiteflies (*Trialeurodes vaporariorum*),[8] and *Ascia* larvae.[9] Intercropping strategy has been widely explored in tea (*Camellia sinensis* L.) plantations in recent years, establishing diverse scenarios such as aromatic plant–tea, fruit–tea, and legume–tea intercropping systems.[10–16] Intercropping trap plants provide alternative strategies for pest population control.[17,18] However, successful applications of intercropped trap plants in tea plantations remain limited.

As a perennial crop, tea provides habitat for an estimated 1000 arthropod species globally.[17] Indeed, intricate interactions among pests and natural enemies in tea plantations form a complex network, showing seasonal dynamics that coincide with the growth stages of tea plants.[19] Hence, individual arthropod species can be considered as nodes within the network, interconnected by other species.[20,21] The structures of arthropod networks in tea plantations exhibit associations with biodiversity. Forest tea plantations establish more complex arthropod networks than monoculture tea plantations, with fewer herbivores and more natural enemies.[19] In addition, intercropped plants have been demonstrated to alter the spatial-temporal distribution of pests and their natural enemies in tea plantations, depending on the identity of the species. For instance, aromatic plants efficiently repelled leafhoppers (*Empoasca onukii*) from tea plants through volatile emissions and simultaneously enhanced natural enemies.[10] Furthermore, the legume *Flemingia macrophylla* mitigated

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the damage caused by green leafhopper (*E. onukii*) on tea buds as a pull module.[22,23]

The tea aphid, *Toxoptera aurantia*, is a destructive and widespread pest in tea plantations.[24–26] It is estimated to cause more than 30% economic reduction in tea plantations in Zhejiang province, China.[25] Traditional treatments for tea aphids predominantly rely on chemical pesticides, exacerbating 3R issues (resistance, residue, and resurgence).[27] Tea aphids are embedded in a complex network involving ants and predators within tea plantations. On the one hand, tea aphids engage in mutualistic relationships with attending ants, such as *Prenolepis mpairs* and *Lasius alienus*, by secreting honeydew as a reward.[28,29] On the other hand, tea aphids establish antagonistic relationships with natural enemies, including ladybeetles,[30] and parasitoid wasps (*Aphelinus* spp.).[25] In addition, there are competitive interactions between attending ants and natural enemies that ants drive away predators to protect aphids.[31–33] Until now, studies have focused on the individual components of tea aphids, ants, or natural enemies rather than examining the intricate interactions within the community.[34,26] A prior field study revealed that intercropped *F. macrophylla* significantly alleviated arthropod damages in a tea plantation.[35] Analyzing the potential effects of *F. macrophylla* as a trap plant on the networks associated with tea aphids would provide valuable insights into the complex dynamics of the arthropod community, leading to improved effectiveness of this strategy in tea plantations.

In this study, we intercropped the legume plant (*F. macrophylla*) in tea plantations to (1) assess their impact on tea aphid, ant, and predator guilds and (2) examine dynamic variations of networks over 2017–2019. (3) In March 2019, the potential effects of this legume on both tea quality and yields were explored. We proposed that intercropping *F. macrophylla* has the potential to trap tea aphids and increase both species richness and abundance of natural predators to enhance aphid-associated network complexity when compared to monoculture management. In addition, intercropped *F. macrophylla* ultimately leads to improvements in terms of tea quality and yields.

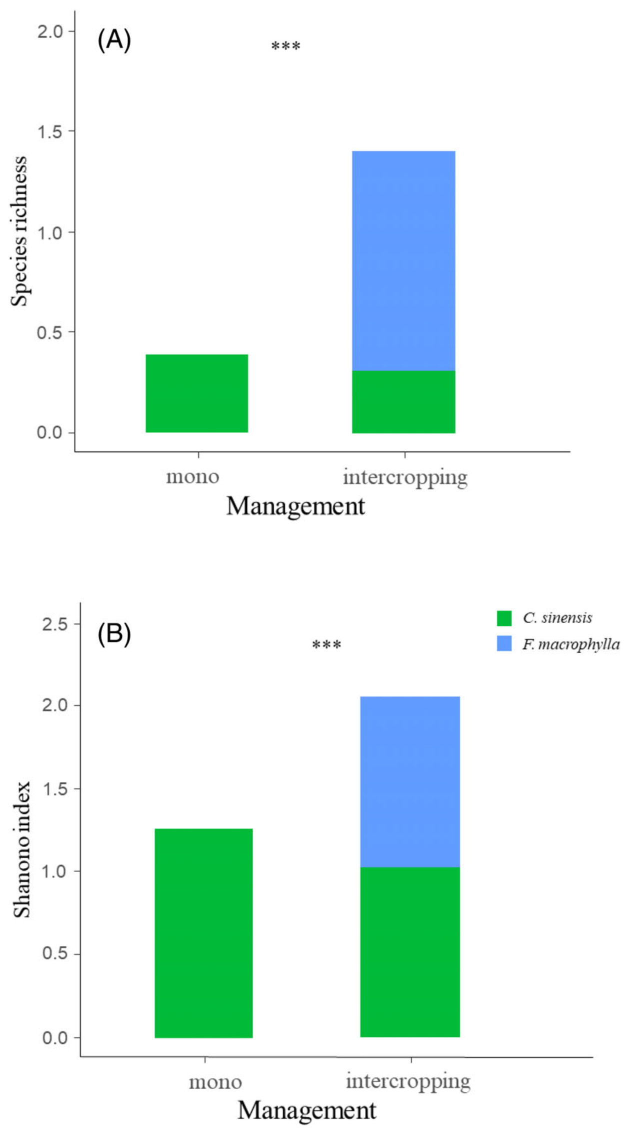

Figure 1. Means of species richness (A) and Shannon index (B) of monoculture and intercropping management strategies in tea plantations over 2017–2019, showing *Camellia sinensis* and *Flemingia macrophylla* in intercropping plantations, respectively. *** above bars (mean ± standard error) indicate significant differences ($P < 0.001$).

2 MATERIALS AND METHODS

2.1 Study site

The field study was carried out in a tea plantation located in Dadugang country (22°30′ N, 100°43′–101°12′ E), Xishuangbanna, Yunnan Province in the southwest of China during 2017–2019. This area has a subtropical monsoon climate, with an annual precipitation of 1400–1800 mm, average yearly temperature of 17–18 °C, and annual sunshine of 1800–2300 h. The soil type is mainly acidic red soil, with a pH ranging from 3.98 to 4.76. The tea plantation was founded in 1986 using seeds of big-leaf tea (*Camellia sinensis* var. *assamica*), modeling with two lines of tea in a row. The rows were spaced 1 m apart. The tea plantation was under organic management, prohibiting chemical pesticides. Organic fertilizers were applied during winter ploughing activities.

The intercropping of the tea plantation was conducted in 2012 by introducing *F. macrophylla* seedlings between rows of tea trees. The management of intercropping tea plantations was consistent with monoculture tea plantations. As a perennial legume,

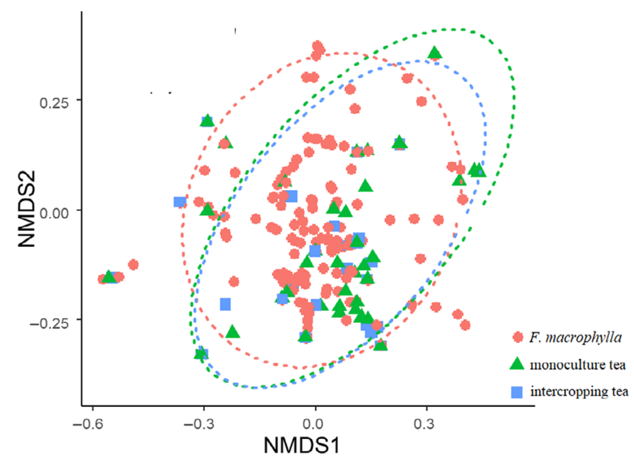

Figure 2. Community composition of aphid–ant–predator harboring on monoculture tea (*Camellia sinensis*), intercropping tea, and trap plant (*Flemingia macrophylla*) over 2017–2019, displaying in the ordination space of a non-metric multidimensional scaling (NMDS). Panels are Bray–Curtis dissimilarity distances and different ellipses represent 95% confidence.

F. macrophylla was cut down twice each year, one in summer after the peaks of tea aphids and another in winter after the yearly tea harvest finished aligning with tea garden ploughing. These pruning periods were chosen to mitigate the risk of tea aphid reinfecting the tea shoots. The pruned branches covered the ground between rows of tea trees, serving as green manure.

2.2 Field survey for arthropods

The repeated examinations were conducted in fixed plots from 2017 to 2019. Each 25 fixed plots (1 m × 1 m) were established in monoculture and intercropping tea plantations, covering the canopies of both tea tree and *F. macrophylla*. These plots were located at five corners along diagonal lines in five sites (10 m × 10 m) distanced at least 20 m. Each plot was examined repeatedly in mid-January, March, May, July, September, and November over 2017–2019, approximately every 60 days coincident with the different growth stages of tea. In each plot, leaves of tea or *F. macrophylla* were checked carefully, and the aphids including winged morphs were collected and counted. Meanwhile, canopies of tea and *F. macrophylla* per plot were scanned ten times to collect flying insects. Additionally, four branches of tea or legume were beaten ten times to collect immobile insects following the method described by Morente *et al.*[36] Ants and predators collected in the same plot were pooled, and the abundance of each species was counted. Then, samples per plot were kept in 70% alcohol for species identification in the laboratory. The obtained ants and predators were identified at least to the genus level, and species-level identifications were made whenever possible. The density of aphids, ants and predators measured as individuals per guild in each sampling plot (1 m × 1 m). The species of ants and predators were estimated as the number of taxa in each plot. The total species richness and Shannon–Wiener index of each plot over the years under different managements were evaluated using 'vegan' package in R.[37]

2.3 Quality and yield of tea buds

It is difficult to directly evaluate tissue loss caused by aphids due to their phloem-feeding behavior. The shoot density and weight of 100 shoots per plot were used to assess aphid damage on tea quality and yields. Fresh shoots (one bud and two leaves) were collected in a 0.5 m × 0.5 m frame as wide as the tea canopy in a total of 50 fixed plots in March 2019 under intercropping and monoculture managements. One hundred shoots per plot were put in an ice box to estimate tea quality. The shoot density (1 m × 1 m) was evaluated using shoot number per plot/0.25 m^2. Consequently, tea productions (g/m^2) of each management were calculated using shoot density × (100 shoots weight/100).

Quality properties, including water-soluble contents, soluble sugars, total amino acids, and total polyphenols, were assessed after tea shoots were dried (103 ± 2 °C). Water soluble contents were extracted with hot water following the national standard (GB/T 8305-2013). Soluble sugars were measured using the anthrone colorimetric method.[38] Total amino acids were determined using the ninhydrin colorimetry method according to national standards (GB/T 8314-2013). The total polyphenols were detected using a Foline–Ciocalteu assay with gallic acid as the standard.[39] The ratio of polyphenols to amino acids was estimated by dividing total polyphenols by total amino acids.

2.4 Network analysis

Networks of aphids, ants, and predators were constructed based on Spearman's correlation matrices per year under monoculture and intercropping management strategies. Network topological characteristics such as the number of nodes and edges, average path length, network diameter, average degree, and modularity were assessed to determine the effects of intercropping practice on network structure and dynamics. Then, the impacts of *F. macrophylla* were disentangled from those of *Camellia sinensis* in intercropping using heatmaps and filtered by correlation coefficient ($P < 0.05$). All heatmap analyses, network analyses, and visualization were performed with the 'igraph' package in the R environment.[40]

2.5 Statistical analyses

The effects of management on total species richness and the Shannon index over 2017–2019 were assessed by a one-way analysis of variance (ANOVA). To evaluate the effects of introducing *F. macrophylla* on aphid–ant–predator communities, non-metric multidimensional scaling (NMDS) based on Bray–Curtis distances was performed on monoculture tea, intercropping tea, and intercropped *F. macrophylla* datasets with the 'vegan' package. The annual density of aphid, ant, and predator guilds in monoculture and intercropping managements was evaluated using a two-way ANOVA with management and year as factors, followed by Tukey *post hoc* comparisons. Additionally, the same method was used to disentangle intercropped *F. macrophylla* effects on monthly variations of aphids, ants and predators from intercropping tea with management-plant and months as factors. Aphid data were log(number + 1) transformed to fit the normal distribution containing many zeroes. The correlations between aphids and ants,

Table 1. Two-way analysis of variance for the effect of management on annual density of tea aphid, ant, and predator guilds, and the effect of management-plant on monthly density of three guilds from 2017 to 2019

	Tea aphid		Ant		Predator	
Effect	*F*-Value	*P*	*F*-Value	*P*	*F*-Value	*P*
Annual density						
Management (M)	15.80	**<0.0001*** **	12.32	**0.0004*** **	16.67	**<0.0001*** **
Year (Y)	49.65	**<0.0001*** **	5.98	**0.0026** **	5.50	**0.0042** **
M × Y	1.824	0.16[ns]	1.86	0.16[ns]	8.60	**0.0002*** **
Monthly density						
Management-plant (MP)	36.84	**<0.0001*** **	16.86	**<0.0001*** **	28.11	**<0.0001*** **
Month (MO)	138.28	**<0.0001*** **	12.33	**0.0005*** **	13.78	**0.0002*** **
MP × MO	33.45	**<0.0001*** **	6.01	**0.0025** **	20.57	**<0.0001*** **

ns indicates non–significant, ** indicates significant $P < 0.01$, and *** indicates significant $P < 0.001$.

aphids and predators were explored with a regression model. The relation between winged morph and aphid was estimated using a regression model, while the mean abundance of winged was compared between monoculture tea, intercropping tea, and intercropped *F. macrophylla* with an unpaired *t*-test.

To evaluate the effects of intercropped *F. macrophylla* on tea yields and quality, such as shoot density, weight of 100 shoots, and tea yield, as well as water-soluble contents, soluble sugars, and the ratio of polyphenols to amino acids were compared between monoculture and intercropping practices with non-parametric pairwise Wilcoxon tests. Statistical significance was considered at $P < 0.05$.

Structural equation modeling (SEM) was conducted to estimate the direct and indirect effects of management strategies on Shannon diversity associated with network stability. The random factors such as plot, month, and year were removed from generalized mixed linear regression models for no significant effects. Model fit was determined by Fisher's C and P values. The best model was selected with a low Akaike information criterion (AIC) value compared to other candidate models. The SEMs were analyzed and visualized using the 'piecewise SEM' package.[41]

3 RESULTS

3.1 Aphid, ant, and predator communities

A total of 4282 and 24 360 arthropods, including tea aphids, ants, and predators, were collected in monoculture and intercropping tea plantations, respectively, over 2017–2019. The arthropods were categorized into five orders: Homoptera, Hymenoptera, Coleoptera, Diptera, and Neuroptera. Tea aphid was the predominant pest in the tea garden, comprising 93.48% of total abundance in monoculture and 93.23% in intercropping. The domain attending ant species belonged to *Lasius* spp., accounting for 0.82% in monoculture and 1.41% in intercropping. Syrphidae were the main predators in monoculture, presenting 2.21%, but only 0.38% in intercropping. In addition, six genera of lady beetles

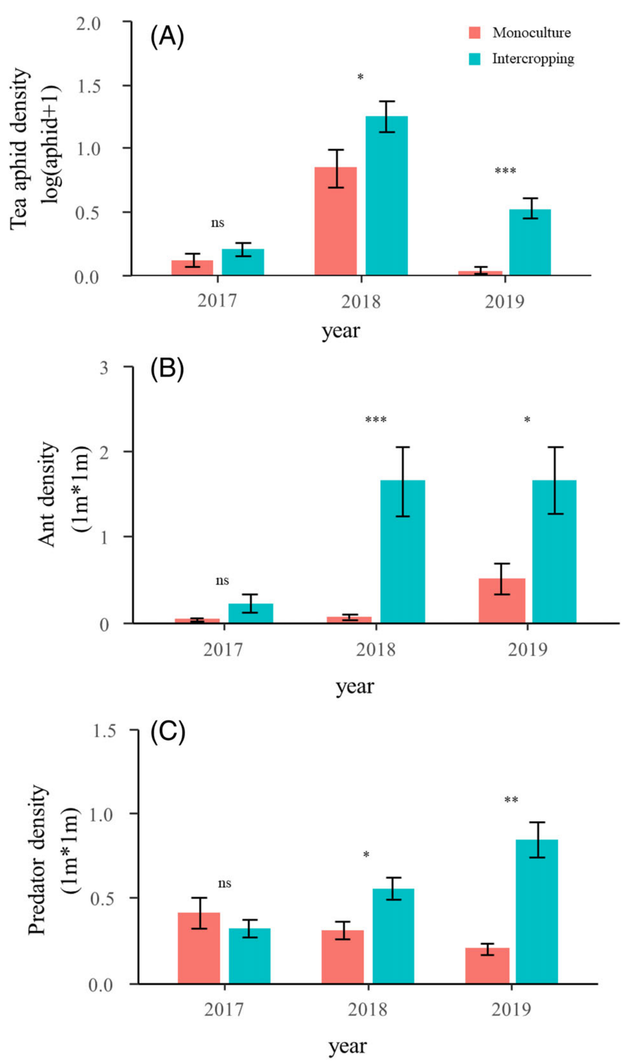

Figure 3. The annual variation of the aphid density (A), ant density (B), predator density (C) in monoculture tea and intercropping tea gardens, respectively. Different characters above the bars (mean ± standard error) indicate significant differences between treatments, * indicates $P < 0.05$, ** indicates $P < 0.01$, *** indicates $P < 0.001$, and ns indicates no significant difference.

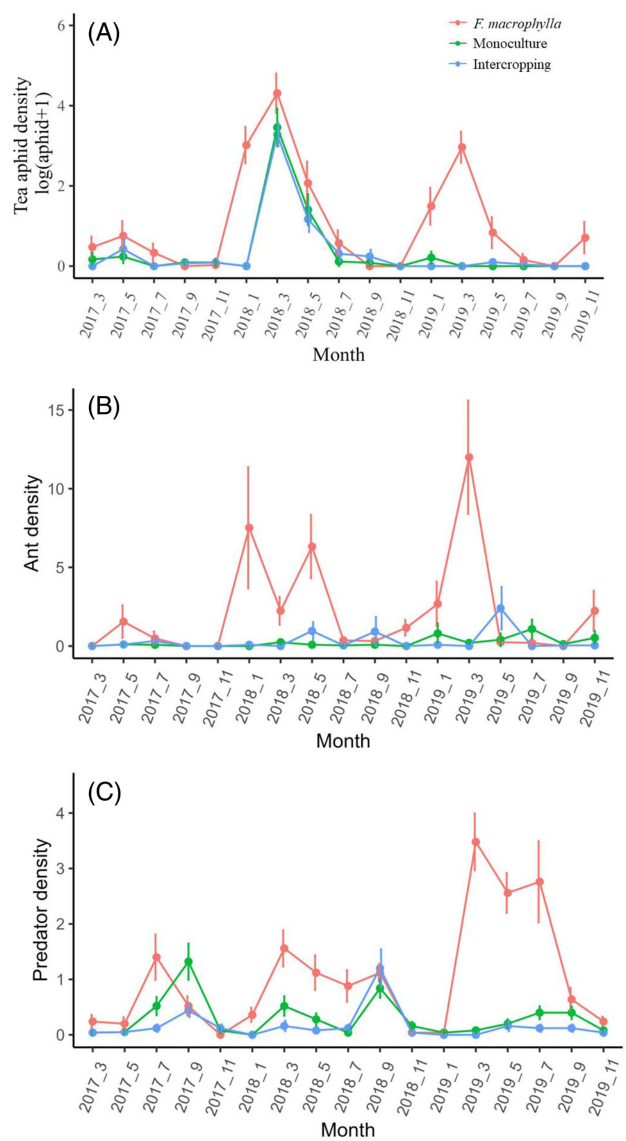

Figure 4. The monthly variations of tea aphid density (A), ant density (B), predator density (C) harboring on monoculture tea, intercropping tea, and *Flemingia macrophylla* over 2017–2019.

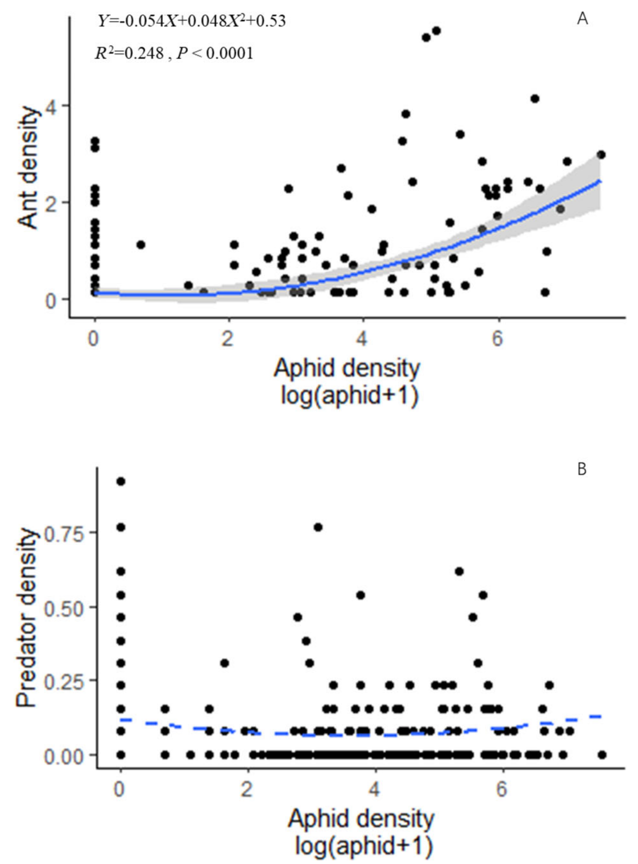

Figure 5. Scatter plot illustrates the density of ant (A) and density of predator (B) in relation to the density of tea aphid, which had been log-transformed, showing the regression line (blue) and 95% confidence area (gray area).

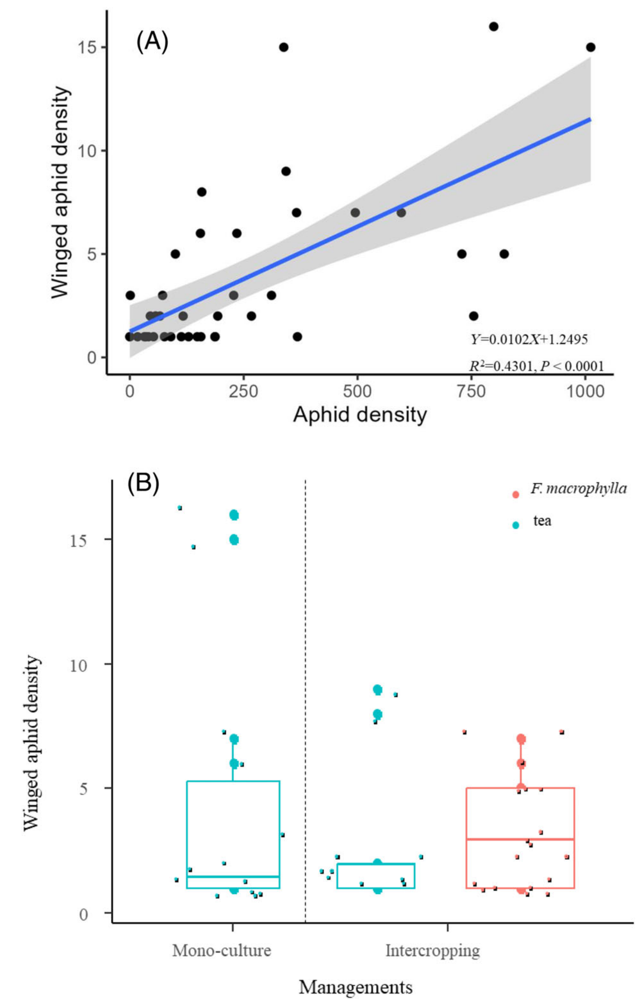

Figure 6. The line regression between winged aphid and aphid density (A), including total individuals collected on both tea and *Flemingia macrophylla* in monoculture and intercropping management in March 2018. Winged aphid density (B) distribution in monoculture tea, intercropping tea, and *F. macrophylla*. The figure shows mean (lines) in per box with error bars, and outliers are also shown in plots.

were identified in monoculture, and ten genera were found in intercropping with a 31-fold increase in total abundance.

The intercropping management significantly increased total species richness ($F_{2,1257} = 108.90$, $P < 0.0001$) (Fig. 1(A)) and the Shannon index ($F_{2,1257} = 75.81$, $P < 0.0001$) (Fig. 1(B)) when compared with the monoculture management over 2017–2019. Furthermore, the NMDS analysis showed no obvious difference in the aphid–ant–predator community between monoculture tea, intercropping tea, and *F. macrophylla* (Fig. 2).

Intercropping management significantly increased annual densities of the aphid, ants and predators (Table 1). *Post hoc* comparison showed that intercropping significantly elevated the densities of aphid, ant and predator in 2018 and 2019, but had no significant effect on them in 2017 (Fig. 3). Intercropped *F. macrophylla* effectively attracted and stimulated tea aphids, which were followed by ants and predators (Fig. 4) (Table 1). The aphid population exhibited two peaks on *F. macrophylla* in 2018 and 2019. In contrast, it displayed a single peak on tea in the spring of 2018 regardless of management (Fig. 4(A)). The ant showed a positive correlation with aphids ($R^2 = 0.248$, $P < 0.0001$) (Fig. 5(A)). In addition, an outbreak of winged aphids occurred in March 2018. Winged aphids exhibited a positive correlation with aphids ($R^2 = 0.43$, $P < 0.0001$) (Fig. 6(A)), and intensively accumulated on *F. macrophylla* (Fig. 6(B)).

3.2 Networks of aphids and their associated ants and predators

Intercropped *F. macrophylla* enhanced the complexity of aphid–ant–predator networks compared to monocultures over 2017–2019 (Fig. 7). The networks in monoculture displayed relatively simple structure with fewer species, fewer links per species, and smaller modularity values (Table 2). Intercropping networks exhibited more complexity, comprising more species and nodes and higher links per species and modularity (Table 2).

Moreover, *F. macrophylla* hosted more complexity networks than intercropping tea by attracting species away from it (Fig. 8). The aphid-associated networks showed annual dynamics on *F. macrophylla* that tea aphid predominantly established positive connections with *Tetramorium* spp. in 2017; shifted to *Lasius* spp. in 2018; related with *Tetramorium* spp., *Crematogaster* spp., and *Lasius* spp. in 2019. Meanwhile, tea aphids exhibited negative connections with *Harmonia axyridis* in 2018, *Illeis* spp., and Syrphidae in 2019. In contrast, settling on tea shoots in monoculture and intercropping strategies, tea aphids were consistently negatively connected with Syrphidae in 2017 and 2018 (Fig. 8).

3.3 Tea quality and yields

Intercropped *F. macrophylla* did not affect tea yields because it had no significant impact on the weight of 100 shoots

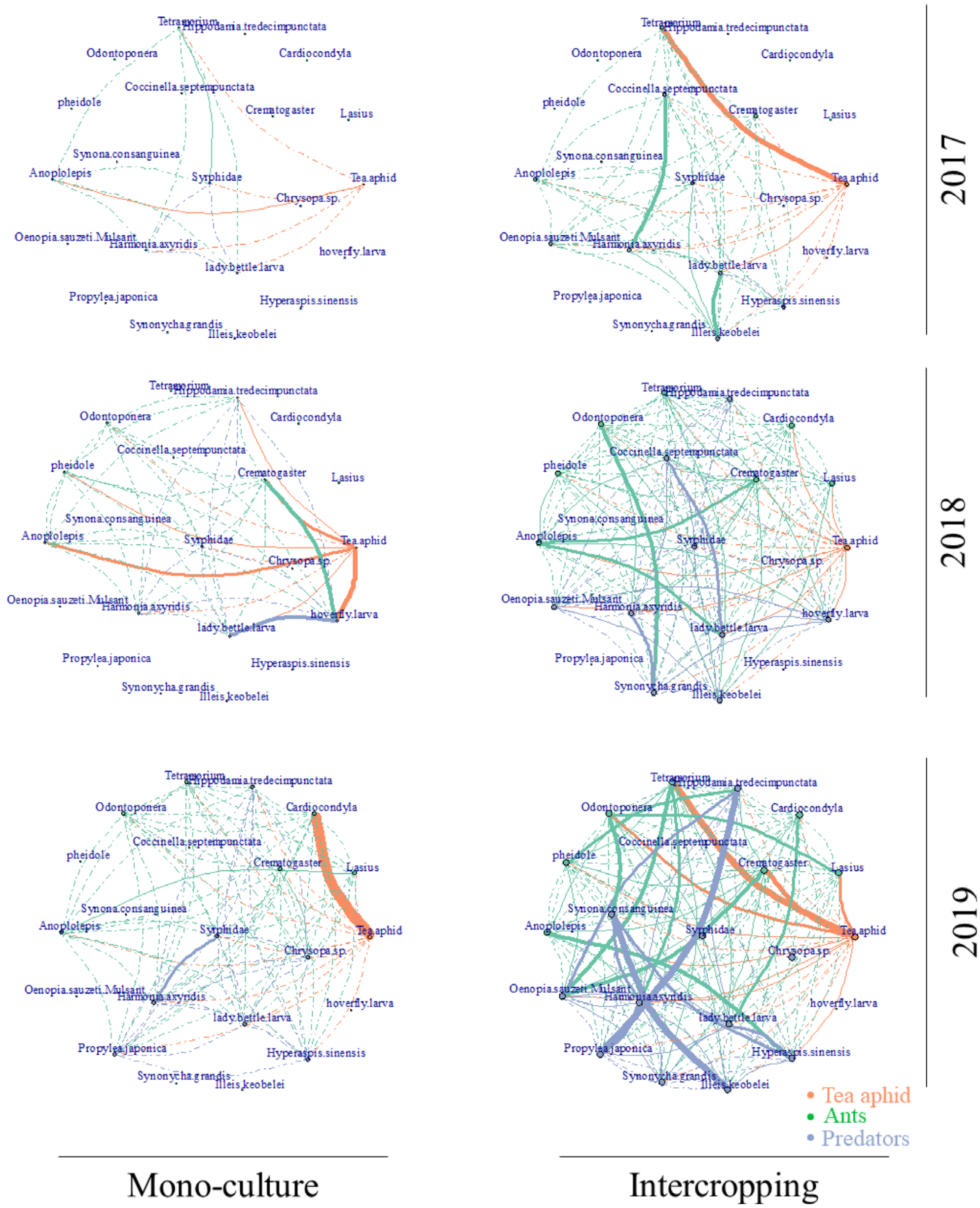

Figure 7. Annual dynamics of aphid–ant–predator networks in monoculture and intercropping tea plantations over 2017–2019. The solid line represents a positive correlation, and the dotted line indicates a negative correlation. Different colors of lines represent links originating from tea aphids (orange), ants (green), and predators (blue). The width of the line corresponds to its correlation ecoefficiency, with wider lines denoting stronger correlations, and the node size reflects its degree, with bigger nodes denoting more connections from it.

Table 2. Topology properties of ant–aphid–predator networks in monoculture and intercropping management strategies from 2017 to 2019

Year	Management	Nodes numbers	Edges numbers	Average degree	Density	Degree centralization	Modularity
2017	Monoculture	6	15	1.4286	0.0357	0.0938	0.0089
	Intercropping	11	55	5.2381	0.1310	0.125	0.0264
2018	Monoculture	10	45	4.2857	0.1071	0.1238	0.0247
	Intercropping	17	136	12.9534	0.3238	0.0800	0.0378
2019	Monoculture	14	91	8.6667	0.2167	0.1138	0.0338
	Intercropping	19	171	16.2857	0.4071	0.0450	0.0402

($P = 0.229$) or shoot density ($P = 0.675$) per plot. Instead, this legume significantly enhanced tea quality by increasing soluble sugars ($P = 0.037$) and reducing the ratio of polyphenol/amino acid ($P = 0.0022$) in the same amount of water extracted ($P = 0.85$) compared to that of monoculture tea shoots in March 2019 (Fig. 9).

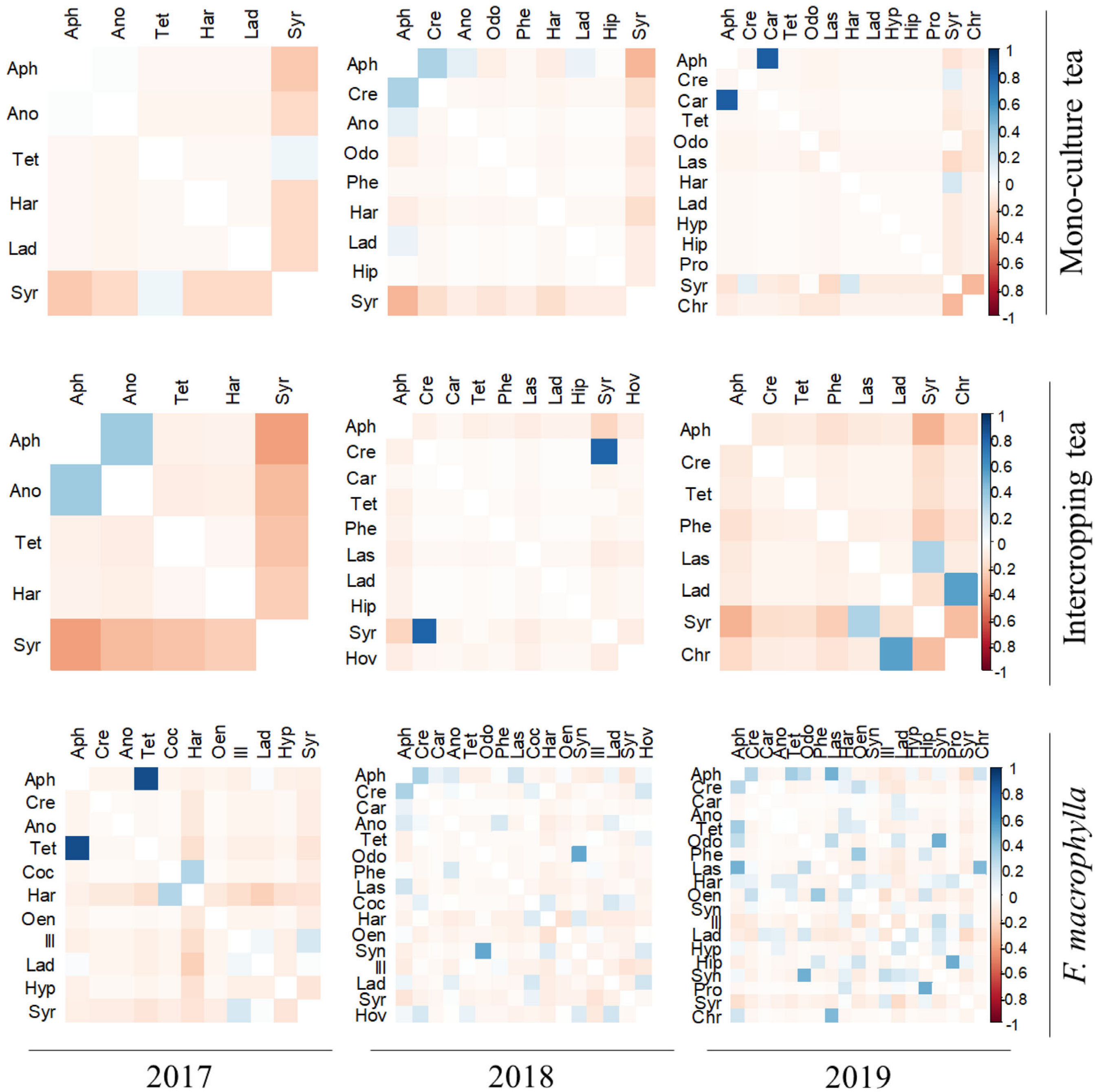

Figure 8. Correlation matrix of aphid, ant, and predator communities occurring on monoculture tea, intercropping tea, and *Flemingia macrophylla* over 2017–2019. Abbreviations in the correlation matrix indicate the following: Aph, *Toxoptera aurantia*; Cre, *Crematogaster* spp.; Car, *Cardiocondyla* spp.; Ano, *Anoplolepis* spp.; Tet, *Tetramorium* spp.; Odo, *Odontoponera* spp.; Phe, *Pheidole* spp.; Las, *Lasius* spp.; Har, *Harmonia axyridis*; Oen, *Oenopia sauzeti* Mulsant; Syn, *Synonycha grandis*; Ill, *Illeis keobelei*; Lad, Lady beetle larva; Hyp, *Hyperaspis sinensis*; Hip, *Hippodamia tredecimpunctata*; Syn, *Synona consanguinea*; Pro, *Propylea japonica*; Syr, Syrphidae spp.; Chr, *Chrysopa* spp.

The SEM demonstrated that intercropped *F. macrophylla* significantly strengthened both direct and indirect connections, leading to increases in the Shannon index (model fit, monoculture, Fisher's $C = 0.37$, $df = 2$, $P = 0.831$; intercropping, Fisher's $C = 9.528$, $df = 2$, $P = 0.049$) (Fig. 10).

4 DISCUSSION

Intercropped *F. macrophylla* proved an effective trap plant for tea aphids (*Toxoptera aurantia*), attracting wingless and winged morphs. This trap legume successfully reduced aphid population on the nearby focal tea, consistent with oilseed rape (*Brassica napus* L.), significantly decreasing the population of peach aphids (*Myzus persicae*) on the tobacco plants.[42] Intercropping management did not have a significant impact on aphid, ant and predator densities in the year 2017. This may be attributed to intrinsic fluctuations within the aphid population. Indeed, *F. macrophylla* stimulated the population of shifting tea aphids as a bottom-up regulator, resulting in two peaks compared to the single peak on tea in both monoculture and intercropping managements.

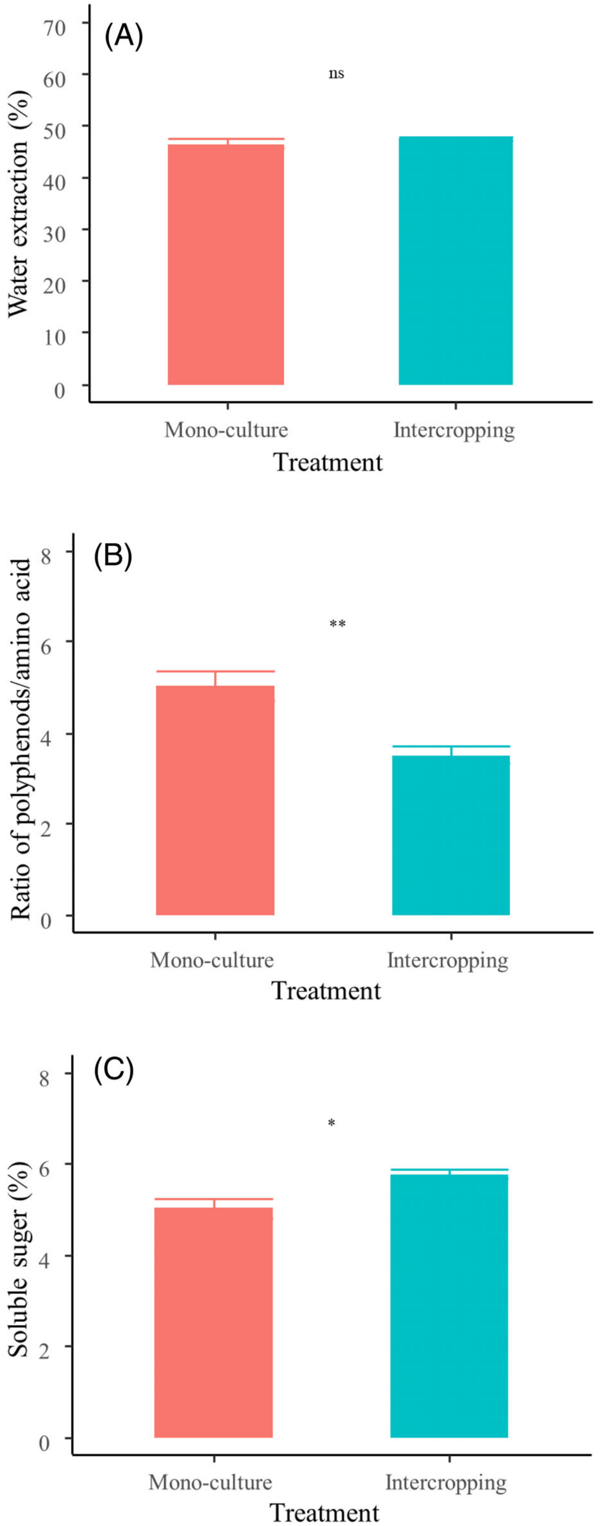

Figure 9. Quality properties of tea shoots harvested in March 2019 in monoculture and intercropping tea plantations, respectively, including water extraction (A), ratio of polyphenols to amino acids (B), and soluble sugar (C). Values are means ± standard error. Characters indicate significant levels; for example, ns indicates not significant, * indicates significant $P < 0.05$, and ** indicates significant $P < 0.01$.

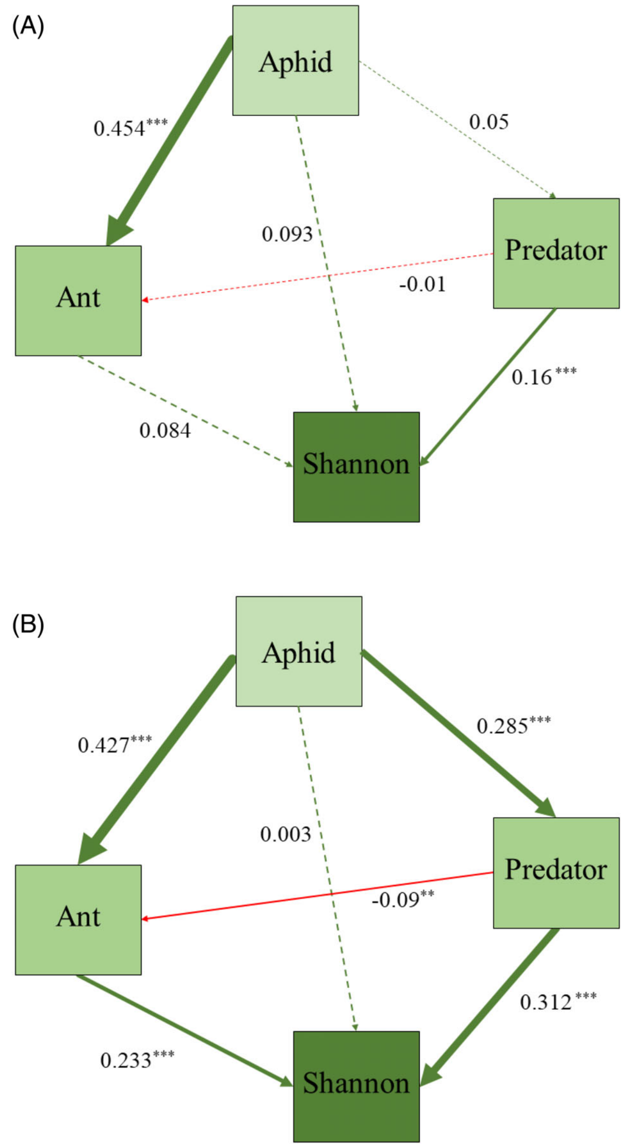

Figure 10. Structural equation modeling (SEM) showing the bottom-up effects of tea aphids on Shannon index, associated with network stability in monoculture (A) and intercropping (B) tea plantations. Numbers on arrows are standardized regression coefficients. Arrows indicate positive (green solid line), negative (red solid line), and statistically non-significant (dotted line) relationships. The thickness of lines qualifies the magnitude of the path coefficients, and the number of asterisks represents the level of significance (**$P < 0.05$, ***$P < 0.01$).

The second peak was linked to the winged male morph outbreak in 2018, which facilitated overwinter egg production. The surviving eggs ultimately led to a population increase in the spring of the following year, consistent with the previous study.[43] The accumulation of winged aphids may be explained by the volatile properties of this legume and attending ants.[44] Certain attractive compounds have been identified in *F. macrophylla* leaves, such as *cis*-3-hexenyl acetate, nonanal, α-farnesene,[22] and *cis*-3-hexen-1-ol, which are attractive to winged aphids.[45] Additionally, considering the relatively short lifespan of tea aphids (40 days), our experiments over 3 years have confirmed that tea aphids successfully colonized on *F. macrophylla*, which effectively prevented its spread back to tea trees.

The effects of *F. macrophylla* cascaded up to higher trophic levels of ants and predators through tea aphids, enhancing both species richness and abundance of these two guilds by providing food resources and shelter.[46-48] Moreover, the NMDS demonstrated that

F. macrophylla did not alter the aphid–ant–predator community, suggesting that intercropping did not introduce new pests into the tea plantation. Shifting ant and predator guilds lagged behind the aphid population, consisting of predatory mites (*Anystis baccarum*) followed by leafhoppers (*E. onukii*) in an intercropping tea plantation.[47] The ant populations exhibited two peaks on *F. macrophylla* due to its regression to tea aphid. In contrast, predators showed more variations and no coordination with aphids, partly attributed to intense disturbance from competitive ants. These patterns demonstrated that *F. macrophylla* can indirectly benefit ant and predator guilds through cascade effects.

Therefore, intercropped *F. macrophylla* enhanced aphid–ant–predator network complexity by increasing node numbers and strengthening connections. Stimulated tea aphids trapped by intercropped *F. macrophylla* can be considered the creator,[49] shaping these networks, including positive and negative connections. The positive connections represent cooperative relationships,[50] such as aphids and attending ants (*Tetramorium* spp., *Crematogaster* spp., and *Lasius* spp.), and negative connections represent competitive associations, encompassing aphid–predator (Coleoptera and Syrphidae) and ant–predator competitions in tea plantations. The more complex networks in intercropping tea plantations may indicate greater resilience when confronting disturbances, in line with tea plantations intercropped with green manure exhibited enhanced and multifunctional resistance to drying–rewetting cycles.[15]

The intercropped *F. macrophylla* in tea plantations significantly improved the quality of spring tea despite no significant effects on tea yield. Tea shoots from intercropping tea plantations exhibited a 26% lower ratio of polyphenols to amino acids and an 8% increase in soluble sugar compared with those from monoculture plantations, consistent with previous findings that intercropping with legumes enhanced tea quality.[14] However, *F. macrophylla* did not affect tea shoot density and weight, in contrast to reports that intercropping increased tea length and weight, leading to elevated tea yield.[11,51] The enhancement of tea quality under the intercropping strategy attributed to *F. macrophylla* alleviates tea aphid damage by trapping tea aphids away from tea plants, while increased predators facilitated biocontrol activities. In addition, previous studies have revealed that intercropping legumes usually enhances soil fertility, especially in terms of bacterial community.[52,53] These combined benefits allow tea to allocate more energy into shoot organs, improving tea quality.[11,12,14]

The SEM demonstrated that *F. macrophylla* strengthened bottom-up and top-down regulations through cascading effects in aphid associated networks, ultimately leading to a higher Shannon index. Enhanced tea aphids on trap legume positively mediated ant and predator populations as a bottom-up regulator, consistent with a previous study.[54] In turn, the stimulated predator populations not only directly suppressed the aphid population but also drove away attending ants to reduce protection of the aphid population indirectly as a top-down regulator. Consequently, a higher Shannon index is related to higher biodiversity in intercropping tea plantations, ultimately leading to higher quality of tea production.

5 CONCLUSION

This study provides valuable insights into applying trap legumes in tea plantations. Intercropped *F. macrophylla* efficiently traps tea aphids and enhances the natural biocontrol of predators through cascade effects. Future studies will focus on the chemical relationships within the aphid-associated networks, exploring the attractive volatiles of *F. macrophylla* and the composition of honeydew secreted by aphids feeding on *F. macrophylla*. In addition, combining with other IPM practices, such as a push module,[22] different seasonal plants,[15] or multiple plants,[52] could further improve the application of trap plants in tea plantations as an efficient IPM strategy.

AUTHOR CONTRIBUTIONS

JG and JT conceived and designed this study. JG, SZ and CZ conducted experiments. JG analyzed data and wrote the manuscript. All authors read and approved the manuscript.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

CONFLICT OF INTEREST STATEMENT

The authors do not have any conflicts to declare.

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