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ORIGINAL RESEARCH

The associational effects of host plant and mistletoe functional traits on leaf herbivory in mistletoe

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Abstract

Associational effects are a phenomenon in which herbivore damage on co-occurring plant species is influenced by neighboring plants. Mistletoes are a group of shrubs that obtain nutrients from host plants through haustoria. Despite the potential for mistletoe herbivory to be affected by associational effects with their hosts, the effects of host and mistletoe functional traits on mistletoe herbivory have been largely overlooked. This study aimed to evaluate the associational effects of host plants and the direct effects of mistletoe functional traits on mistletoe herbivory. To achieve this, we measured leaf herbivory and leaf traits of three mistletoe species (*Dendrophthoe pentandra*, *Scurrula chingii* var. *yunnanensis*, and *Helixanthera parasitica*) and their associated 11 host species during both dry and wet seasons. Our results showed that leaf herbivory of *D. pentandra* and *S. chingii* var. *yunnanensis* differed significantly on their respective host species, but *H. parasitica* did not. The relationships between mistletoe and the paired host herbivory differed between seasons, with a stronger positive relationship observed during the dry season. Furthermore, significant relationships were observed between paired leaf carbon, leaf nitrogen, and condensed tannin in mistletoes and their host plants, indicating that host plants can affect mistletoes' leaf functional traits. A group of mistletoe leaf traits provided significant predictions for leaf herbivory: leaves with higher leaf thickness and leaf total nitrogen showed higher herbivory. Overall, our study reveals that mistletoe leaf herbivory is directly affected by its leaf traits and indirectly affected by host associational effects, primarily through changes in mistletoes' leaf traits.

Keywords Mistletoe–host interaction · Plant–herbivore interaction · Herbivore damage · Neighborhood effect · Parasitic plants

Introduction

The interaction and coevolution between plants and insect herbivores is a fundamental subject in the fields of ecology and evolutionary biology. Insect herbivores, as primary consumers, consume plant materials for their growth, survival, and reproduction, which has significant effects on plant growth, reproduction, and overall fitness (Sarmento et al. 2011). Plants have evolved various defense mechanisms to avoid or repel phytophagous insects. These defenses include direct defense, which involves physical and chemical resistances, and indirect defense, which involves the production of volatile organic compounds and extrafloral nectar to attract natural enemies of insect herbivores (Becerra et al. 2009; Chen 2008; Núñez-Farfán et al. 2007). Therefore, the level of herbivory on plants is partially determined by their defense strategies. However, when plants grow in a community, the consumption of a particular plant may also be influenced indirectly by neighboring plants, either of the same or different species (Barbosa et al. 2009; Hambäck et al. 2014; Underwood et al. 2014). Certain plant associations can either decrease or increase the likelihood of herbivore detection or damage, which is known as associational resistance and associational susceptibility, respectively (Barbosa et al. 2009; Underwood et al. 2014).

Numerous studies have been conducted to investigate the factors that influence the associational resistance or susceptibility of plants to herbivores, as well as the underlying

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mechanisms. These studies have examined the apparency, physical, and chemical defense traits of neighbors, which can hinder herbivores from detecting, locating, and touching the target plant (Castagneyrol et al. 2013; Nesbit et al. 2016; Tagawa and Watanabe 2021). Plants located next to highly defended neighbors may experience reduced herbivore damage (Akashi et al. 2021; Baraza et al. 2006; Callaway et al. 2005). Conversely, when outbreaks of generalist herbivores occur, unpalatable individual plants near preferred neighbors may suffer high herbivore loads due to “spillover effects” (White and Whitham 2000). The extent and direction of the associational effects also depend on the spatial patterns of neighboring plants (Champagne et al. 2016; Emerson et al. 2012; Tsegai et al. 2013; Wang et al. 2010). Recent studies have suggested that the identity of heterospecific neighbors, interspecific phenotypic variation, and genotypic variation within species can all contribute to associational effects (Coverdale et al. 2018; Damien et al. 2016; Field et al. 2020). Additionally, the chemical compounds emitted by neighbors before or after being damaged may distract or repel insect herbivores to navigate and feed their host, or induce neighbors to resist herbivory (Huang et al. 2019; Karban et al. 2014; Quintana-Rodriguez et al. 2015). Nonetheless, the "background" or community of plants has been emphasized in the research on the associational effects of herbivore–plant interactions.

Parasitic plants are a group of plants that extract water and nutrients from other flowering plants by using haustoria. They have close physical and physiological connections and interactions with their host plants, which often possess different defensive traits or leaf quality (Pennings and Callaway 2002; Pennings and Simpson 2007; Watson 2009; Watson et al. 2022). This makes them a valuable system for studying interactions between plants, animals, and other plants, especially in terms of associational effects. In contrast to the associational effects observed among plants within the same community, parasitic plants may also transfer their defensive chemicals to or from their hosts (Adler 2000, 2003; Shen et al. 2023), potentially leading to different patterns of associational effects. Despite this, only a few studies have examined the effects of parasitic plants on host plant–herbivore interactions (Belchior et al. 2022; Guerra et al. 2021; Lázaro-González et al. 2019). These previous studies have mainly focused on how parasitic plants affect host–herbivore interaction through changes in host plant physiology, biochemistry, and morphology. Surprisingly, there have been few attempts to investigate how host plants affect parasitic plant herbivory and the interactions between parasites and host plants (but see Adler 2000, 2003; Marvier 1996).

Mistletoe, a diverse group of hemiparasitic shrubs, exhibits taxonomic variation and parasitizes the branches and stems of various angiosperms and gymnosperms (Liu and Le 2018; Nickrent et al. 2010; Watson 2001). Mistletoes, like other parasitic plants, obtain water and minerals from their host plants by means of the haustorium, which connects to the host plants’ vascular system (Zhang et al. 2023). The parasitic nature of mistletoe can negatively impact the health of its host, leading to reduced growth rates, reproductive capacity, and even death of infected branches or entire host plants under severe infection (Aukema 2003). However, mistletoe also serves beneficial roles in the forest and woodland ecosystem by providing food sources, nesting sites, and resting places for birds, mammals, and insects (Mathiasen et al. 2008; Watson 2001). Research has indicated that mistletoe can influence the interactions between host plants and herbivores by inducing changes in the defensive traits of the host plants or by providing shaded habitats for herbivores (Belchior et al. 2022; Chu et al. 2021; Guerra et al. 2021). Despite extensive studies on the effects of mistletoes on host plants, ecosystems, other organisms, and host–herbivore interactions, limited knowledge exists regarding the impact of host plants on mistletoe herbivory.

In this study, we aim to investigate the impact of host species on parasitic mistletoe herbivory by examining the herbivory rates and defensive traits of three mistletoe species growing on a combined total of 11 host species. We have formulated three hypotheses: H1: The presence of mistletoe on host species can lead to two contrasting outcomes in terms of herbivory. On the one hand, mistletoe may evade herbivory on host species that possess strong defensive mechanisms. On the other hand, mistletoe may experience increased herbivory if the host plants exhibit attractive traits. Consequently, there exists a positive correlation between mistletoe herbivory and the herbivory levels observed on its host plants (Fig. S1a). H2: Differences in mistletoe herbivory are linked to alterations in the defensive traits of mistletoe itself, which are impacted by the variations in nutritional and defensive chemistry of the host species. As a result, we expect the following outcomes: (1) there will be a positive correlation between the functional traits, particularly the chemical traits, of mistletoe and host plants (see Fig. S1b); and (2) the leaf herbivory of mistletoe is influenced by the functional traits of the mistletoe (see Fig. S1c). H3: Considering the significant influence of seasonality on plant–herbivore interactions, including defensive traits, nutritional quality, and herbivorous insect populations (Coley and Barone 1996), we hypothesize that the relationship between mistletoe leaf traits and its herbivores will be more pronounced during the dry season compared to the rainy season (Fig. S1a–c). This is due to the occurrence of more severe herbivore damage in the dry season within the framework of the seasonal tropical climate (Zhao et al. 2021).

Materials and methods

Study site and system

This study was conducted at Xishuangbanna Tropical Botanical Garden (XTBG), Chinese Academy of Sciences, located in Yunnan Province, southwestern China (21°56′N, 101°15′E, 580 m a.s.l.). The climate in the study area is characterized by a southwest monsoon, with a distinct dry season from November to April and a wet season from May to October. The average annual temperature is 22.7 °C, with monthly mean range from 14.8 to 25.5 °C. The average annual precipitation is approximately 1500 mm, with 80% occurring during the wet season and 20% during the dry season (Cao et al. 2006). The XTBG covers a total area of 1125 ha, and is surrounded by a river, and contains a patch of ~ 255 ha of relatively undisturbed tropical rainforest. The garden follows a long-term organic management strategy, which prohibits the use of pesticides and chemical fertilizers. This strategy allows many natural herbivores to colonize plants growing within the garden.

For this study, we chose three species of mistletoe, specifically *Dendrophthoe pentandra*, *Scurrula chingii* var. *yunnanensis*, and *Helixanthera parasitica*, which all belong to the Loranthaceae family. These mistletoe species are widely distributed in XTBG (Table 1). According to our previous observations, we have noted a gradient in the host ranges of these three mistletoes species in Xishuangbanna. For example, *D. pentandra*, *S. chingii* var. *yunnanensis*, and *H. parasitica* can parasitize approximately 235, 86, and 35 host species, respectively, in this region (Wang and Zhang 2017). We selected the host species based on the frequency of mistletoe infection and the accessibility of leaf sampling. The selected host plants were adult trees with a height exceeding 2 m, and were scattered along the roadside or forest edges. However, we did not consider their origin. Most host plants were grown together with various tree species in XTBG. We tried to select host individuals that were as far away from each other as possible. The farthest distance between selected host plants was approximately 3 km, while the nearest distance was around 5 m. The average distance between host individuals for each host species is provided in Table S1.

Data collection

Measurement of leaf herbivory

In tropical rainforests, insect herbivores cause more leaf damage than vertebrate herbivores and pathogens (Coley and Barone 1996). Our previous observations at XTBG revealed the absence of vertebrate herbivores consuming mistletoe and host leaves. Instead, we mainly observed lepidopteran herbivores, which are insect herbivores that chew on leaves. Therefore, our study specifically focused on these leaf-chewing insect herbivores. The herbivore damage (%) of chewing insects on leaf area for the paired collections of host and mistletoe was assessed in both the wet season (4-Jul to 5-Aug-2021) and dry season (6-Nov to 26-Dec-2021). In tropical rainforest in southwest China, the season is a primary predictor that can influence plant–herbivore interactions (Wenda et al. 2023). Additionally, mistletoe and host may exhibit different physiological responses to seasonal climate (Richards et al. 2021). To measure leaf herbivory, we collected the same mistletoe and host species during both seasons. For each interaction between host and mistletoe species, 3–15 individuals were selected and tagged. Approximately 80 leaves were collected from each paired

Table 1 Selected mistletoe species, host species, and sample size

Mistletoe species	Host plants (Family)	Host abbreviation	Sample size	
			Wet season	Dry season
Dendrophthoe pentandra	*Mangifera indica* (Anacardiaceae)	MI	5	10
	Citrus maxima (Rutaceae)	CM	3	9
	Ficus religiosa (Moraceae)	FR	5	10
	Kopsia arborea (Apocynaceae)	KA	5	11
	Bauhinia blakeana (Fabaceae)	BB	5	8
	Elaeocarpus hainanensis (Elaeocarpaceae)	EH	5	10
	Syzygium polypetaloideum (Myrtaceae)	SP	5	15
Scurrula chingii var. *yunnanensis*	*Citrus maxima* (Rutaceae)	CM	5	20
	Bauhinia blakeana (Fabaceae)	BB	5	10
	Camellia sinensis var. *assamica* (Theaceae)	CS	5	10
	Ficus hispida (Moraceae)	FH	5	10
Helixanthera parasitica	*Cinnamomum heyneanum* (Lauraceae)	CH	5	15
	Knema tenuinervia (Myristicaceae)	KT	4	5

host individual and mistletoe clump (usually 1–3 clumps growing on the same host tree) using pruning scissors. The leaves were collected from 4–5 branches extending in different cardinal directions. The collected leaves were stored in plastic bags and transported to the laboratory for scanning to obtain images of all the leaves. The consumed leaf area and reconstructed leaf area were then measured using ImageJ (Schneider et al. 2012). The percentage of consumed leaf was estimated using the average at the individual level for the host and at the clump level for the mistletoes.

Measurement of leaf functional traits

The study measured eight leaf functional traits of mistletoe and its paired host plants in terms of insect herbivore defense in both seasons. These traits included leaf toughness, leaf thickness (mm), moisture (%), specific leaf area (SLA, cm^2/g dry mass), total carbon (TC) (g/kg), total nitrogen (TN) (g/kg), C:N ratio, and condensed tannin (CT) (%). These functional traits are known to affect the nutritional quality and plant defense, which in turn can influence herbivorous insects (Agrawal 2007; Agrawal and Fishbein 2006; Pérez-Harguindeguy et al. 2016). In each host and mistletoe species interaction, three to five individuals were selected and sampled when measuring the leaf herbivory. For each host individual and mistletoe clump, 20 undamaged, fully expanded leaves were collected, and transported to the laboratory. To prevent water loss, the collected leaves were stored in a refrigerator and leaf functional traits were measured promptly. The SLA was determined by dividing the one-sided area of a fresh leaf (cm^2) by its dry weight (g). Leaf moisture content was calculated by subtracting the dry weight from the fresh weight, dividing the result by the fresh weight, and multiplying by 100% (Farias et al. 2020). Leaf thickness (mm) was measured using a digital micrometer, excluding primary and secondary veins. Leaf toughness was assessed using a leaf punch at three positions, again avoiding primary and secondary veins (Sanson et al. 2001). The leaves were then dried in an oven at 75 °C for 72 h, and the dry weight was measured to determine the water content. The average values of the measured leaf functional traits were calculated for each individual host plant and mistletoe clump. Additional leaves were collected, dried, and ground into a fine powder for chemical analyses, as 20 leaves were not sufficient for measuring chemicals. Leaf TC and TN were determined by a wet digestion procedure (Kalra and Maynard 1991), and the C:N ratio was subsequently calculated. The CT content was extracted using a modified version of the ISO 9648 method (GB/T 15686—2008), in which the supernatant was mixed with ferric ammonium citrate and ammonia solution, and the absorbance value at 525 nm measured with water as blank control. The CT content was then determined using a standard curve of Merck reference 773 tannic acid. All chemical analyses were conducted in the laboratory central of XTBG.

Statistical analyses

To investigate the impact of the host species and season on mistletoe leaf herbivory, we conducted an analysis of variance (ANOVA) separately by mistletoe species, and a Tukey post hoc comparison test was used to compare mistletoe herbivory among host species. Herbivory was used as response variables, while host species and season were employed as independent variables. Linear mixed effect models (LMMs) were employed to investigate the association between mistletoe herbivory and host herbivory. In this analysis, host herbivory, season, and their interactions were treated as fixed effects, while host species and mistletoe species were treated as random effects. To address issues of non-normality and heteroscedasticity in the residuals, a square root transformation was applied to the mistletoe and host leaf herbivory data.

To examine the relationship between paired functional traits of the mistletoes and host plants (*traits model*) and the impact of mistletoe functional traits on mistletoe herbivory (*herbivory model*), we conducted LMMs. The *traits model* incorporated fixed effects such as host functional traits, season, and their interactions. Similarly, the *herbivory model* included fixed effects of mistletoe functional traits, season, and their interactions. Host and mistletoe species were treated as random effects in both models. Prior to conducting the herbivory model, we conducted a Pearson correlation test to identify variables with high correlation. To avoid multicollinearity, only variables with a correlation coefficient (r) below 0.65 were included in the global models. The models were fitted using restricted maximum likelihood methods and the lmer function of the "lme4" package (Bates et al. 2015). The best fitting model was automatically selected based on the lowest Akaike information criterion value using the dredge and get.models functions of the "MuMIn" package (Bartoń 2023). After model fitting, we assessed the normality and heteroscedasticity of residuals through graphical analysis. In the *traits model*, all variables, except for leaf moisture and CT, were log-transformed. The results of the LMMs were visualized using the tab_model and plot_model function in the "sjPlot" package (Lüdecke 2023).

In order to examine the potential indirect influence of host functional traits on mistletoe herbivory by altering mistletoe traits, we employed principal component analysis (PCA) to reduce the dimensionality of the mistletoe variables and host variables. Subsequently, we utilized the PC axes obtained from the PCA to reduce the dimensionality of the host functional traits as exogenous variables, and to reduce the dimensionality of the mistletoe functional traits as endogenous variables for a structural equation model. The

PCA was performed using the PCA function in the "FactoMineR" package, with the variables standardized using the scale function (Lê et al. 2008). A structural equation model (SEM) is a statistical technique used in scientific research to analyze complex multivariate relationships among a set of interconnected variables. In SEM, paths are used to represent hypothesized causal relationships between variables, with some variables acting as predictors in one path and as responses in another. This approach allows for the exploration and quantification of indirect or cascading effects. Due to its ability to uncover hidden relationships, SEM has found extensive application in the fields of ecology and evolution (Lefcheck 2016). The SEM was conducted using the psem function in the "piecewiseSEM" package (Lefcheck 2016). All statistical analyses and data visualizations were carried out in R 4.3.0 ® Core Team 2023).

Results

The impact of host species on herbivory intensity of mistletoes

The herbivory intensity of *Dendrophthoe pentandra* was significantly affected by both host species ($P < 0.001$) and season ($P = 0.02$), but not by their interactions (Table 2). *Dendrophthoe pentandra* exhibited higher herbivory intensity on *Bauhinia blakeana* and *Mangifera indica* than on *Kopsia arborea* and *Ficus religiosa*, and greater herbivory intensity on *Citrus maxima* than on *Kopsia arborea* (Fig. 1A). The herbivory intensity of S*currula chingii* var. *yunnanensis* was significantly affected by the host species ($P = 0.005$), but not season and/or their interactions (Table 2). There were differences in herbivory intensity among different host species, with higher herbivory intensity observed on *Camellia sinensis* var. *assamica* than on *Citrus maxima*, *Ficus hispida*, and *Bauhinia blakeana* (Fig. 1B). However, the herbivory intensity of *Helixanthera parasitica* was not affected by the host species, the season, or their interactions (Table 2). Therefore, there was no significant difference in herbivory intensity between *Cinnamomum heyneanum* and *Knema tenuinervia* (Fig. 1C).

Table 2 Effects of host species, season, and their interactions on mistletoe herbivory based on two-way ANOVA analysis

Mistletoe species	*df*	*F*	*P*
Dendrophthoe pentandra			
Host	6	8.16	**< 0.001*****
Season	1	6.62	**0.012***
Host:Season	6	1.38	0.233
Scurrula chingii var. *yunnanensis*			
Host	3	4.85	**0.005****
Season	1	0.70	0.407
Host:Season	3	1.54	0.241
Helixanthera parasitica			
Host	1	0.03	0.857
Season	1	0.29	0.593
Host:Season	1	3.42	0.076

***$P \le 0.001$; **$P \le 0.01$; *$P \le 0.05$

Statistically significant *P* values are shown in bold

The study found a positive relationship between herbivory mistletoes and host plants during the dry season (coefficient = 0.19, $P = 0.009$). However, no significant relationship was detected during wet season. The variation in mistletoe herbivory was only explained by 2.4% by factors such as host herbivory, season, and their interactions (Table 3; Table S2; Fig. 2).

The relationship between host plants and mistletoe paired leaf functional traits

The study found significant relationships between the TC, TN, C/N, and CT content of mistletoes and the corresponding traits of their host plants (Table S3). However, no significant relationships were observed between mistletoes and host plants in terms of paired leaf moisture, leaf thickness, leaf toughness, and SLA (Table S3). Mistletoe leaf TC, TN, C/N ratio, and TC content increased with the paired traits of host plants (Fig. 3), but no significant effect of season on these relationships between the mistletoes and the host plants was detected (Table S3).

The impact of leaf functional traits of mistletoes on mistletoe herbivory

The mistletoes' TN, leaf thickness, season, and the interaction between season and TN were found to have significant impacts on mistletoe herbivory (Table S4). There was a positive correlation observed between mistletoe herbivory and TN, as well as leaf thickness (Table S5; Fig. 4B). Furthermore, the relationship between herbivory and TN was found to be more pronounced during the wet season (Fig. 4A). However, no significant relationship was found between mistletoe herbivory and CT (Table S5).

In the analysis of mistletoe traits variables, the first principal component (PC1) axis of PCA accounted for 40.1% of the total variation. It showed a positive correlation with leaf toughness, C/N, and thickness, while it had a negative correlation with TN and SLA (hereafter M-PC1) (Table S6; Fig S2). The second principal component (PC2) explained 26.4% of the variation and exhibited a positive relationship with CT, TC, and C/N ratios, but a negative relationship with leaf moisture, leaf thickness and TN (hereafter M-PC2) (Table S6; Fig. 2A). The third principal component (PC3)

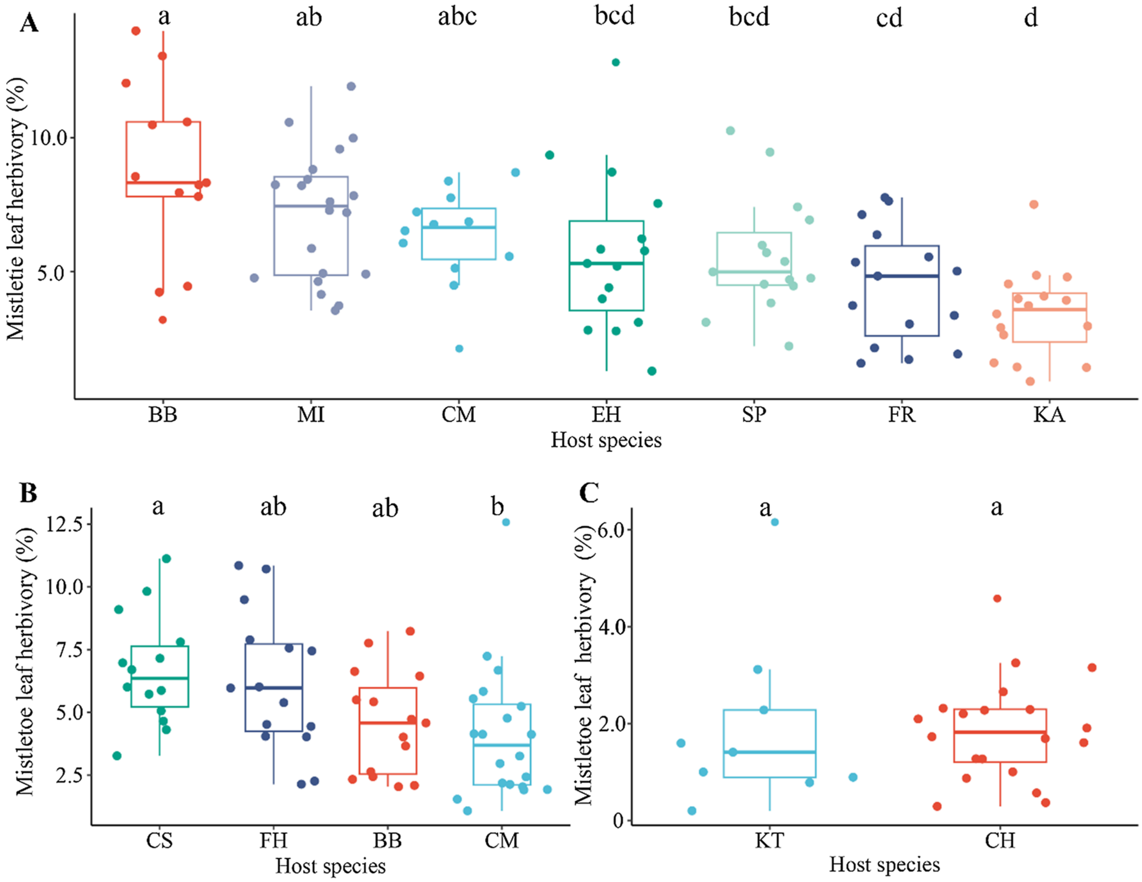


Fig. 1 The leaf herbivory intensity of mistletoes parasitizing different host species. **A**, *B*, and **C** the herbivory intensity of *Dendrophthoe pentandra*, *Scurrula chingii* var. *yunnanensis*, and *Helixanthera parasitica*, respectively. *BB Bauhinia blakeana*, *CM Citrus maxima*, *EH Elaeocarpus hainanensis*, *FR Ficus religiosa*, *KA Kopsia arborea*, *MI Mangifera indica*, *SP Syzygium polypetaloideum*, *CS Camellia sinensis* var. *assamica*, *FH Ficus hispida*, *CH Cinnamomum heyneanum*, *KT Knema tenuinervia*. *Different lowercase letters* mark significant differences ($P < 0.05$)

explained 15.5% of the variation and showed a positive relationship with leaf moisture, C/N ratio, SLA, and CT, while it was negatively related with TN and TC (hereafter M-PC3) (Table S6; Fig S2B). Additionally, we observed a significant negative association between mistletoe leaf herbivory and the M-PC2 and M-PC3 axes of PCA (Table S5; Fig. 4C), although the relationship between M-PC1 and herbivory varied depending on the season (Table S8).

The effect of host plants on mistletoe herbivory

Regarding the host functional traits, the first principal component (PC1) of PCA explained 50.1% of the total variation, and showed a positive relationship with host TN, SLA, moisture, and thickness, while exhibiting a negative relationship with host C/N, TC, CT, and toughness (hereafter H-PC1) (Table S7; Fig. S2 C). The second principal component (PC2) of PCA explained 2.2% of the variation and displayed a positive relationship with TC, TN, and SLA, and a negative relationship with leaf toughness and thickness (hereafter H-PC2) (Table S7, Fig. S2 C). The third principal component (PC3) of PCA explained 10.0% of the variation and exhibited a positive relationship with leaf moisture, CT, SLA, thickness, and C/N, while showing a negative relationship with TN (hereafter H-PC3) (Table S7; Fig. S2 D).

The piecewise SEM revealed significant associations between H-PC1 and M-PC1, M-PC2, and M-PC3. H-PC2 was significantly associated with M-PC2 and M-PC3, and H-PC3 was also significantly related with M-PC1 (Fig. 5). Furthermore, we observed a significant relationship between M-PC2 and mistletoe herbivory (Fig. 5).

Discussion

This study presents a distinct pattern of associational effects mistletoe herbivory in host plants. Leaf herbivory by *D. pentandra* and *S. chingii* var. *yunnanensis* varied significantly among different host species, while *H.*

Table 3 Effects of host herbivory, season, and their interactions on mistletoe herbivory based on linear mixed-effects model

Fixed effects			
Predictors	Estimates	CI	*P*
(Intercept)	1.72	1.05 – 2.39	**< 0.001**
Host herbivory	0.19	0.05 – 0.34	**0.009**
Season [wet]	0.31	– 0.04 to 0.66	0.078
Host herbivory:Season [wet]	– 0.31	– 0.56 to – 0.06	**0.015**
Random effects			
σ^2	0.26		
$\tau_{00\ \mathrm{Host}}$	0.12		
$\tau_{00\ \mathrm{Mistletoe}}$	0.27		
ICC	0.61		
N_{Host}	11		
$N_{\mathrm{Mistletoe}}$	3		
Observations	199		
Marginal R^2/Conditional R^2	0.024/0.617		

Marginal R^2 and *conditional* R^2 are the variation explained by fixed effects and the variation explained both by fixed and random effects, respectively

Statistically significant *P* values are shown in bold

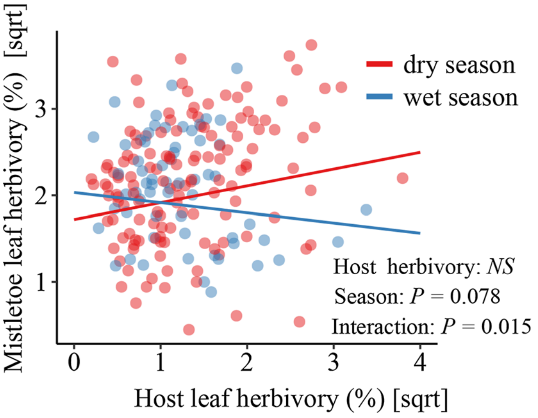


Fig. 2 The relationship of leaf herbivory between mistletoes and host plants; *points* are raw data, *lines with different colors* represent model-fitted slopes; *red points* and *red line* dry season, *blue points* and *blue line* wet season, *NS* non-significant

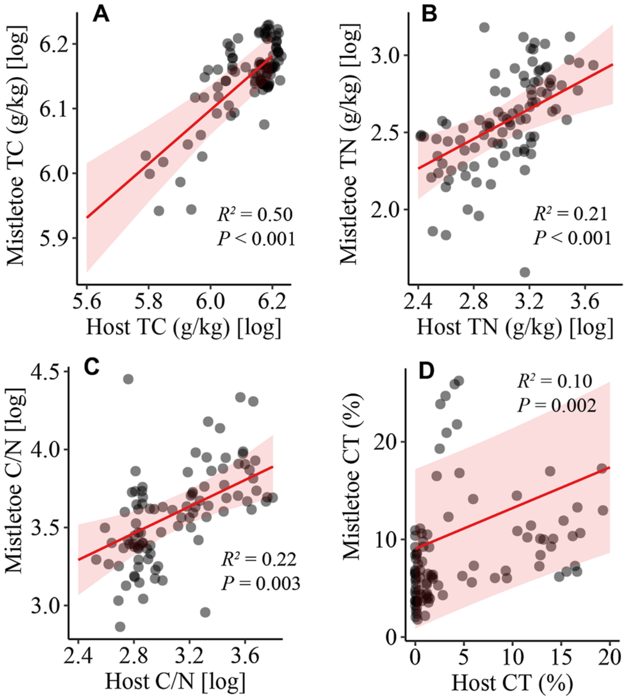


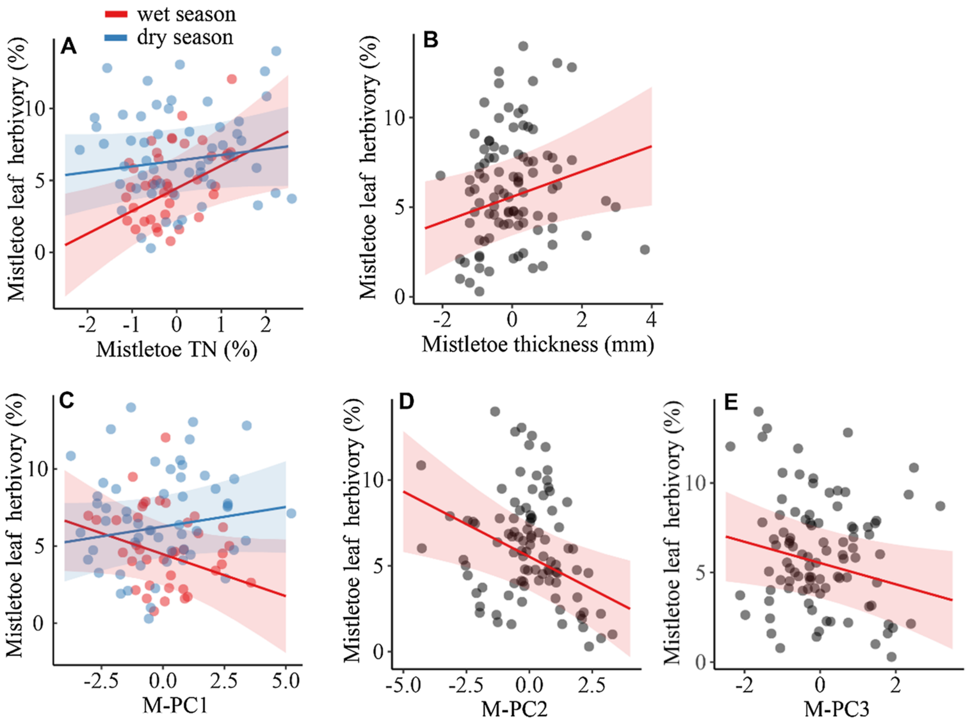
Fig. 3 The relationship of paired leaf functional traits between mistletoes and host plants, based on the predicted results of the best model of linear mixed-effects models; *red line* model-fitted slope, *black points* mixed data for both dry and wet seasons

parasitica did not show significant variation. Additionally, mistletoe herbivory was positively related with host plant leaf herbivory, with a strong positive correlation during the dry season. Certain leaf chemical traits, such as leaf TN, TC, C/N ratios, and CT, showed a significant positive association between mistletoes and host plants. However, no similar relationships were found for leaf moisture, leaf toughness, leaf thickness, and SLA, indicating that mistletoe leaf chemical traits can be influenced by their host traits. Mistletoe leaf herbivory was best predicted by a combination of mistletoe leaf traits, including TN and leaf thickness. The effect of TN on mistletoe herbivory is stronger during the wet season compared to the dry season. Overall, this study suggests that mistletoe leaf herbivory is directly affected by its leaf traits and indirectly affected by host associational effects, primarily through changes in the mistletoes' leaf traits.

Host plants displayed significant associational effects upon mistletoe leaf herbivory

Our study supports the first hypothesis (H1) that the leaf herbivory of mistletoes is influenced by the host species and is positively correlated with it. This relationship can be explained by the concept of associational susceptibility or associational resistance, where neighboring plants can affect the foraging behavior of herbivores and their natural enemies through emitting volatile organic compounds or by being more noticeable (Barbosa et al. 2009; Kim 2017). The palatability of the host plants plays a crucial role in determining associational susceptibility and resistance. When the host plants are highly palatable (low protection, high nutrition), such as *Bauhinia blakeana* and *Citrus maxima* in this study, they attract generalist herbivores, which can subsequently spread to the mistletoe plants, resulting in high

Fig. 4 The relationships between mistletoe herbivory and mistletoe leaf nitrogen (TN), leaf thickness, and the PC axis of PCA, based on the predicted results of the best model of linear mixed-effects models; *red points* and *red line* dry season, *blue points* and *blue line* wet season for **A** and **C**, *red line* model-fitted slope, *black points* mixed data for both dry and wet seasons for *B*, **D**, and **E**



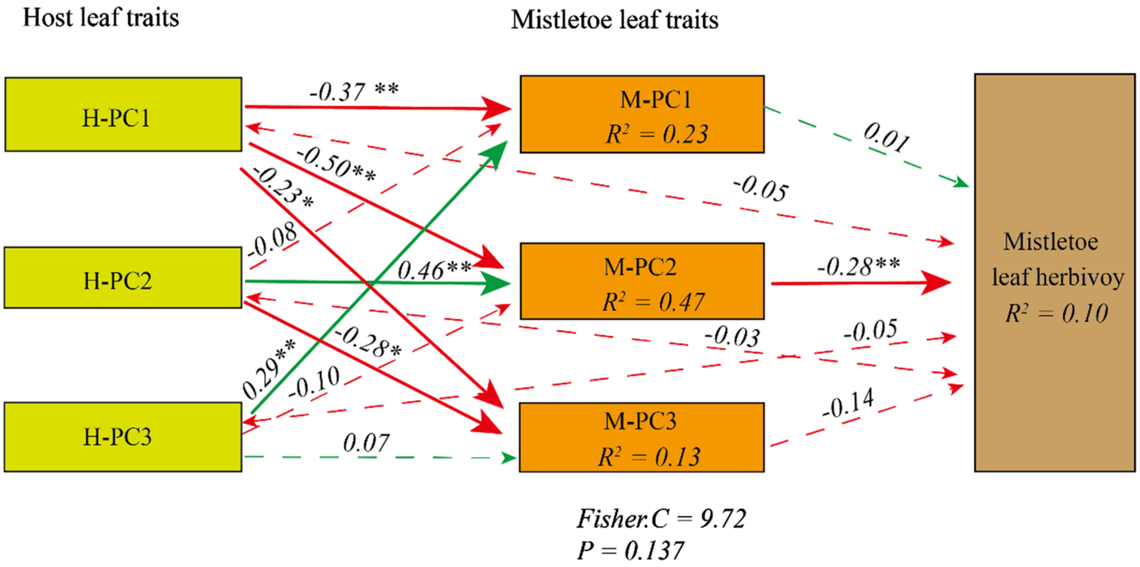


Fig. 5 The effect of host plant on mistletoe herbivory via changing the functional traits of mistletoe. Structural equational models (SEM) show how the host plant affects mistletoe leaf herbivory (Fisher's $C = 11.94$, $P = 0.063$); *solid green arrows* significant positive paths ($P \leq 0.05$ piecewise SEM), *solid red arrows* significant negative paths ($P \leq 0.05$ piecewise SEM), *dotted arrows* non-significant paths ($P \leq 0.05$ piecewise SEM); the *thickness* of the significant paths represents the magnitude of the standardized regression coefficient or effect sizes, given on the *arrows*. R^2 for component models are given under the *circles* or *squares* of endogenous variables

herbivore loads on the mistletoes. On the other hand, if the host plants are unpalatable (low nutrition, high defense), such as *Elaeocarpus hainanensis* and *Syzygium polypetaloideum* in this study, they can deter herbivores from consuming them (Table S10), by providing protection for the mistletoes, leading to lower herbivory on both the mistletoes and the host plants. We also found that the relationship between the mistletoes and host herbivory was stronger during the dry season, which can be attributed to changes in leaf traits (Richards and Coley 2007; Yoneyama and Ichie 2019) or the seasonal fluctuation of the resource–herbivore relationship. Additionally, the variation in mistletoe leaf herbivory was weakly explained by the leaf herbivory of the host plant, possibly due to differences in insect herbivore composition between the mistletoes and the host plants, or to different mechanisms of associational effects among mistletoe–host species pairs. For example, previous research has demonstrated that Hemiptera insects, specifically Psylloidea, display a strong preference for specific hosts and exhibit variations in their composition when comparing box mistletoe (*Amyema miquelii*) and its host *Eucalyptus* species (Burns et al. 2015). Therefore, we speculate that different herbivore composition between mistletoe and host species and different underlying mechanisms may weaken the predictive capacity of mistletoe herbivory using host herbivory as an indicator. These findings suggest that further exploration is needed to understand the direction and strength of associational effects of host plants on mistletoe herbivory and the underlying mechanisms.

The associational effects of host plants can vary depending on the mistletoe species. For instance, *D. pentandra* and *S. chingii* var. *yunnanensis* have a great number of host species in their natural environment (235 and 86 host species, respectively) compared to *H. parasitica* (which has only 35 host species recorded in this area). The former two species also exhibited significant differences in leaf herbivory among their host species. On the other hand, *H. parasitica* shows higher defensive traits and experiences less herbivory in nature compared to the other two species (Fig S3). It even contains a higher condensed tannin level than its host species (Tables S9, S10), indicating that this species has a strong defensive capacity against herbivore consumption, which may reduce or eliminate the associational effect of host plant. These findings suggest that the strength of associational effect may be more pronounced in mistletoe species with lower defensive traits.

Host plants exert indirect effect on mistletoes leaf herbivory via traits change in mistletoes

Our study revealed a positive correlation between the chemical characteristics of mistletoe and specific traits of their host plants. These traits include leaf TC, leaf TN, C/N ratio, and condensed tannin. This suggests that mistletoe leaf chemical traits can be influenced by the host species, and, in some cases, the influence can also be reciprocated. These findings provide support for our second hypothesis (H2). Previous studies have demonstrated that mistletoes possess the ability to acquire dissolved carbon and nitrogen from the xylem of their host plants, known as the "carbon–parasitism hypothesis" and "nitrogen–parasitism hypothesis" (Ehleringer et al. 1985; Marshall and Ehleringer 1990; Bannister and Strong 2001; Scalon et al. 2015). The pattern of the relationships in leaf functional traits between mistletoe and its host plant may be explained by these hypotheses, indicating the dependence of mistletoe on host plant quality (Watson 2009). Furthermore, our findings are supported by a study in Yunnan Province, southwest China, which revealed the similarity between mistletoes and host plants in nutrition elements, with host nutrient concentration being the best predictor of mistletoe nutrients (Zhang et al. 2023). However, the relationships between mistletoes and host plants in terms of secondary metabolites have not been explored and understood (Mathiasen et al. 2008). Although investigations on the interactions between mistletoe and host plant secondary metabolites are limited, it has been observed that parasitic plants, such as *Castilleja indivisa*, can extract secondary metabolites, including alkaloid lupanine, as a defense mechanism against herbivores (Adler 2002, 2003). This phenomenon is facilitated by the close physiological connections between parasitic plants and host plants, which are established through specialized organs known as haustoria. These haustoria also enable mistletoes to acquire nutrients and secondary metabolites from their hosts (Glatzel and Geils 2009; Mathiasen et al. 2008). Therefore, the observed correlation between mistletoes and host plants in CT may be due to the absorption of this substance or basic elements required for its synthesis from host plants, which requires further exploration.

It is important to note how the host plant influences changes in functional traits and how these changes affect interactions between mistletoes and herbivores. Our study used PCA and SEM to examine the functional traits of host plants collectively impacting mistletoe leaf traits and subsequently affecting mistletoe leaf herbivory. Specifically, traits such as leaf TC, leaf NC, C/N ratio, and CT are significantly influenced by host plants, and play a significant role in determining mistletoe herbivory. These traits have been reported to have a significant impact on leaf palatability and nutrient availability to herbivores (Agrawal and Fishbein 2006; Mattson 1980; Zhao et al. 2021).

The effects of mistletoe leaf functional traits on mistletoe leaf herbivory

The herbivory levels of plants are typically influenced by their defensive characteristics and nutritional quality. In this study, we have examined the herbivory of mistletoes and found that the consumption of their leaves by herbivores was positively correlated with leaf TN. This aligns with previous studies that have shown that herbivores prefer foliage with high nitrogen levels (Agrawal 2007; Pérez-Harguindeguy et al. 2016). Surprisingly, we also found a positive correlation between leaf thickness and mistletoe herbivory, contradicting previous findings that suggested that herbivory decreases with increasing leaf thickness (Lobregat et al. 2017). We propose that this inconsistency may be explained by the fact that thick leaves contain more moisture, which can dilute the CT and carbon content in mistletoes (Fig S2A).

Mistletoe leaves are classified as hemi-succulent, meaning that they have fewer structural defenses but higher nutrient content compared to other plants (Richards et al. 2021; Watson 2001). Tannins are known to reduce herbivory by decreasing leaf protein digestibility, damaging the digestive system, and interfering with metabolism and growth (Moles et al. 2011; Peters and Constabel 2002). In our study, we found that mistletoe species with higher CT-containing leaves (*H. parasitica*) experienced less herbivory compared to other mistletoe species. This suggests that the difference in CT leaves among the three mistletoe species contributes largely to the differences in leaf herbivory. However, when considering mistletoe species as a random effect, the effects of CT on mistletoe leaf herbivory was not significant. This finding further suggests that the differences in mistletoe species themselves, rather than changes in CT induced by the host, influence mistletoe leaf herbivory. Nonetheless, we did observe a slight negative relationship between CT and herbivory (Table S5).

Interestingly, the correlation between mistletoe herbivory and leaf TN was unexpectedly stronger in the wet season, contradicting our third hypothesis (H3). This may be due to older leaves often containing more chemical defenses and being less palatable compared to young leaves (Coley and Barone 1996; Wenda et al. 2023; Yoneyama and Ichie 2019). We propose that herbivores prefer leaves with higher nutrient content when there is an ample supply during the wet season. Our analysis using PCA and LMMs further revealed that mistletoes possess multiple functional traits that collectively contribute to their leaf herbivory. Specifically, leaf TN, C:N ratio, CT, leaf toughness, and SLA play critical roles. These traits, in combination, provide an efficient defensive strategy against herbivores (also see Agrawal and Fishbein 2006; Zhao et al. 2021).

Limitations and conclusions

Ee would like to acknowledge several limitations in our study. Firstly, the assessments of leaf herbivory for both mistletoes and host plants were based on single time-points. This approach may underestimate the actual rates of herbivory, as leaves that have been completely consumed cannot be evaluated. However, it is important to note that this limitation is common to studies employing similar methods that are not conducted over an extended period (Coley and Barone 1996). Secondly, our study was conducted in a botany garden with a limited number of mistletoe species. Therefore, it is challenging to determine whether other factors, such as climate or mistletoe species, were relatively consistent across different hosts for a particular mistletoe species. Additionally, we believe that there may be other unconsidered factors that could influence the effects of host plants on mistletoe herbivory, such as the interactions between herbivorous insects and their predators in mistletoes and host plants. Thirdly, we must acknowledge the limited sample size of mistletoe species, host species, and the number of mistletoe–host species pairs. This limitation may restrict the generalizability of our findings. Therefore, it is necessary to expand this study to a regional or global scale, including a greater variety of mistletoe and host species, to retest the effects of host plants on mistletoe–herbivore interactions. This could also involve manipulating mistletoe herbivores, their predators, or the defenses of mistletoes, among other mechanisms.

Our study examined how host plants influence mistletoe's leaf herbivore. We have described a distinct associational effect for the parasitic–host plants upon herbivores, which differs from the neighboring plants in same community. This is because mistletoe leaf herbivory is influenced by both its own leaf traits and the effects of the host plants, which can alter the mistletoes' leaf traits.

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Author contribution statement LZ and G S designed the research and collected the data. GS analyzed the data and drafted the manuscript; JC and LZ revised manuscript, and all authors critically approved the manuscript.

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

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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