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Host-mediated effects on the reproductive phenological asynchrony of a generalist mistletoe in China

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Abstract

Host-mediated effects on hemiparasitic mistletoes were hypothesized to contribute to mistletoes reproductive phenological asynchrony, thus providing a longer period of food supply to its mutualistic pollinators and dispersers. However, studies with empirical data interrogating this hypothesis are lacking. Weekly monitoring of flowering and fruiting patterns on a generalist mistletoe *Dendrophthoe pentandra* (Loranthaceae) was conducted for two consecutive years in tropical Xishuangbanna, Southwest China. We examined whether flowering and fruiting patterns were seasonal, quantified the degree of stagger within *D. pentandra* populations and determined the factors influencing the first flowering date (FFD) of *D. pentandra*. Furthermore, the effect of change in the number of host species on reproductive phenological asynchrony of mistletoe was examined. We found that (i) both flowering and fruiting exhibited unimodal peaks in the two consecutive years of the study; (ii) the FFD was significantly influenced by crown area of mistletoe and light, such that clump with larger crown and more light exposure had an earlier FFD and longer flowering and fruiting durations; (iii) different host species had a significant impact on the phenology of mistletoes. However, contrary to our hypothesis, the number of host species did not significantly change the asynchrony of reproductive phenology of mistletoe. Therefore, these results suggest that alternative hypotheses are needed to interpret the ecological significance of the number of host species and phenological asynchrony of generalist mistletoes.

Keywords asynchrony, *Dendrophthoe pentandra*, first flowering date, host effect, mutualism

一种泛性桑寄生植物繁殖物候异步性的寄主介导效应

摘要：寄主介导效应被认为会导致半寄生性的桑寄生植物的繁殖物候异步性，并由此为与桑寄生植物互惠共生的传粉者和种子散布者提供更长时间的食物资源供应，但目前关于此方面的研究还缺乏相关的实证数据。本研究以广泛分布于中国西南西双版纳地区的一种泛性桑寄生科植物五蕊寄生(*Dendrophthoe pentandra*)为材料，每周监测其开花、结果物候，检测了其开花和结果物候是否呈季节性格局，量化了五蕊寄生繁殖物候的异步程度，并检测了影响该植物始花期早晚的因素。最后，本研究还检验了五蕊寄生繁殖物候的异步性随寄主种类数量变化的效应。研究结果表明：(i)在连续两年的物候观测中五蕊寄生的花期和果期都呈单峰分布格局；(ii)始花期显著受到植物大小和光照强度的影响，即冠幅越大和受光程度越高的植物个体有更早的始花期和更长的花期和果期；(iii)不同的寄主种类对五蕊寄生的繁殖物候

有显著的影响，但与假设相反的是，随着寄主种类数量的增加，五蕊寄生繁殖物候的异步性没有显著提高。这项研究表明，在解释泛性桑寄生植物的繁殖物候异步性及寄主种类的数量对其影响的生态学意义还需进行更深入的探究。

关键词：异步性，五蕊寄生(*Dendrophthoe pentandra*)，始花期，寄主效应，互利共生

INTRODUCTION

The timing of reproductive phenology of plants with seasonal and periodic cycles is a critical life-history trait and a fitness factor that drives mutualistic network structure and diversity (Elzinga *et al.* 2007; Encinas-Viso *et al.* 2012), which affects pollination, seed dispersal and quality of offspring, as well as the animals depending on these plants (Craine *et al.* 2012; Newstrom *et al.* 1994; Sun and Frelich 2011; Wright and Meagher 2003). Likewise, high asynchrony of flowering in populations with a low density may further decrease the number of available mating partners, thereby weakening reproductive success, especially for species with self-incompatibility mechanisms (de Assis Pires *et al.* 2014; Ollerton and Lack 1998). On the other hand, high levels of asynchrony in plant phenology can also prolong the spatiotemporal availability of nectar and fruit resources for mutualistic partners (Quintana-Rodríguez *et al.* 2018), and can represent the complementarity of resources at the community level (Watson 2001). Asynchrony also reduces the risk of pollination uncertainty when weather or resource conditions are unpredictable (Rathcke and Lacey 1985), and achieve asynchronous fruit ripening can increase successful seed dispersal (Gorchov 1988; Thompson and Willson 1979). In general, phenological patterns within conspecific populations, such as the first flowering date (FFD) (a phenological event), the flowering/fruiting duration (a phenophase) and the asynchrony index are important for understanding mutualism, especially for plants which need reciprocal pollinators and dispersers (Reid 1990; Sakai 2001; SanMartin-Gajardo and Morellato 2003).

The frequency and duration of reproductive phenology in tropical seasonal forests range from complete intraspecific synchrony to extreme asynchrony and from constant activity to recurrent short pulses (Bush *et al.* 2017; Pau *et al.* 2013; Sakai *et al.* 1999; Vanschaik *et al.* 1993). The reproductive phenology of species is driven by biotic factors (such as other sympatric plants, pollinators and seed dispersers) (Elzinga *et al.* 2007; Wright and Meagher 2003) and abiotic factors (e.g. temperature and precipitation) (Dunham *et al.* 2018; Pau *et al.* 2013). Importantly, light condition is vital for non-autotrophic shrubs, like mistletoes, which influences seed establishment and/or subsequent growth (Kelly *et al.* 2000; Norton *et al.* 1995). Phenological patterns may be scale- and density-dependent (de Assis Pires *et al.* 2014; Jensen *et al.* 2019) and plants in different locations may differ in phenology (Napier *et al.* 2014). Biological characteristics, such as height and age, can also influence reproductive phenology (Herrera 1991; Ollerton and Lack 1998). In some trees and hemiparasitic annual herbs, larger plants bloom earlier and flower for longer than smaller plants, and they also often have high levels of asynchrony (Dieringer 1991; Otárola *et al.* 2013).

Mistletoes are polyphyletic shrubby aerial stem parasites that depend on their hosts for water and nutrients and can conduct photosynthesis, and vary in their interaction with their hosts (Ehleringer *et al.* 1985; Griebel *et al.* 2017). They belong to the Santalales, which comprises 5 families, 88 genera and approximately 1600 species, and are distributed across terrestrial ecosystems, other than some alpine, desert and polar areas (Liu *et al.* 2018; Nickrent *et al.* 2010; Watson 2011). Structural host affiliations of mistletoes range from extreme generalization to extreme specialization (Milner *et al.* 2020; Norton and Carpenter 1998). For a particular mistletoe species that has interacted with different host species often shows certain functional differences or even genetic differentiation (Rodriguez-Mendieta *et al.* 2018; Yule *et al.* 2016; Zuber and Widmer 2009). In addition, as keystone species, mistletoes can provide food resources (leaves, nectar and fruits) and nest sites for many birds and other fauna, particularly to frugivore mistletoe specialists (Amico and Aizen 2000; Aukema 2003; Barea and Gerardo Herrera 2009; Reid 1990; Watson 2001). Meanwhile, they are heavily dependent on various birds for pollination and seed dispersal, thereby maintaining asymmetric and diffuse mutualistic relationships with their partners (Guerra and Pizo 2014; Watson 2001).

Asynchronous reproductive phenology of mistletoes plays an important role in maintaining mutualism with pollinators and seed dispersers by prolonging the spatiotemporal allocation of food resources (Davidar 1983b; Watson 2001). For example, *Amyema miquelii* (Loranthacea) plants have different onset and duration of flowering and fruiting at different locations in south-western Australia (Napier *et al.* 2014). Fruit ripening of *Psittacanthus calyculatus* (Loranthaceae) occurs asynchronously from November to March in Mexico (Lara *et al.* 2009). It is hypothesized that some host-mediated effects (e.g. host species, deciduous vs. evergreen host) have been key in developing phenological asynchrony in mistletoes (Teixeira-Costa *et al.* 2017). Host species identity is the most important factor influencing flowering time of desert mistletoe (*Phoradendron californicum*) in American deserts (Overton 1997; Yule and Bronstein 2018). However, few empirically based comprehensive studies of the reproductive phenology of mistletoe have been undertaken, and the extent to which host-mediated effects influence reproductive phenology remains poorly understood.

Parasitism is the most successful life-history strategy among all organisms, and interactions with their hosts play an important role in parasite ecology and evolution (Krasylenko *et al.* 2021; Yule and Bronstein 2018). In animal parasitology, phenotypic (e.g. body size) and genetic differentiation induced by the use of distinct host species (i.e. host-mediated effects) have received much attention (Mccoy *et al.* 2001; Ruiz-Montoya *et al.* 2005), but these have been less studied in plant parasites. In this study, we investigated the reproductive phenology (flowering and fruiting) of a generalist mistletoe, *Dendrophthoe pentandra*, for 2 years to evaluate traits and to explore if host-mediated effects contribute to the phenological asynchrony of the mistletoe. We addressed the following: (i) Is flowering and fruiting of this mistletoe seasonal in tropical rainforests, and what is the reproductive phenology of *D. pentandra* at plot, site and host species level? (ii) Which factors trigger the FFD of this hemiparasitic shrub and does plant size influence the FFD? (iii) To what degree does flowering and asynchrony occur in *D. pentandra* and is asynchrony influenced by site and host-mediated effects?

MATERIALS AND METHODS

Study area

We conducted fieldwork for two consecutive years (2018–2019) in secondary forests with some level of human disturbance in Xishuangbanna (XSBN), Yunnan Province, Southwest China. The dry season (November–April) and the rainy season (May–October) are typical of the tropical monsoon climate in Xishuangbanna (Zhu *et al.* 2015). In our study, the average monthly temperature ranged from 17 to 27 °C, and the annual mean temperature over the 2 years was 22.6 °C, with minimum and maximum temperatures in February and May, respectively. Average monthly rainfall ranged from 8 to 356 mm, and annual rainfall was 1899.4 mm for 2018 and 832.6 mm for 2019, with maximum rainfall in August (climate data from National Forest Ecosystem Research station at Xishuangbanna, 21°55′37″ N; 101°15′53″ E; 570 m a.s.l.) as shown in Supplementary Fig. S1. Details on floristic composition and forest physiognomy in the study area are provided in Zhu *et al.* (2015).

Plant species

Dendrophthoe pentandra is a hermaphroditic evergreen xylem hemiparasite that aggregates primarily in open forests and plantations (Luo *et al.* 2016; Wang and Zhang 2017). In Xishuangbanna, *D. pentandra* was the most generalized mistletoe species and parasitized up to 361 host species, belonging to 224 genera and 72 families (Xiao and Pu 1988). It obtains water and nutrients through primary haustoria (Fig. 1a) and secondary haustoria (Fig. 1b) on epicortical roots from host xylem. Like many mistletoe species from the Loranthaceae family, *D. pentandra* has a mass flower display and produces large amounts of dilute nectar (Fig. 1e) and plentiful fruits (Fig. 1f), with a red exocarp and a viscid nutritious pulp during the reproductive period. It attracts omnivorous and frugivorous birds to facilitate pollination and seed dispersal, namely the flowerpecker (e.g. *Dicaeum concolor*), the bulbul (*Pycnonotus aurigaster*) and the white-eye (*Zosterops japonica*) (Luo *et al.* 2016). Several species of flowerpecker defaecate seed strings on perches and multiple infections at the same point on the host branch occasionally occur (Fig. 1c). If these seeds germinated, a larger, visually complex clump is formed. This can also occur in other mistletoes (see Reid 1991; Reid and Smith 2000). However, some studies have already shown that seedling establishment probability decreased with the number of seeds deposited per faeces or seed string in mistletoes (Amico *et al.* 2017; Davidar 1983a). In addition, intraspecific competition within a single host individual also occurred (Nabity *et al.* 2021). These reduce the likelihood of multiple individuals grafting together in the field. To avoid

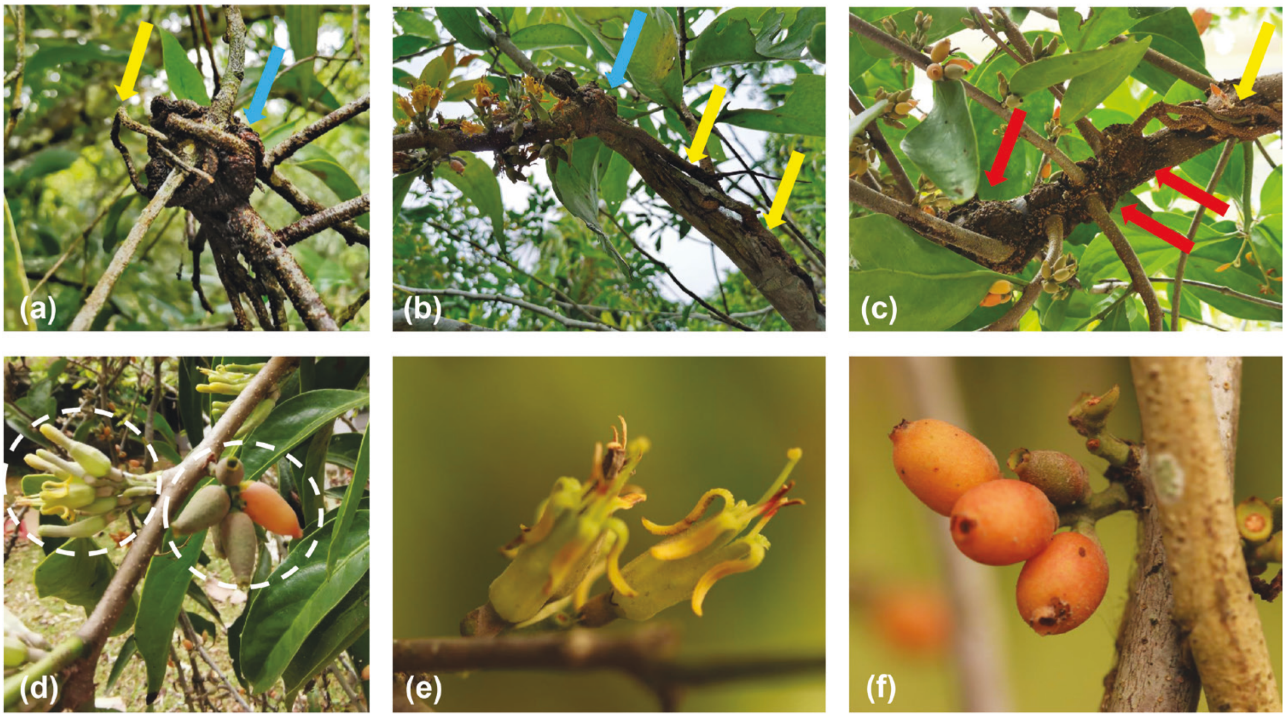

Figure 1: The haustoria, flowers and fruits traits of *Dendrophthoe pentandra*. (**a**)–(**c**) show the different types of haustorium in *D. pentandra*. Blue, yellow and red arrows represent primary haustoria, secondary haustoria on epicortical roots and potential combination of primary haustorium, respectively; (**d**)–(**f**) show flowers and fruits of *D. pentandra*.

potential ambiguity, we treated a mistletoe clump as an available unit (i.e. a clump = an individual) during the phenological observation and analysis process regardless of whether it was composed of multiple different genetic individuals. Most mistletoe individuals that we studied possessed a large primary haustorium, and there was a very low proportion of clumps in our study.

Phenological observation

Three sites with natural distribution and relative abundance of the species, namely Dadugang (DDG), Menglun (ML) and Xiangming (XM) (21°58′ to 22°17′ N; 101°00′ to 101°25′ E, at 959–1147 m a.s.l.) (Supplementary Fig. S2), were selected to study the phenological patterns and factors influencing the reproductive phenology of *D. pentandra*, as detailed in previous surveys (Wang and Zhang 2017; Xiao and Pu 1988). Three plots (20 m × 20 m) separated by >200 m were established at each site. Two plots remained at XM in the 2018 flowering period, after one (i.e. XM1, see Supplementary Fig. S2) was flattened during landscaping. No mistletoes had started to flower prior to survey commencement, and the fruits of all mistletoes were wilted by the end of the survey period. We identified all host trees infected by *D. pentandra* at each plot and marked each tree with a numbered aluminium band. Mistletoe density (the number of individuals per plot) and the name of the host species were recorded. Hosts were measured for height, diameter at 1.3 m above the ground (DBH), crown area as a surrogate for plant size (for formula, see Sayad *et al.* 2017) and infection intensity (the number of mistletoe clumps per host tree) (Aukema 2004). The height (from ground to infection attachment point of the host) and the corresponding crown area of the mistletoe were measured. The levels of light exposure were estimated visually on a scale of 0–10 for each mistletoe in the first census. A score of 10 indicates that the entire foliage of the mistletoe was exposed to full sunlight throughout the day (Montgomery *et al.* 2003).

Some mistletoe clumps did not flower and/or died during the study period because of nutrient shortage or competition within a single host individual (e.g. Nabity *et al.* 2021). A total of 212 and 158 mistletoes flowered in 2018 and 2019, respectively, and a total of 200 and 135 mistletoes produced fruit in 2018 and 2019, respectively. We observed reproductive phenology (flowering and fruiting) of *D. pentandra* at weekly intervals (5–8 days; min = 5 days; max = 8 days; mean ± SD = 7 ± 1.5 days) over 2 years (97, 97 and 96 census dates in total for DDG, ML and XM, respectively).

One year of the study corresponded to one calendar year (Soler *et al.* 2015). Each mistletoe clump was checked visually for the presence of open flowers (green-yellow colour) and evidence of pollination, and for ripe fruits (orange-red colour) and evidence of foraging by birds, which enables seed dispersal (Adamescu *et al.* 2018). Binoculars were used for observations when necessary. Data were obtained for four primary phenological variables: (i) the FFD, (ii) the last flowering date (LFD), (iii) the first ripe date (FRD) of fruit and (iv) the last ripe date (LRD) of fruit. First and last dates of flowering and fruiting were estimated based on field records indicating colour change in flowers and fruits between two consecutive sampling dates for each observed clump (Yule and Bronstein 2018). Secondary phenological variables were calculated, namely flowering and fruiting duration and the index of asynchrony of a given individual with its conspecifics for flowering and fruiting (modified from Augspurger 1983). The index of asynchrony ranged between 0 (total overlap) and 1 (no overlap). The asynchrony index was formulated as follows:

$$\text{Asynchrony}_i = 1 - \left(\frac{1}{n-1}\right) \times \left(\frac{1}{f_i}\right) \times \sum_{j=1}^{n} e_{i \neq j} \quad (1)$$

where e_i is the number of days where flowering of individual i overlaps with that of individual j; f_i is the total number of days individual i is flowering and n is the number of individuals observed. Phenological strategy (continual, sub-annual, annual or supra-annual) and duration of phenophases (brief, intermediate or extended) for *D. pentandra*, were classified according to the system developed by Newstrom *et al.* (1994) and Nobrega Gomes *et al.* (2019), respectively.

Comparison of mistletoe's phenology with other tree species at the community level

In order to understand the complementarity of reproductive phenology of *D. pentandra* at the community level, we compared our study with the only earlier phenology study in the Xishuangbanna tropical seasonal rainforest (Mohadass *et al.* 2018) In this research, they investigated reproductive phenology of 76 woody and shrub tree species (70 genera, 37 families) from 2004 to 2007 in the 1-ha permanent plot located in Menglun, near our ML study site. We mapped our phenology of *D. pentandra* in 2018 onto their figure showing 76 species' phenology to evaluate whether mistletoe can be complementary to other species at the community level. With the authors' permission, we used WebPlotDigitizer software to extract data from Fig. 3 of Mohadass *et al.* (2018). We extracted the average number of tree species that bloomed and bore fruit every month from 2004 to 2007. Because sampling frequency was inconsistent, we directly compared the individual number of flowering or fruiting of mistletoes to their number of reproductive tree species.

Statistical analyses

We used circular statistics in Oriana 4.0 software (http://www.kovcomp.co.uk) to interpret the phenological patterns of *D. pentandra*, specifically annual seasonal patterns and their relationship with phenological variables (Morellato *et al.* 2010). As there is no natural start and/or endpoint to a year, characteristics that vary on an annual cycle were analysed as 'circular' variables (Ting *et al.* 2008). The four primary phenological variables were transformed to an angle on a circular scale. The mean vector (μ) and mean date at which the event occurred were calculated, referring to the date on which the highest concentration of individuals in each phenophase was recorded. The circular standard deviation and the length of the mean vector (r) were also calculated, indicating the concentration of individuals (0–1) around the mean date, as well as the degree of seasonality. First, Rayleigh tests were performed to assess the significance of the mean vector (μ) for all unimodal distributions, which were considered seasonal when the mean vector was significant ($P < 0.05$) (Morellato *et al.* 2010; Nobrega Gomes *et al.* 2019). Second, we calculated the circular–circular correlation coefficients for the four primary phenological variables and the circular–linear correlation coefficients for the four primary phenological variables, the two secondary phenological variables (flowering and fruiting durations) and the biological traits (height and crown area of mistletoe). The significance of the correlation was tested using the jackknife method (Morellato *et al.* 2010; Müller *et al.* 2019).

The reproductive phenological patterns of *D. pentandra* at plot, site and host species levels were described and compared. At first, we used the Watson–Williams F test in Oriana software to determine the significance of the mean dates of the four primary phenological variables. This was used to verify differences in mean dates of concentration of the phenological events between the years, plots, sites and host species. Then we used the Kruskal–Wallis *H* and the Mann–Whitney *U* tests for the four secondary phenological variables, depending on the number of groups subjected to comparison. In particular, we compared the asynchrony index of flowering and fruiting between plots, sites and years to determine the factors influencing the asynchrony index.

We applied a generalized linear mixed-effects model (GLMM) with a Poisson error structure, using the package *lme4* in R v4.0.3 (R Core Team 2020), to identify factors that influence the FFD of mistletoe. We checked for collinearity in the biological characteristics of host and mistletoe, using Spearman's rank correlation coefficient to create correlation matrices, a method suitable for non-normal data. When the correlation coefficient between two variables is >0.7 neither variable should be used in the same model (Dormann *et al.* 2013; Harrison *et al.* 2018). We selected host species, plot and mistletoe identity (ID) nested within the host ID as random factors. Host height, crown area and DBH, and mistletoe height, crown area, light exposure level and year were selected as fixed factors. These were incorporated into a model based on the results of collinearity. Mistletoe ID was added as a random factor when modelling overdispersion. Marginal R^2 indicates the explanatory rate of the fixed factor to the response variable. Mean ± 1 SE values were calculated across all data unless otherwise specified.

We checked whether the number of host species influenced the asynchrony index of flowering and fruiting to determine if the number of hosts influenced the asynchrony index of the reproductive phenology. The calculation considered all individuals infected with *D. pentandra* as a group when there was one host species and calculated the asynchrony index for each *D. pentandra* clump on the host (i.e. there were C1 19 combinations for 19 host species). For two host species, all individuals infected with *D. pentandra* were considered as a whole and the asynchrony index was calculated for each *D. pentandra* clump (i.e. there were C2 19 combinations for 19 host species). This process was completed for the maximum number of host species for the corresponding phenological variables (flowering and fruiting). The *mean()* and *sd()* functions were used to calculate the average value and standard deviation of the asynchrony index for each combination in R v4.0.3.

RESULTS

Host and mistletoe traits

Overall, 19 host species and 104 host individuals were infected by *D. pentandra*, representing 217 connections between hosts and mistletoe clumps (Fig. 2; Supplementary Fig. S3). Interactions between hosts and mistletoes varied greatly. *Anneslea fragrans* (Pentaphylacaceae) hosted the most parasitic individuals (60 connections, 23 host individuals), followed by *Apodytes dimidiata* (Icacinaceae) (37 connections, 18 host individuals) and *Wendlandia tinctoria* subsp. *intermedia* (Rubiaceae) (33 connections, 20 host individuals), while the remaining connections accounted for approximately 40% of the total. *Castanopsis echidnocarpa* (Fagaceae) and *Elaeocarpus austroynnanensis* (Elaeocarpaceae) at DDG, and *Dalbergia stipulacea* (Fabaceae), *Lithocarpus fohaiensis* (Fagaceae) and *Macaranga indica* (Euphorbiaceae) at ML had the fewest host species, where only one host individual was infected by *D. pentandra* (Fig. 2). *Cratoxylum cochinchinense* (Hypericaceae) was the only deciduous host species. In total, seven host species (18 individuals) were dioecious (i.e. *Eurya groffii*, *Ilex godajam*, *Aporosa yunnanensis*, *Macaranga denticulata*, *C. echidnocarpa*, *Aporosa dioica* and *M. indica*, Supplementary Table S1). Among these, female *E. groffii* have higher infection intensity than do males at XM site.

The mean height, DBH and crown area of hosts were 12.26 ± 0.82 m, 8.22 ± 0.24 cm and 5.87 ± 0.53 m^2, respectively. Host height highly correlated with host crown area ($r = 0.74$, $P < 0.001$, Supplementary Fig. S4). The average infection intensity was 2.3 ± 0.2 (1–8 mistletoe per host plant). There were marginally significant differences in infection intensity between seven host species that more than three infected individuals per host species (Kruskal–Wallis *H* test, $P = 0.0501$); this difference mainly occurred in *A. fragrans* and *C. cochinchinense*. Mistletoe infection intensity increased with the increase of host DBH, height and crown area, although these correlation coefficients were low (Supplementary Fig. S4). Mistletoe density at DDG was highest for each phenophase in both years, followed by XM and ML (100 individuals at DDG, 68 at XM and 44 at ML for flowering in 2018). The mean mistletoe height and crown area were 6.02 ± 0.12 m and 0.33 ± 0.02 m^2, respectively. The mean light exposure level of mistletoes was 5.65 ± 0.14.

Mistletoe phenological pattern

The length of the mean vector was $r > 0.95$, and the Rayleigh test ($P < 0.001$) indicated that flowering and fruiting of *D. pentandra* was notably seasonal (Table 1). The phenological strategy of *D. pentandra* was a one flowering/fruiting cycle in a year. The duration of phenophases was intermediate (average flowering and fruiting duration in 2 years were >44 days, Fig. 3).

Correlation among phenological variables

Circular–circular correlation of the four phenological variables over 2 years showed that they were significantly correlated with each other ($P < 0.05$), although some had low correlation coefficients (Supplementary Table S2). The FFD and the LFD, or the FRD had higher positive correlation coefficients, which confirmed that the earlier the FFD, the earlier the LFD and the earlier the FRD ($r = 0.429$ and 0.515 in 2018, $r = 0.456$ and 0.531 in 2019, Supplementary Table S2). However, for the FFD and the LRD, the correlation coefficient was very low and was negative in 2019, which meant that the earlier the FFD, the later the LRD ($r = -0.096$). The high correlation coefficient for FFD between 2018 and 2019 ($r = 0.311$) suggested that the onset

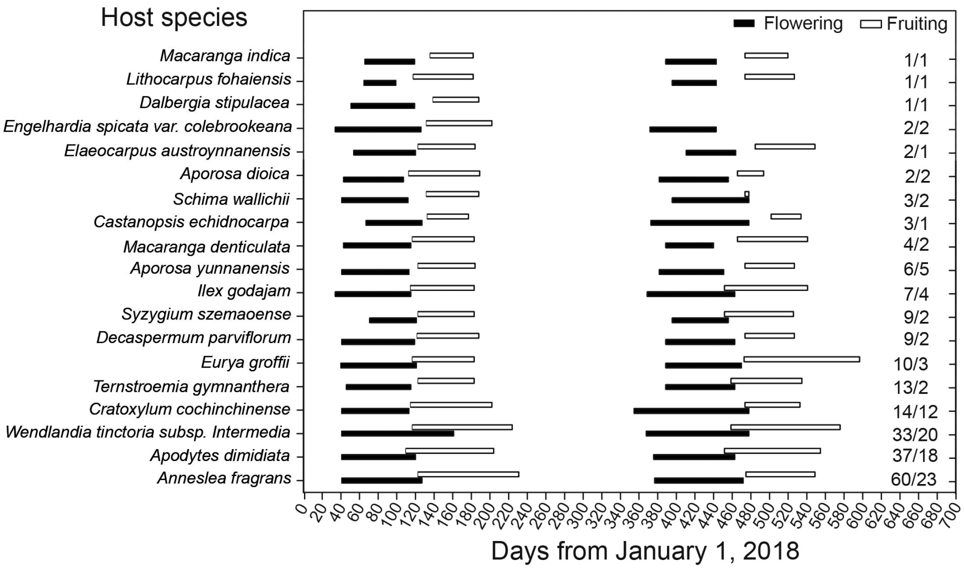

Figure 2: The reproductive phenological variation of *Dendrophthoe pentandra* on different hosts species in the study area. The *x*-axis represents the number of days from 1 January 2018. Black and grey horizontal bars indicate the flowering and fruiting duration, respectively, of *D. pentandra* on each host species. The left *y*-axis represents different host species ordered by the number of *D. pentandra* clumps growing on them. The right *y*-axis represents the number of *D. pentandra* clumps and corresponding infected host trees at the first census in 2018.

Table 1: The circular statistical analysis for the occurrence of *Dendrophthoe pentandra* seasonality in Xishuangbanna

	FFD		**LFD**		**FRD**		**LRD**	
	2018	**2019**	**2018**	**2019**	**2018**	**2019**	**2018**	**2019**
Number of observations	212	158	212	158	200	135	200	135
Mean vector (μ)	64.425	35.978	109.753	82.255	131.105	110.211	182.744	153.229
Mean date	7 March	6 February	22 April	25 March	13 May	22 April	5 July	5 June
Circular standard deviation	17.114	17.45	8.232	12.244	8.726	13.032	8.059	17.729
Length of mean vector (r)	0.956	0.955	0.99	0.977	0.988	0.974	0.990	0.953
Rayleigh test (Z)	193.905	144.004	207.668	150.947	195.415	128.194	196.082	122.674
Rayleigh test (P)	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Note: Rayleigh test for uniform of phenological events, $r > 0.5$ indicating high seasonality refer Nobrega Gomes *et al.* (2019).

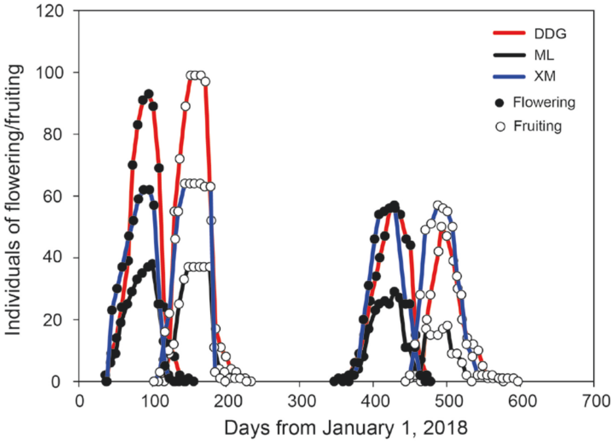

Figure 3: Reproductive phenological variations of *Dendrophthoe pentandra* at the three study sites over 2 years. The *x*-axis represents the number of days from 1 January 2018. The red, black and blue lines represent DDG, ML and XM sites, respectively. The solid and hollow points represent the number of mistletoe individuals that are flowering and fruiting, respectively.

of flowering in *D. pentandra* had a certain degree of stability throughout the year. The FRD showed a similar trend ($r = 0.303$), and this correlation was significant ($P < 0.05$). The circular–linear correlation between the four phenological variables with flowering or fruiting in the 2 years showed that earlier FFD resulted in a longer flowering duration ($r = 0.888$ in 2018, $r = 0.735$ in 2019). The earlier the FRD, the longer the fruiting duration ($r = 0.724$ in 2018, $r = 0.503$ in 2019, Supplementary Table S2).

Correlation between phenological and biological variables

Circular–linear correlation between the four phenological variables and mistletoe height/crown area over 2 years showed a weak positive correlation. The correlations between the FFD and mistletoe height ($r = 0.199$, $P < 0.001$ in 2018, $r = 0.207$, $P = 0.001$ in 2019) and crown area ($r = 0.305$, $P < 0.001$ in 2018, $r = 0.174$, $P = 0.009$ in 2019) were significant, confirming that mistletoe with higher height and larger crowns had earlier FFDs (Supplementary Table S3). The degree of asynchrony of flowering and fruiting duration increased with the crown area of *D. pentandra* in 2018 ($R^2 = 0.02$, $P = 0.02$ for flowering, $R^2 = 0.07$, $P = 0.02$ for fruiting) although this trend was not apparent in 2019 (Supplementary Fig. S5).

Effect of years on mistletoe phenology

All four primary phenological variables over the 2 years differed significantly, and were observed 1 month earlier in 2019 than in 2018 ($P < 0.001$, Table 1; Supplementary Table S4). Flowering onset was later in 2018 (66 days) than in 2019 (37 days) ($P < 0.001$, Table 1). In 2018, *D. pentandra* flowered from February to May, and approximately 50% flowered in February. The flowering duration in March coincided with the dry season. The flowering durations were 46.2 ± 1.1 and 47.1 ± 1.3 days in 2018 and 2019, respectively. The fruiting period from April to July coincided with the rainy season (Fig. 3; Supplementary Fig. S1). Fruiting duration differed significantly over the 2 years (52.7 ± 0.8 days in 2018 and 44.2 ± 1.8 days in 2019) ($P < 0.001$). In 2018, the asynchrony index of flowering was 0.28 ± 0.01 ($n = 212$) and the asynchrony index of fruiting was 0.14 ± 0.01 ($n = 200$). In 2019, the flowering and fruiting asynchrony indices were 0.33 ± 0.01 ($n = 158$) and 0.33 ± 0.01 ($n = 135$), respectively (Table 2). Furthermore, the asynchrony index of fruiting in 2018 was significantly lower than that of both flowering and fruiting in 2019 ($P < 0.001$). In 2018, the mistletoe clumps surviving for 2 years had an earlier FFD (FFD = 64 days, $n = 153$) than those that were lost in 2019 (FFD = 71 days, $n = 59$) ($F = 8.583$, $P = 0.004$).

Effects of sites and plots

Over 2 years, three primary phenological variables (FFD, LFD and FRD) ($P < 0.05$), together with flowering and fruiting duration, showed a significant difference between DDG and XM ($P < 0.001$, Supplementary Table S5). Significant differences for the FRD and fruiting duration were also detected between ML and XM ($P < 0.001$). However, there was no significant difference in the LRD between the three sites. The asynchrony index for flowering showed a significant difference between the sites (DDG: 0.24 ± 0.01, $n = 100$; ML: 0.34 ± 0.02, $n = 44$; XM: 0.26 ± 0.01, $n = 68$ in 2018 and DDG: 0.37 ± 0.01, $n = 68$; ML: 0.32 ± 0.02, $n = 31$; XM: 0.24 ± 0.02, $n = 59$ in 2019. There was only a significant difference in asynchrony index of fruiting between DDG and XM (DDG: 0.15 ± 0.01, $n = 99$; XM: 0.08 ± 0.01, $n = 64$ in 2018; and DDG: 0.39 ± 0.02, $n = 57$; XM: 0.20 ± 0.02, $n = 57$ in 2019; Table 2).

Within each site, the two primary phenological variables (FFD and LRD) and three secondary phenological variables (flowering duration, fruiting duration and the asynchrony index of fruiting) showed no significant difference over the 2 years (Supplementary Table S6). At ML, the FRD ($F = 5.039$, $P = 0.03$) and fruiting duration

Table 2: Flowering and fruiting asynchrony index of *Dendrophthoe pentandra* in Xishuangbanna

	Flowering		**Fruiting**	
Pop code	**2018**	**2019**	**2018**	**2019**
DDG1	0.15 ± 0.01 (42)^{a}	0.32 ± 0.02 (20)^{a}	0.12 ± 0.02 (42)	0.31 ± 0.03 (19)^{ab}
DDG2	0.21 ± 0.03 (11)^{ab}	0.21 ± 0.04 (9)^{b}	0.21 ± 0.05 (11)	0.25 ± 0.04 (7)^{a}
DDG3	0.29 ± 0.02 (47)^{b}	0.39 ± 0.02 (39)^{ac}	0.13 ± 0.01 (46)	0.39 ± 0.03 (31)^{b}
DDG	0.24 ± 0.01 (100)^{A}	0.37 ± 0.01 (68)^{A}	0.15 ± 0.01 (99)^{A}	0.39 ± 0.02 (57)^{A}
ML1	0.31 ± 0.02 (11)	0.43 ± 0.06 (7)^{a}	0.15 ± 0.04 (10)	0.60 ± 0.10 (3)^{a}
ML2	0.31 ± 0.04 (20)	0.32 ± 0.03 (16)^{ab}	0.11 ± 0.03 (16)	0.35 ± 0.03 (12)^{b}
ML3	0.30 ± 0.02 (13)	0.18 ± 0.04 (8)^{c}	0.12 ± 0.03 (11)	0.10 ± 0.03 (6)^{c}
ML	0.34 ± 0.02 (44)^{B}	0.32 ± 0.02 (31)^{B}	0.14 ± 0.02 (36)^{AB}	0.36 ± 0.03 (21)^{AB}
XM2	0.29 ± 0.01 (24)	0.26 ± 0.02 (24)	0.07 ± 0.01 (20)	0.22 ± 0.03 (23)
XM3	0.25 ± 0.01 (44)	0.22 ± 0.02 (35)	0.08 ± 0.01 (44)	0.20 ± 0.02 (34)
XM	0.26 ± 0.01 (68)^{C}	0.24 ± 0.02 (59)^{C}	0.08 ± 0.01 (64)^{C}	0.20 ± 0.02 (57)^{C}
Total	0.28 ± 0.01 (212)	0.33 ± 0.01 (158)	0.14 ± 0.01 (200)	0.33 ± 0.01 (135)

Note: Mean ± SE, uppercase letters indicate the differences among sites, lowercase letters indicate the differences among plots in each site.

($P < 0.001$) were significantly different between the ML2 and ML3 plots. At DDG, the LFD ($F = 7.168$, $P = 0.009$) and the FRD ($F = 5.576$, $P = 0.02$) at DDG2 were later than those at DDG3. The FRD at DDG1 was earlier than at DDG2 (Supplementary Table S6). The asynchrony index of flowering at DDG1 (0.15 ± 0.01, $n = 42$) was lower than at DDG3 (0.29 ± 0.02, $n = 47$) in 2018. In 2019, the asynchrony index of flowering at DDG1 (0.32 ± 0.02, $n = 20$) was higher than that at DDG 2 (0.21 ± 0.04, $n = 9$), and ML1 (0.43 ± 0.06, $n = 7$) was higher than at ML3 (0.18 ± 0.04, $n = 8$). No significant difference was detected for the asynchrony index of fruiting in 2018. However, in 2019, the asynchrony index of fruiting at DDG2 (0.25 ± 0.04, $n = 7$) was lower than that at DDG3 (0.39 ± 0.03, $n = 31$. At ML, the asynchrony index of fruiting was significantly different at all three plots (ML1: 0.60 ± 0.10, $n = 3$; ML2: 0.35 ± 0.03, $n = 12$; ML3: 0.10 ± 0.03, $n = 6$; Table 2).

Effect of host species

There were significant differences between host species for all four primary phenological variables. The difference for each phenological variable was apparent on different host species (for those host species with more than three mistletoe clumps, Supplementary Table S7). The flowering duration of mistletoe on *A. dimidiata* was longer than that on *Syzygium szemaoense* ($P = 0.007$, Fig. 2). The fruiting duration of mistletoe on *A. dimidiate* was longer than on the other three host species, *A. fragrans* ($P = 0.051$), *Decaspermum parviflorum* ($P = 0.047$) and *Ternstroemia gymnanthera* ($P = 0.047$). The asynchrony index of fruiting showed no significant difference between host species, but the asynchrony index of flowering showed more complexity between host species. There was a significant difference in the asynchrony index of flowering for *D. pentandra* on *A. dimidiata* compared with three other host species, namely *A. fragrans* ($P = 0.023$), *S. szemaoense* ($P = 0.002$) and *T. gymnanthera* ($P = 0.009$). *Syzygium szemaoense* and three other host species, *E. groffii* ($P = 0.049$), *I. godajam* ($P = 0.015$) and *W. tinctoria* subsp. *intermedia* ($P = 0.005$) infected by *D. pentandra* also showed significant differences. Likewise, *T. gymnanthera* and *I. godajam* ($P = 0.034$) and *W. tinctoria* subsp. *intermedia* ($P = 0.035$) infected by *D. pentandra* were significantly different (Supplementary Table S7).

Factors influencing the FFD

Collinearity of biological characteristics between host and mistletoe showed that host DBH and host crown area were strongly correlated (Supplementary Fig. S4), and host crown area was thus selected for use in the GLMM models. GLMM analysis indicated that the FFD was significantly influenced by the mistletoe crown area in 2018 ($P < 0.001$) and 2019 ($P = 0.02$), and in the 2 years combined ($P < 0.001$). The level of light exposure was significant for the FFD in 2018 ($P = 0.004$) and the year was also significant in the combined model for the 2-year study period ($P < 0.001$, Table 3). Flowering duration was influenced by mistletoe crown area ($P < 0.001$) in 2018, and there was no significant interannual factor in the combined model for the 2-year study period. No factor was found to influence flowering and fruiting duration significantly in 2019. Similarly, no factor was found to influence the FRD significantly in the combined model for the 2-year study period.

Effects of the number of host species

The number of host species did not significantly influence the degree of flowering asynchrony for mistletoe in 2018 (from 0.25 ± 0.14 in any host species to 0.28 ± 0.11 in 19 host species, Fig. 4a) or in 2019 (from 0.32 ± 0.17 in any host species to 0.34 ± 0.12 in 18 host species, Fig. 4c). A similar trend was found in the degree of fruiting asynchrony in 2018 (from 0.12 ± 0.11 in any host species to 0.14 ± 0.10 in 19 host species, Fig. 4b) and in 2019 (from 0.27 ± 0.18 in any host species to 0.33 ± 0.13 in 17 host species, Fig. 4d). All the values indicated in this section are mean ± SD.

Complementarity of reproductive phenology of *D. pentandra*

In 2018, the flowering duration of *D. pentandra* was from February to May, and flowering peaked in April, while the fruiting duration was from April to August, and the fruiting peaked in May–June. Most individuals of *D. pentandra* flowered during February–April and fruiting during May–July (Fig. 5). In Mohandass *et al.*

Table 3: GLMM results for the analysis of reproductive phenological variables of *Dendrophthoe pentandra*

Phenological variables (year)	N	Predictors	Incidence rate ratios	CI	P	Marginal R^2
FFD (2018)	212	Intercept	78.29	70.71–86.68	<0.001	0.124
		Mistletoe crown area	0.80	0.72–0.89	<0.001	
		Mistletoe light level	0.98	0.96–0.99	0.004	
FFD (2019)	158	Intercept	36.13	31.23–41.80	<0.001	0.034
		Mistletoe crown area	0.74	0.58–0.95	0.020	
FFD (2018 and 2019)	370	Intercept	67.57	61.36–74.42	<0.001	0.394
		Mistletoe crown area	0.77	0.68–0.87	<0.001	
		Year (2019)	0.55	0.51–0.59	<0.001	
Flowering duration (2018)	212	Intercept	34.08	29.57–39.29	<0.001	0.093
		Mistletoe crown area	1.31	1.14–1.50	<0.001	
		Mistletoe light level	1.03	1.00–1.05	0.022	
Flowering duration (2018 and 2019)	370	Intercept	40.37	37.92–42.99	<0.001	0.050
		Mistletoe crown area	1.28	1.14–1.44	<0.001	
FRD (2018 and 2019)	335	Intercept	132.66	130.53–134.83	<0.001	0.461
		Mistletoe crown area	0.97	0.94–1.00	0.023	
		Year (2019)	0.84	0.83–0.86	<0.001	
Fruiting duration (2018)	200	Intercept	49.07	45.40–53.03	<0.001	0.058
		Mistletoe crown area	1.18	1.08–1.28	<0.001	
Fruiting duration (2018 and 2019)	335	Intercept	48.55	43.58–54.08	<0.001	0.122
		Mistletoe crown area	1.15	1.03–1.29	0.012	
		Year (2019)	0.77	0.71–0.83	<0.001	

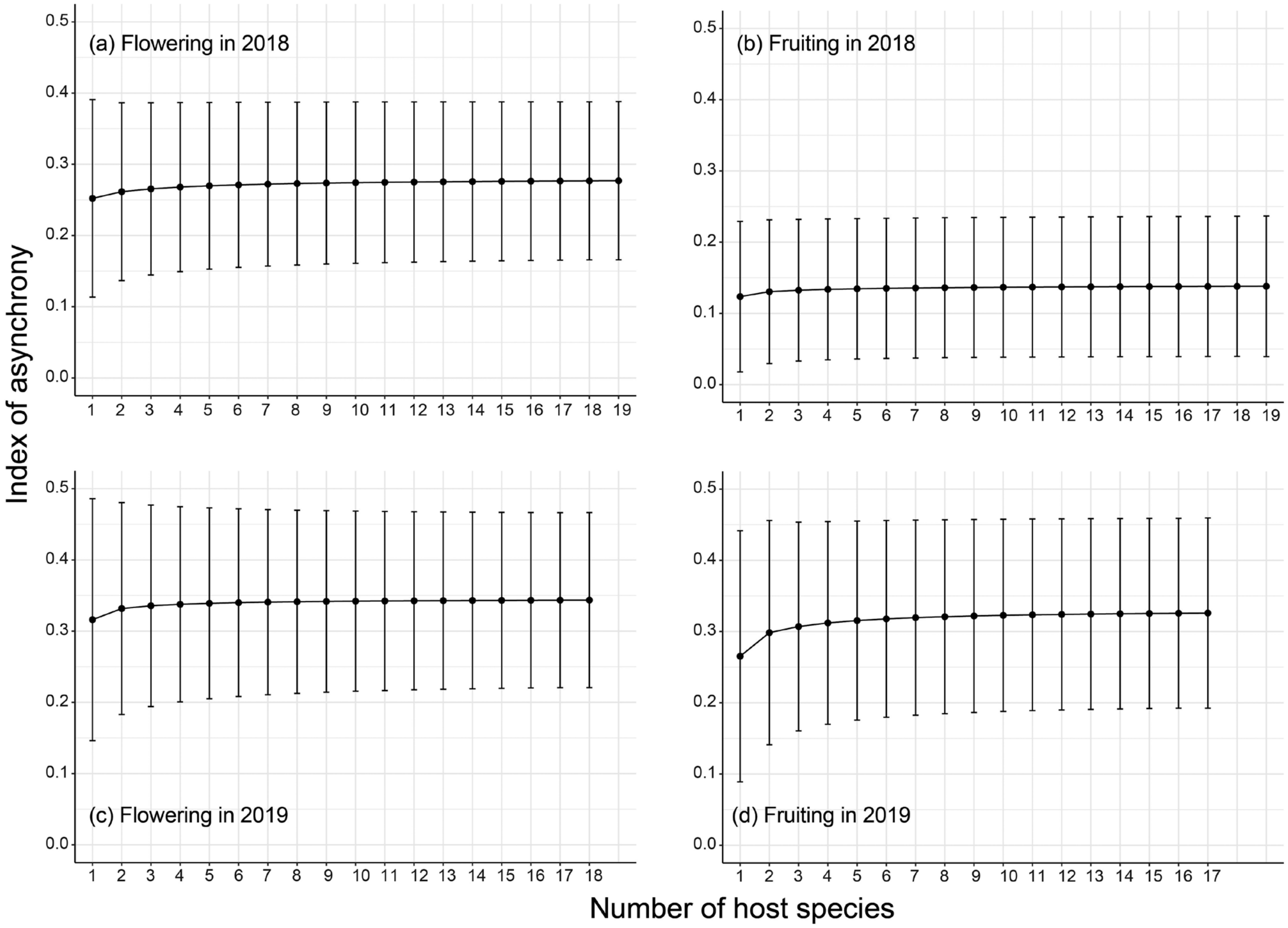

Figure 4: The asynchrony index of *Dendrophthoe pentandra* in different number of host species during flowering (**a**, **c**) and fruiting (**b**, **d**) periods. The *x*-axis represents different number of host species. The black dots represent the mean asynchrony index of *D. pentandra* individuals on different number of host species. Points indicate the mean (±SD) asynchrony index.

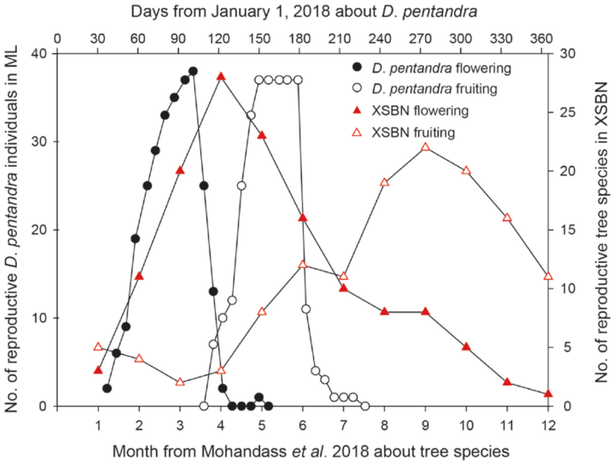

Figure 5: The reproductive phenology of *Dendrophthoe pentandra* in 2018 and reproductive phenology of 76 tree species from 2004 to 2007 in Xishuangbanna (XSBN). The average number of tree species that bloom and bear fruit every month from 2004 to 2007 in XSBN were provided by Mohadass *et al.* (2018) with the authors' permission.

(2018), most species flowered in April–May, and flowering peaked in April. Most species fruited August–November, and fruiting peaked in September (Fig. 5).

DISCUSSION

The reproductive phenological patterns of a generalist mistletoe were studied at plot, site and host species levels in tropical seasonal rainforests, to understand phenology and phenological asynchrony. Our results showed that the FFD was significantly influenced by crown area of mistletoe clump and light exposure. Plot, site and host species were shown to significantly influence mistletoe phenology. Contrary to our hypothesis, asynchrony in reproductive phenology did not significantly change when related to the number of host species.

Heterogenetic distribution of *D. pentandra* between study sites and hosts

Like most other generalist mistletoe species, *D. pentandra* infected a large number of host species.

It showed a preference for some host species in specific locations. This heterogeneous distribution of mistletoe on hosts at different sites may be influenced by abiotic and biotic factors (e.g. canopy cover of habitat and host, behaviour of seed dispersers, the size of individual hosts and branch diameter) (Amico *et al.* 2017; Luo *et al.* 2016; Rawsthorne *et al.* 2012; Reid and Smith 2000; Sasal *et al.* 2021). The canopy cover at DDG and XM was less than at ML, which is in a nature reserve with a dense canopy. Previous studies found that mistletoe density was higher in more fragmented sites (Kelly *et al.* 2000). Open microenvironments encourage birds to find fruits and disperse seeds, which influences mistletoe infection patterns (Magrach *et al.* 2013). Meanwhile, canopy cover of host had a significant positive effect on seed deposition probability (Amico *et al.* 2017). The difference in host tree size (e.g. tree height, diameter and basal area) at different sites may contribute to the heterogenic distribution of mistletoe (Sayad *et al.* 2017; Sreekar *et al.* 2016). Mistletoe infection intensity of dioecious *E. groffii* female trees is greater than on male trees, and it shares avian dispersers with mistletoe, as Carlo and Aukema (2005) mentioned in other mistletoes, although this phenomenon needs further investigation in our study sites.

Factors influencing the reproductive phenology of *D. pentandra*

Flowering and fruiting patterns of *D. pentandra* were seasonal and corresponded to the dry and rainy seasons, respectively. In tropical areas, rainfall is the main stimulus that determines seasonality of phenology (Dunham *et al.* 2018) and is a climatic driver of phenology (Mendoza *et al.* 2017). Flowering in the dry season prevents rain washing of pollen and enhances pollination efficiency for plants dependent on animals for pollination, such as some vector-dependent mistletoes (Bach and Kelly 2004; Wright and Calderon 1995). Seeds of *D. pentandra* have no dormancy and can germinate during the rainy season. Due to non-dormancy traits, ripening of fruit during the rainy season maximizes the likelihood of mistletoe seedling establishment.

A low degree of overlap in flowering and fruiting can increase flower and fruit display, attracting more pollinators and seed dispersers (Augspurger 1981; Buide *et al.* 2002; Nobrega Gomes *et al.* 2019). High asynchrony in mistletoes can extend the duration of flowering and fruiting displays to maintain long-term relationships with pollinators and seed dispersers (Quintana-Rodríguez *et al.* 2018; Watson 2001). However, complete synchrony in the reproductive phenology of plants is impossible because of microclimatic influences and variations in genotypes (Elzinga *et al.* 2007). The fruiting asynchrony index is constrained by the flowering asynchrony index, hence fruiting usually has a higher degree of stagger (Gorchov 1990). In this study, however, the fruiting asynchrony index was lower than the flowering asynchrony index which might be an adaptation to allow for fruiting during the rainy season. Besides, the water limitation is more significant for the non-autotrophic mistletoe than for the trees (Scalon and Wright 2015).

There were distinct differences in phenology between sites and years. Phenological events at DDG were later than at XM, and the asynchrony of fruiting differed significantly in the 2 years. This may have resulted from the shorter flowering and fruiting duration at DDG than at XM. Although we considered the formula for the asynchrony index to be more suitable than other formulas, it may be more accurate to measure the asynchronization of plants based on the length of time and intensity of the phenological characteristics (Bolmgren 1998; Freitas and Bolmgren 2008). Significant differences in the FRD were detected between the plots at DDG and ML. Phenological staggering at different locations may be a strategy for mistletoes to attract and maintain mutualistic partners on a spatiotemporal scale (Napier *et al.* 2014). Terrain and factors within the microenvironment contribute to these differences (Müller *et al.* 2019; Wright and Calderon 2018).

Host species significantly impacted the duration and phenological events of mistletoe. Mistletoe with more individuals may have a longer flowering duration than those with fewer individuals for any host species (Fig. 2). Yule and Bronstein (2018) reported that host species influenced mistletoe peak flowering time. In our study, host species also influenced mistletoe flowering and fruiting duration, and asynchrony of flowering at the host species level (Supplementary Table S7).

In this study, clump size significantly influenced the phenology of mistletoe. Larger clumps bloomed earlier and flowered for longer than smaller clumps. They also had high asynchrony, although this trend was marginal. Plant size represents resource assimilation, which is often size dependent (allometric); larger plants direct more resources to reproduction than smaller ones, further influencing plant phenological traits at the individual level (Ramirez-Parada *et al.* 2020). This effect could be obvious for mistletoe, as it depends on hosts to supply water and nutrition. Flower numbers, FFD and length of flowering can also be related to plant size (Schmitt 1983). In turn, plant size and phenology can influence fitness (Ollerton and Lack 1998). For example, larger individuals of the desert mistletoe, *P. californicum* had more flowers and floral resources (Yule and Bronstein 2018). In a dense forest, mistletoe mainly infects taller trees that receive adequate light (Soler *et al.* 2015). More light assists germination and seed establishment (Luo *et al.* 2016). We note that this result should be quoted carefully in future work considering that the larger clump may be composed of multiple individuals. However, they also represent more functional floral and fruits resource at the clump level in a community.

Number of host species did not contribute significantly to phenological asynchrony of mistletoe

It was hypothesized that the number of host species infected by mistletoe contributes to their reproductive phenological asynchrony so that they can provide food for their mutualistic pollinators and dispersers for longer. Our investigation did not reveal this pattern; instead, the number of host species did not appear to enhance the reproductive phenological asynchrony of mistletoe noticeably. Not all potential host species were included in the study, which may influence this finding. The 19 host species in our study do not include most host species in this area. *Dendrophthoe pentandra* has 361 host species in Xishuangbanna (Xiao and Pu 1988), and the 19 host species in our study accounted for only 5% of the potential host species. The number of host species can influence mistletoe phenology to some extent, but this effect weakens as the number of host species increases. Likewise, advantages for insects disappeared with an increase in host phenological asynchrony in the willow psyllid (*Cacopsylla groenlandica*) as they were unable to exploit the full range of host options (Hodkinson 1997).

Complementarity of reproductive phenology of mistletoe at the community level

The reproductive phenology period (floral and fruit resource) of *D. pentandra* complements period of food shortage (Fig. 5), suggesting that the parasitic plants play an important role in resource supply at the community level. The complementarity of resources provided by mistletoe is particularly important during winter in temperate climates (Aizen 2003). Phenological asynchrony of mistletoes, which is critical to maintaining mutualistic pollinators and dispersers, may also be attributed to the sympatric distribution of different mistletoe species, especially for mistletoes that rely on the same vector assemblages (Davidar 1983b). In Xishuangbanna Tropical Botanical Garden (authors observations), four sympatric mistletoe species (*D. pentandra*, *Helixanthera parasitica*, *Macrosolen cochinchinensis*, *Scurrula chingii*) dispersed by birds also presented a staggered and complementary reproductive phenology.

CONCLUSIONS

This study indicated that *D. pentandra* has a unimodal seasonal reproductive phenology, where flowering and fruiting coincided with the dry and rainy seasons, respectively. Phenological variables can also influence the occurrence of phenological events sequentially and can change noticeably at the start and end of phenological events in successive years. Several factors, such as plot, site, host species and mistletoe clump size significantly influenced phenology in our study. Contrary to our expectations, the number of host species did not significantly enhance the asynchrony of reproductive phenology. Our study demonstrated that the number of host species may not necessarily be beneficial for the phenology of a generalist mistletoe to maintain diffuse coevolution. The reproductive phenology of mistletoe generally has an important adaptive significance for interacting species in 'host–mistletoe–pollinator/seed disperser' systems. Further investigation is required to understand the effects of host species and host phenology on mistletoe reproductive phenology. It is recommended that future studies investigate how mistletoes support pollinators and dispersers and how this complex interaction responds to dominant anthropogenic disturbances and climatic changes.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Table S1: Information summarizing host species in the study area.

Table S2: Correlations of phenological variables of *Dendrophthoe pentandra*.

Table S3: Circular–linear correlation of the four primary phenological variables and mistletoe height and crown area over 2 years.

Table S4: Mean date as compared for the four primary phenological variables between 2018 and 2019, using the Watson–Williams *F* test.

Table S5: Mean date for the four primary phenological variables as compared at the different sites using the Watson–Williams *F* test.

Table S6: Mean date for the four primary phenological variables as compared within each site using the Watson–Williams *F* test.

Table S7: The comparison of mean date for phenological variables between host species.

Figure S1: Mean maximum and minimum temperatures and accumulated monthly precipitation from 2018 to 2019 in Xishuangbanna, China.

Figure S2: The locations of populations investigated in this study in Xishuangbanna, Southwest China.

Figure S3: Mistletoe and host species connections in the study area.

Figure S4: Correlation between host and mistletoe traits.

Figure S5: The relationships between asynchrony of flowering and fruiting duration and crown size of *Dendrophthoe pentandra* over 2 years (upper: 2018; below: 2019).

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

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