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Absence of consistent pattern between seasons or among species in effect of leaf size on insect herbivory

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ABSTRACT

Insect herbivory on plant leaves is a major determinant of plant fitness, especially the growth and survival of tree seedlings in forests. Leaf size is believed to significantly affect the intensity of herbivory. Studies often assume the relationship between leaf size and herbivory to be monotonic; however, this relationship is influenced by many factors—the magnitude and direction of which are different—indicating a complex non-monotonic pattern. In this study, we investigated the herbivory of 5754 leaves of 422 seedlings belonging to 42 subtropical tree species over two seasons in southwest China. The effects of leaf size on herbivory differed among seasons; a hump-shaped pattern was detected in December, while a pattern of monotonic increase was detected in September. A variety of patterns, including complex non-monotonic hump-shaped patterns, as well as patterns indicating monotonic decrease and increase existed among species, although most species displayed no significant correlations. The relationship between leaf size and insect herbivory did not follow a constant rule, but differed across species and seasons, indicating that the effects of leaf size on the foraging preferences of insect herbivores may be contingent on both external (e.g., temperature) and intrinsic (e.g., other leaf traits) factors. Therefore, a one-off survey focusing on few species may not provide complete understanding of the overall pattern of the effect of leaf size on herbivory. Similar variations may also exist in other ecological processes, which should be given due consideration in future studies on biotic interactions.

1. Introduction

Leaf size varies dramatically both across and within species, and even in the same individual plant (Poorter and Rozendaal, 2008; Hulshof and Swenson, 2010; Diaz et al., 2016; Zhang et al., 2017; Wright et al., 2017). Many studies have discussed the potential explanations for such large variations in leaf size, for example, considering factors, such as precipitation, moisture, temperature, irradiance, soil fertility, genotype, and crown position (McDonald et al., 2003; Hulshof and Swenson, 2010; Wright et al., 2017; Eisenring et al., 2021). Consequently, variations in leaf size influences many ecological processes, including leaf expansion time, photosynthesis, transpiration rate, thermal regulation, and self-shading (Moles and Westoby, 2000; Falster and Westoby, 2003; Yates et al., 2010; Leigh et al., 2017; Hu et al., 2020).

Insect herbivory (hereafter referred to as herbivory) is a major factor that causes leaf damage and death, and can in turn alter plant fitness, especially the growth and survival of tree seedlings in forests (Schowalter et al., 1986; Eichhorn et al., 2010; Barton and Hanley, 2013; Jactel et al., 2021). Leaf size is believed to significantly influence the intensity of herbivory at both intraspecific and interspecific levels (Brown and Lawton, 1991; Moles and Westoby, 2000; Cardenas et al., 2014; Li et al., 2021). Several hypotheses have been presented: 1) logically, a larger leaf would provide the insect herbivores (also referred to as herbivores in this article) more absolute nutrients because of its larger area (Moles and Westoby, 2000); 2) larger leaves often require longer expansion time, which may in turn accumulate more damage by herbivores (Li et al., 2021).Therefore, larger leaves may be expected to suffer heavier herbivory. However, insects rarely consume the entire

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leaf, and they often have to change feeding site possibly due to the rapid plant responses (e.g., deterioration of food quality) and due to attraction of natural enemies to the damaged leaf (Rodriguez-Saona et al., 2005; Mertens et al., 2021); therefore, large leaves may have a lower herbivory rate (the ratio of the area loss to the whole leaf area) when a given area was consumed by insects. Furthermore, the underlying mechanisms of the association between leaf size and herbivory at intraspecific level may be different from that at interspecific level. Within a given species, the leaf size is often correlated with leaf age (i.e., growth stage), and the nutrients and/or defenses may also change with the development stage of a leaf, therefore indirectly alters the foraging preferences of insect herbivores (Coley, 1980; Aide, 1993; Boege and Marquis, 2005; Low et al., 2009; Moreira et al., 2016). Young shoot tips are more vulnerable to herbivory than base leaves, and the interspecific differences of the correlation between leaf size and leaf age may lead to differences in the preference of leaf size by insect herbivores; for example, insect herbivores prefer small leaves of *Betula pubescens*, but larger leaves of *Salix phylicifolia* (Bogacheva, 1994). Furthermore, leaf size is also related to many other leaf traits, such as specific leaf area, chemical and physical defenses, and nutrient content, all of which may potentially influence the leaf size preference of herbivores (Ackerly et al., 2002; Cardenas et al., 2014; Zava and Cianciaruso, 2014); therefore, the relationship between leaf size and insect herbivory may differs among species because of the interspecific variation in other leaf traits.

As discussed above, the relationship between leaf size and herbivory is influenced by many factors, and the magnitude and direction of the effects differ among different factors, indicating that the relationship between leaf size and herbivory may show a complex non-monotonic pattern that has also been observed during other ecological processes (Elliott and Irwin, 2009; Yan and Zhang, 2014; Thein et al., 2021; Zhang et al., 2021). Current evidence seems to support the above hypothesis that herbivory can be positively or negatively related to, or be independent of leaf size (Bogacheva, 1994, 2002; Moles and Westoby, 2000; Potter et al., 2012; Cardenas et al., 2014). Furthermore, the overall intensity of insect herbivory often differs across seasons, mainly because of the seasonal variation in (i) the quality and quantity of plant leaves, (ii) the species composition and abundance of insect community, and (iii) the activity and metabolic intensity (Awmack and Leather, 2002; Richards and Coley, 2007; Savilaakso et al., 2009). Therefore, a more thought-provoking question may be asked: do such seasonal effects influence the relationship between leaf size and insect herbivory? For example, if an extremely severe herbivory occurs in a given season because of the insect outbreaks or shortage of leaf production or both, and most of the leaves are consumed by insects no matter they are small or big, therefore a clear relationship between leaf size and herbivory may be not detectable.

To gain a more comprehensive understanding of how leaf size affects insect herbivory, we investigated the herbivory of 5754 leaves of 422 seedlings belonging to 42 tree species in a subtropical evergreen broadleaf forest for two seasons. We aimed to address the following three questions: 1) Does a non-monotonic pattern exist between leaf size and insect herbivory across different plant species? 2) Whether the relationship between leaf size and insect herbivory follows a same pattern among plant species? 3) Whether the relationship between leaf size and insect herbivory follows a same pattern among seasons?

2. Material and methods

2.1. Study site

This study was conducted in a subtropical forest in the Ailao Mountains, in southwest China (24°32′ N, 101°01′E, altitude ~2000 m). The dominant species in this forest are *Lithocarpus hancei, Lithocarpus xylocarpus*, and *Castanopsis wattii*. In January 2015, a heavy snowfall caused extreme damage to the forest, with approximately 50% of tree canopies being destroyed. In April 2015, we initiated a long-term project to monitor seedling regeneration after the snow damage. In total, 388 permanent sample plots (1 $m \times 1$ m) were established in the forest with $\geq$ 10 m apart from each other to monitor seedling survival dynamics.

2.2. Experimental design

This study was conducted in September and December 2020. We randomly selected 30 and 45 plots in September and December, respectively, with 15 plots being sampled in both months. During each survey, we identified all seedlings of woody species in each plot. For individuals with no more than 30 leaves, we measured the leaf size and herbivory of each leaf, whereas for individuals with a large number of leaves, 30 leaves were randomly selected. For species with compound leaves (i.e., 4 and 3 species in September and December, respectively), each leaflet was treated as a measurement unit (Paul et al., 2012; Wright et al., 2017).

The length and width of each leaf were measured, and the leaf size was calculated using the ellipse area formula (Pennings et al., 2009; Kavanagh, 2015). Furthermore, our pilot experiment showed that the leaf size estimated from the ellipse area formula was highly correlated with that accurately measured using the scanner (based on 210 leaves of 42 species, Fig. S1). For a few leaves that could not be measured due to excessive feeding, we measured the size of the leaf nearest to the leaf under focus. Leaf damage was defined as the proportion of leaf area consumed by leaf chewers, which were the dominant insect herbivores in the forest. The damage to all leaves was visually estimated by a single investigator, to reduce errors caused by the introduction of subjectivity; the proportions of leaf damage visually estimated by the investigator and those accurately measured using the scanner showed good correlation (Pearson correlation coefficient, $r = 0.877$, $P<0.001$, $n = 60$).

2.3. Data analysis

All analyses were performed using R (version 4.2.0). We analyzed the effects of leaf size both across and within different species. The phylogenetic tree including all our study species were constructed with the R package “V. PhyloMaker” (function “phylo.maker”, Jin & Qian, 2019). The effects of leaf size on herbivory across the species were tested using phylogenetic generalized least squares regression (function “pgls” in package “caper”), which was fitted by maximum likelihood and using Pagel’s λ under Brownian motion. The intensity of herbivory was estimated by the weighted average herbivory severity, that is, total damaged area for all the sampled leaves divided by the total leaf area (Prado et al., 2014; Barreto et al., 2021). Two alternative models were employed: 1) the herbivory severity was assumed to monotonically decrease or increase with leaf size, and leaf size was treated as a fixed factor; and 2) a unimodal relationship was expected between leaf size and herbivory; therefore, leaf size and the quadratic term for leaf size were treated as fixed factors. The better fitting model was selected based on Akaike information criterion (function “anova” in package “stats”). In order to improve the model performance, the herbivory severity which was proportion data was logit-transformed, while leaf size was ln-transformed to reduce skewness (Kabacoff 2015).

Within each single species, a linear mixed model was introduced to analyze the effect of leaf size on the proportion of damaged leaf area (i.e., herbivory severity) (function “lmer” in package “lme4”). The same two candidate models (i.e., with and without the quadratic term for leaf size being included as a fixed factor) were used to analyze the leaf size effect, and the better fitting model was selected using the Akaike information criterion. In all models, the individual seedling ID nested in plot ID was treated as a random effect.

3. Results

3.1. General patterns of leaf size and herbivory

The sampled 174 seedlings from the 30 plots selected in September belonged to 30 species. In total, 2595 leaves were investigated, of which 54.5% were damaged by herbivores, with the herbivory severity being 8.5%. Both leaf size and severity of herbivory differed greatly among leaves, ranging from 0.02 cm^2 to 105.20 cm^2 and 0% to 98%, respectively. In the 45 plots selected in December, there were 248 seedlings belonging to 37 species. In total, 3159 leaves were investigated, and 58.9% of them were damaged, with the herbivory severity being 6.3%. The leaf size and herbivory severity ranged from 0.06 cm^2 to 88.13 cm^2, and 0% to 80%, respectively.

3.2. Effects of leaf size on herbivory across species

Of the 30 species surveyed in September, the average leaf size ranged from 0.83 cm^2 to 42.30 cm^2, and the herbivory severity ranged from 0 to 29%. Leaf size was positively correlated with herbivory severity (t = 2.74, p = 0.011), indicating that species with larger leaves were consumed more heavily (Fig. 1a). Among the 37 species surveyed in December, both leaf size and herbivory varied greatly, with the ranges being 1.09–35.08 cm^2 and 0–38.8%, respectively. A negative quadratic term for leaf size effect was detected in the expression for herbivory severity ($t = -2.14$, $p = 0.042$), revealing a hump-shaped pattern, which indicated that species producing medium-sized leaves were consumed more than species with either large or small leaves (Fig. 1b). When the species producing compound leaves were excluded, the results showed similar patters (Fig. S2).

3.3. Effects of leaf size on herbivory within species

Among the 30 species surveyed in September, five species showed a positive correlation between leaf size and the proportion of leaf area consumed by herbivores (i.e., larger leaves were consumed more heavily), one species showed a negative correlation (i.e., smaller leaves were consumed more heavily), three species showed a hump-shaped pattern (i.e., medium-sized leaves were consumed more heavily than both small and large leaves), and the other 21 species exhibited no apparent patterns (Table 1). Among the 37 species surveyed in December, five species showed a positive correlation between leaf size and herbivory severity, one species showed a negative correlation, two species exhibited a hump-shaped pattern, and the other 29 species exhibited no apparent patterns (Table 2).

4. Discussion

Overall, our results provided strong evidence that the relationship between leaf size and insect herbivory did not follow a constant rule across seasons; a pattern of monotonic increase occurred in September, while a hump-shaped pattern occurred in December. More complex patterns were detected among species, including hump-shaped pattern, monotonic decrease and increase patterns, although many species showed a leaf-size-independent pattern.

As discussed previously, various mechanisms determine both positive and negative effects of leaf size on herbivory (Bogacheva, 1994; Moles and Westoby, 2000; Low et al., 2009; Moreira et al., 2016). Despite potential interference from other factors (e.g., the rapid plant responses after being attacked and the interspecific variation in other leaf traits, such as specific leaf area, and carbon and nitrogen content) (Ackerly et al., 2002; Cardenas et al., 2014; Zava and Cianciaruso, 2014), our results showed a clear positive relationship between herbivory and leaf size across species in September; larger leaves suffered heavier damage than smaller ones, indicating that the positive effects of leaf size may overcome the negative effects. However, a hump-shaped pattern was found in December, that is, the consumption of medium-sized leaves was higher than that of both large and small ones. In our study area, the temperature was much lower in December than in September (7.2 °C vs. 15.3 °C). In general, ectothermic insect herbivores are sensitive to temperature reduction, and often show a decrease in abundance, activity, and metabolic intensity, as well as reduced energy requirements at lower temperatures (Sinclair et al., 2003; Deutsch et al., 2008; Rho and Lee, 2017). In such situations, based on the predator satiation hypothesis (Janzen, 1971), large-sized leaves may show a smaller proportion of insect damage than medium-sized leaves, as the absolute nutrient content of large leaves far exceeds the energy requirement of the insect herbivores.

Our results showed that the leaf size preference varied considerably among species in both seasons, indicating that the effect of leaf size on

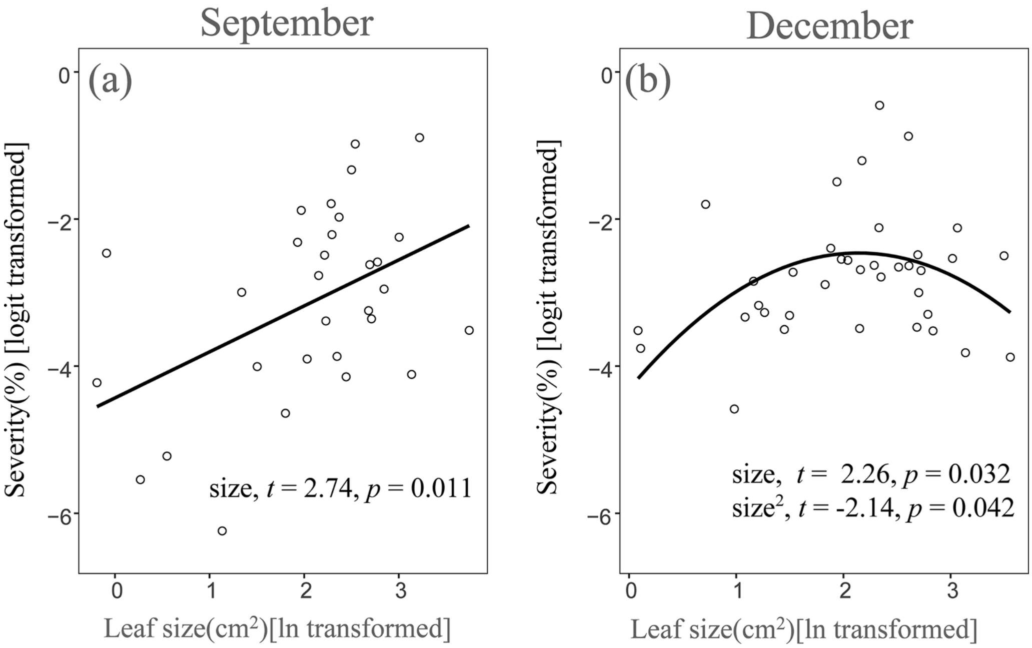

Fig. 1. Effects of leaf size on herbivory severity across species. The regression lines were based on the phylogenetic generalized least squares regression (PGLS).

Table 1

The effects of leaf size on herbivory severity for each of the 30 species in September. The sample size and mean leaf size (cm^2, mean ± SD) are shown in the table, and the minimum and maximum values are shown in the parentheses. The statistical analysis is based on the linear mixed model.

Species	Sample size	Leaf size	Herbivory severity
Rhododendron leptothrium	23	0.83±0.89 (0.02, 2.91)	—
Viburnum erubescens	30	0.92±0.65 (0.09, 2.25)	—
Schefflera shweliensis	8	1.31±1.06 (0.51, 3.49)	—
Ligustrum delavayanum	26	1.74±0.99 (0.19, 3.47)	—
Acanthopanax evodiaefolius	3	3.11±0.21 (2.95, 3.41)	
Ilex corallina	486	3.82±2.65 (0.06, 12.88)	—
Viburnum chingii	43	4.50±2.18 (0.05, 8.12)	∩
Meliosma kirkii	7	6.06±4.49 (2.14, 15.08)	—
Lithocarpus hancei	14	6.89±2.49 (4.24, 12.61)	—
Schima noronhae	72	7.16±6.80 (0.35, 29.55)	↗
Ilex szechwanensis	42	7.63±4.76 (0.39, 18.50)	—
Neolitsea polycarpa	110	8.61±4.88 (0.92, 22.29)	—
Litsea cubeba	26	9.17±4.85 (2.04, 19.96)	—
Eriobotrya bengalensis	14	9.30±7.11 (1.56, 23.56)	↗
Styrax perkinsiae	278	9.83±8.67 (0.60, 41.04)	↗
Litsea elongata	230	9.91±4.71 (1.26, 23.28)	—
Mahonia bracteolata	30	10.46±6.23 (1.45, 26.64)	—
Laurocerasus undulata	15	10.69±8.44 (0.69, 26.86)	—
Lindera thomsonii	12	11.51±6.65 (4.27, 20.62)	—
Symplocos poilanei	30	12.19±6.35 (0.82, 22.62)	↗
Michelia floribunda	19	12.68±7.50 (3.57, 33.98)	—
Daphne papyracea	81	14.60±6.86 (1.90, 32.99)	—
Symplocos ramosissima	390	14.79±9.11 (0.66, 53.13)	↘
Symplocos dryophila	61	15.05±6.84 (4.05, 33.17)	—
Stewartia pteropetiolata	234	16.04±12.27 (0.11,67.85)	↗
Viburnum cylindricum	32	17.20±7.72 (2.16, 36.98)	∩
Machilus gamblei	131	20.16±13.99 (0.51, 105.20)	—
Manglietia insignis	65	23.01±16.41 (2.43, 59.10)	—
Aucuba himalaica	53	25.03±18.52 (0.71, 79.80)	∩
Illicium macranthum	30	42.3±14.43 (31.56, 63.32)	—

↗: positive linear correlation; ↘: negative linear correlation; ∩: hump-shaped; —: means no correlation; and blank: means no analyses were conducted because the sample size was less than 5.

Table 2

The effects of leaf size on herbivory severity for each of the 37 species in December. Details of the explanations of the values in the table, please see the caption of Table 1.

Species	Sample size	Leaf size	Herbivory severity
Ligustrum delavayanum	56	1.09±0.94 (0.06, 3.52)	—
Rhododendron leptothrium	23	1.11±0.86 (0.19, 2.83)	↗
Eurya jintungensis	15	2.04±1.24 (0.38, 4.78)	—
Rhododendron decorum	8	2.67±1.08 (1.27, 4.14)	↘
Viburnum chingii	46	2.95±2.24 (0.16, 9.03)	—
Zanthoxylum esquirolii	30	3.20±1.52 (1.18, 6.68)	—
Ilex coralline	315	3.35±2.26 (0.14, 12.79)	—
Ilex szechwanensis	86	3.54±2.88 (0.19, 14.95)	—
Ilex gingtungensis	15	4.26±2.89 (0.99, 8.95)	∩
Castanopsis wattii	4	4.47±1.13 (2.91, 5.47)	
Schefflera shweliensis	47	4.62±3.03 (1.20, 13.38)	—
Prunus tomentosa	3	6.23±1.46 (4.24, 7.70)	
Litsea elongata	16	6.57±2.48 (2.55, 11.62)	—
Litsea cubeba	7	6.96±6.16 (1.02, 18.50)	—
Laurocerasus undulate	10	7.25±2.73 (2.97, 11.03)	—
Ilex manneiensis	11	7.7±4.21 (0.63, 14.70)	—
Mahonia bracteolate	30	8.60±5.28 (2.20, 27.21)	—
Prunus cerasoides	4	8.66±3.55 (3.39, 13.35)	
Eriobotrya bengalensis	21	8.79±4.93 (2.64, 18.79)	—
Neolitsea polycarpa	469	9.85±6.18 (0.92, 35.12)	↗
Schima noronhae	36	10.30±7.05 (0.82, 30.14)	↗
Lithocarpus hancei	21	10.36±4.09 (3.85, 17.53)	—
Viburnum cylindricum	22	10.50±7.17 (0.28, 22.09)	—
Machilus gamblei	397	12.37±7.05 (1.65, 50.14)	—
Michelia floribunda	16	13.56±7.15 (3.39, 29.71)	—
Symplocos ramosissima	422	13.62±8.83 (0.55, 51.05)	∩
Symplocos anomala	33	14.67±4.74 (3.34, 21.90)	—
Daphne papyracea	103	14.80±6.65 (1.63, 34.00)	—
Cyclobalanopsis stewardiana	30	14.93±4.84 (6.14, 25.92)	—
Stewartia pteropetiolata	381	15.25±12.38 (0.14, 63.15)	↗
Symplocos dryophila	96	16.25±7.44 (2.04, 38.96)	—
Ardisia crenata	26	17.05±10.77 (2.28, 37.89)	—
Lindera thomsonii	29	20.45±3.55 (13.19, 28.27)	—
Symplocos poilanei	90	21.42±12.63 (1.98, 58.17)	↗
Skimmia arborescens	30	23.08±11.06 (7.59, 46.65)	—

(*continued on next page*)

insect herbivory was species-specific. Similar interspecific variation has been reported in other species interactions, such as seed dispersal and predation by small mammals (Feng et al., 2021; Chen et al., 2022). The species measured in our study differed greatly in the mean value (0.83–42.30 cm^2) and range (0.46–104.69 cm^2) of leaf size, and the ratio of maximum to minimum leaf size (2–617-fold). However, most of them did not show distinct effects of leaf size on herbivory within the species. Here, we propose several possible explanations: 1) The limited range of

Table 2 (*continued*)

Species	Sample size	Leaf size	Herbivory severity
Illicium macranthum	58	33.09±13.26 (6.05, 58.69)	—
Manglietia insignis	153	35.08±20.36 (3.47, 88.13)	—

leaf size within a single species may not be sufficient to exhibit a distinct effect of size on herbivory. 2) Plant leaves usually possess physical and chemical defense traits in varying degrees (Moles et al., 2013; Cardenas et al., 2014; Zava and Cianciaruso, 2014; Zhao et al., 2021), which may influence the effects of leaf size on herbivory; for example, if a given leaf contains a large amount of highly toxic chemicals, insect herbivores may reject it regardless of whether it is large or small. 3) Leaves often differ in nutrient content among species (Kattge et al., 2011; Cardenas et al., 2014), which may also contribute to the interspecific variation of the effects of leaf size on herbivory. 4) Many insects are specialist herbivores (Ali and Agrawal, 2012), and different species of herbivores may show different preferences for leaf size. 5) Logically, the intraspecific variation in leaf nutrient and defense content may be much smaller than that at the interspecific level, which may in turn lower the statistical power of the statistical models and lead to undetectable relationship between leaf size and herbivory. 6) The relatively small sample sizes for intraspecific data could also be a potential reason. Furthermore, the neighbor effect also alters insect-leaf interactions; for example, whether a given species of plant would be consumed by an insect herbivore can be influenced by the presence of neighboring plants (Baraza et al., 2006; Hahn and Orrock, 2016; Moreira et al., 2017), which may in turn potentially influence the effect of leaf size on the preference of insect herbivores for a specific species of leaves. In addition, the seedlings surveyed in our study differed greatly in plant height (unpublished data), therefore, based on the apparency theory (Feeny, 1976), such kind of variation in plant height might have some influences on the relationship between leaf size and herbivory.

5. Conclusions

We found that the effect of leaf size on insect herbivory varied across seasons and among plant species. In conclusion, the effects of leaf size on the foraging preferences of insect herbivores may be contingent on both external (e.g., temperature) and intrinsic (e.g., other leaf traits) factors, indicating that a one-off survey with a few species may create a bias in our understanding of the overall pattern of the effect of leaf size on herbivory, especially when many species show no significant relationships between leaf size and herbivory severity. Similar variations may also exist in other ecological processes (e.g., pollination, frugivory, seed predation, etc.), and should be considered in future studies on biotic interactions.

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CRediT authorship contribution statement

Xiang Zhang: Data curation, Formal analysis, Investigation, Software, Visualization, Writing – original draft. **Anting Yang:** Data curation, Formal analysis, Investigation, Software, Visualization, Writing – review & editing. **Li Feng:** Data curation, Formal analysis, Investigation, Software, Visualization. **Zhiyun Lu:** Investigation, Writing – review & editing. **Bo Wang:** Conceptualization, Formal analysis, Funding acquisition, Methodology, Project administration, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.flora.2023.152257.

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