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RESEARCH ARTICLE

Development of defoliating insects and their preferences for host plants under varying temperatures in a subtropical evergreen forest in eastern China

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Abstract The aim of this work was to understand the development of defoliating insects and their preferences for host plants under varying temperatures in a subtropical evergreen broad-leaved forest in China. We measured the main developmental parameters of three typical defoliating insects (i.e., *Ourapteryx ebuleata szechuana*, *Biston marginata*, and *Euproctis angulata*) and their preferences for five host plants at temperatures from 16°C to 31°C at 3°C intervals in the Tiantong National Forest Research station in eastern China. The results showed the following. 1) An appropriate rise in temperature increases the survival rate with an increase in the number of offspring. The developmental durations for these three insects were shortened, and pupal weight increased with an increase in temperature. 2) A shift in the preference for host plants for these three insects was observedat elevated temperatures. They all preferred to feed on *Schima superba* and *Castanopsis sclerophylla* at elevated temperatures, showing an opposite response to the other three plants. The daily leaf consumption of the three insects was positively correlated with their feeding preference, with more leaves being consumed from the plants they preferred. 3) For *O. ebuleata szechuana* larvae, daily leaf consumption initially increased and then decreased with increasing temperatures. In contrast, *Biston marginata* and *Euproctis angulata* larvae consumed more leaves at elevated temperatures. The feeding preferences of *O. ebuleata szechuana* and *Biston marginata* were more sensitive to changing temperatures than that of *Euproctis angulata* laevae. We concluded that increased numbers of offspring and generations, pupal weights, and a shift in preference to two plants for these three defoliating insects might lead to severe damage to these two plants which would enhance the fragmentation and decrease the stability of the forest communities under changing temperatures. Meanwhile, the variations in the responses of defoliating insects to the changing temperatures should be taken into consideration for the pest management of forests to adapt to the changing climate.

Keywords defoliating insects, elevated temperature, development dynamics, feeding behavior, subtropical evergreen forest

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1 Introduction

The rising temperature of the earth's atmosphere is one of the leading characteristics of climate change (Kardol et al., 2010). Numerous environmental monitoring and model simulations have demonstrated that global warming since the industrial revolution is ongoing and enlarged in this century, and it is predicted that the global mean temperature could increase by 2.6°C to 4.8°C by 2100 (IPCC, 2013). In this respect, the predicted increase in temperature in China would be 2.3°C to 3.3°C in the next 50 years. Because many biological and chemical processes and their reaction rates in the natural ecosystems are controlled by their environmental temperatures, an understanding of the impacts of changing temperature on natural ecosystems under predicted climate change is a hot topic (Dieleman et al., 2013; Chung et al., 2013; Peters et al., 2014).

Insects and plants are key components of natural ecosystems (Coley and Barone, 1996; van Velzen and Etienne, 2015). The food webs that are based on these two groups of species play important roles in the maintenance of ecosystem stability and drive the material circulation and energy flow (Bidart-Bouzat and Imeh-Nathaniel, 2008; Dardeau et al., 2014). Leaf damage caused by defoliating insects could weaken the growth of the plants (Weed et al., 2011) and affect the interspecific competition among species (Giffard et al., 2012) and community dynamics (Davidson and Mckey, 1993; Strauss, 2001; Cribb et al., 2010; Delaney, 2012). Temperature is the key-environmental factor that determines insect growth, development, and metabolism (Porter, 1995). Numerous studies have shown that elevated temperatures could lead to insect pest resurgence (Yamanaka et al., 2008), and speed up the development rates and shorten the duration of each generation (Gomi et al., 2009); consequently, voltinism, in turn, might be bolstered (Régnière et al., 2012). The survival rates of the progeny might be affected due to the development of the parental generation having been affected by the rising temperature (Hódar et al., 2003). Additionally, the feeding behavior and food consumption could be affected by the changing temperatures (Everatt et al., 2013). There is long history of study on the interactions between insects and their host plants (Unsicker et al., 2009; Yamazaki and Lev-Yadun, 2015). Most of these shudies have focused on the interactions between the crops and their pests (Karageorgou et al., 2008; Calixto et al., 2015), and some research has been conducted in the tropical rainforest and temperate forest (Borchert et al., 2005; Chuine et al., 2010), whereas little is known about the interaction in the subtropical evergreen broad-leaved forest (Liu et al., 2010).

The subtropical evergreen broad-leaved forest, mainly distributed in China and Japan, is one of the main terrestrial vegetation types. It plays an important role in biodiversity conservation and environmental protection. Interactions between insects and plants play key roles in the maintenance of the biodiversity, stability of the community structure, the circulation of materials, and the flow of energy. One key problem that vegetation faces is fragmentation and structural damage: leaf consumption from defoliating insects likely contributes to this problem, at least in part (Wang, 2007; Liu, 2011). To date, much research has been conducted on leaf herbivory and its influential factors (Coley and Barone, 1996), the spatial and temporal patterns of leaf herbivory (Coley and Barone, 1996; Tian et al., 2007), and the defense strategies of the young leaves adapted to insect attack (Agrawal and Fishbein, 2006). However, little is known about the effects of warming climate on insect development and feeding behavior (Ge, 2011).

The aim of this work was to understand the development of defoliating insects (i.e.,*Ourapteryx ebuleata szechuana*, *Biston marginata*, and *Euproctis angulata*) and their preferences for host plants under varying temperatures in a subtropical evergreen broad-leaved forest in China.

2 Materials and methods

2.1 Study site

This study was conducted at the Tiantong National Forest Ecosystem Observation and Research Station, East China Normal University (29°28'N, 121°47'E), in the eastern part of China (Fig.1). The station has a subtropical, monsoon climate. The mean annual temperature is 16.2°C. The highest average monthly temperature is 28.1°C in July, and the average lowest monthly temperature is 4.2°C in January. The annual precipitation is 1,374 mm, of which 35%–40% occurs from June to August, and the average annual humidity is approximately 82%. This forest reserve is species-rich, acting as an important refugium for unique species, and thus has been an important focus for biodiversity conservation (Song and Chen, 2007). The dominant plant species include *Schima superba* Gardn. and Champ. (Theaceae), *Castanopsis fargesii* Franch. (Fagaceae), *Castanopsis sclerophylla* (Lindl.) Schott. (Fagaceae), and *Cyclobalanopsis sessilifolia* (Blume) Schottky (Fagaceae).

2.2 Growth and development of study insects

In this work, three defoliating insects (i.e., *Ourapteryx ebuleata szechuana* (Lepidoptera: Geometridae), *Biston marginata* (Lepidoptera: Geometridae), and *Euproctis angulata* (Lepidoptera: Lymantriidae) (Fig. 2) were chosen because they are widely distributed in this forest and feed substantially on the leaves of dominant plants. Additionally, the timing of the development of these three insects was well fitted to the leaf early phenology (i.e., leaf emergence and expansion from February to June).

In this work, 5 common host plants for these 3 defoliating insects were chosen; these five plants are dominant plants for this vegetation type, playing important roles in the maintenance of the community structure and their ecological functions. They are as follows: *Schima superba* (Theaceae), *Castanopsis sclerophylla* (Fagaceae), *Cyclobalanopsis glauca* (Fagaceae), *Cyclobalanopsis sessilifolia* (Fagaceae), and *Cyclobalanopsis myrsinaefolia* (Fagaceae). The branch sprout and later leaf expansion was from March to June (Liu, 2011). Previous work determined that feeding by the defoliating insects could affect the plants' resource allocation, reduce their fitness, and even kill the plants (Wang, 2007; Liu, 2011).

2.3 Methods

2.3.1 Collection of target insects

Collection of *O. ebuleata szechuana* and *B. marginata*: Moths were collected with light traps on consecutive

Fig. 1 Location of Tiantong National Forest Research Station in eastern China.

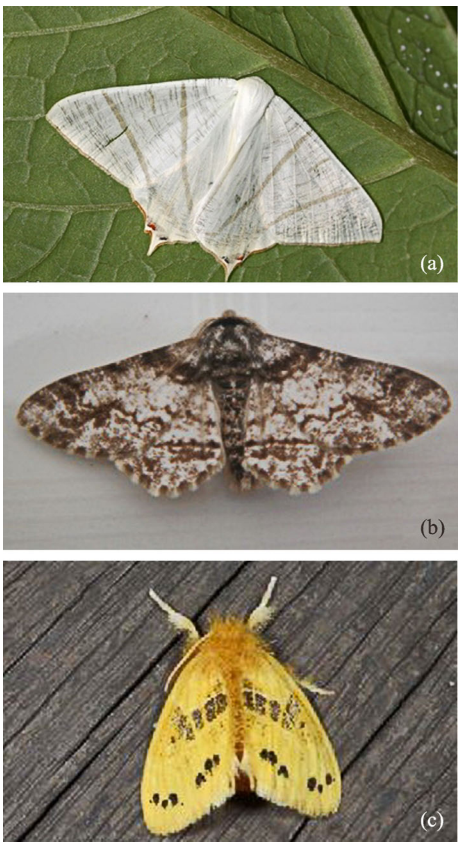

Fig. 2 *Ourapteryx ebuleata szechuana* (a), *Biston marginata* (b) and *Euproctis angulata* (c).

nights in the forest beginning in late February. The filament lamp was covered with transparent gauze to protect the moths from being burned. The collected *O. ebuleata szechuana* (200 males and 200 females) or *B. marginata* (200 males and 200 females) were placed in transparent plastic boxes (20 cm in diameter and 25 cm in height, with 5 females and 5 males in each box). Rayon Balls with sucrose water were placed in the box to provide energy and water for the moths. The experiment began when the females had oviposited 10,000 eggs.

Collection of *E. angulata*: The emergency of *E. angulata* larvae began in late March. The field collection of eggs in clusters was done before March 1st, and then these eggs were retrieved for storage in refrigerators at approximately 7°C. The experiment began when we got 10,000 eggs.

2.3.2 Experimental design and treatments

The measurements of the response of the development and preferences for host plants of the defoliating insects to temperature were conducted for temperatures at 3°C intervals from 16°C to 31°C. The 16°C and 31°C were set based on the maximum and minimum daily mean temperatures observed from February to June in the past 30 years (1983–2013). The greenhouse system consisted of 21 chambers (RXZ-328A, Jiangnan Instrument, Ningbo, Zhejiang, China, 1.5 m in length, 1.5 m in width, and 2.0 m in height) working independently with three replicates for each temperature level: ambient temperature (Con), 16°C, 19°C, 22°C, 25°C, 28°C, and 31°C.

Light intensity was settled at 18,000 lux and the photoperiod was the same as the daily sunshine duration outside, and the humidity was settled at 85%±3% (Ge, 2011).

2.3.3 Development of the 3 defoliating insects

Egg hatching: A total of 300 eggs were placed on a 9-cm-diameter glass Petri dish in each chamber. This treatment was continued until egg hatching. The duration of the hatch was recorded, and the egg stage and hatchability was subsequently calculated.

Development of larvae: The methods used by Jermy et al. (1968) and Lemoine et al. (2013) were applied to the produced larvae. Specifically, after larval emergence, 30 larvae were placed on a 20-cm-diameter glass Petri dish, and every 5 dishes were established as a group. The larvae were fed with fresh leaves at 0800 hours every day. When the larvae were 3rd instar, they were individually placed on a 10-cm-diameter glass Petri dish for further feeding until pupation. At 4 days after pupation, 50 typical pupae were collected for weight determination (LE104E, Switzerland).

The pupation date and pupal weight were recorded, and the duration of larval development and survival rate (i.e., pupation rate) were subsequently calculated.

Pupal experiment: This experiment was conducted only on *O. ebuleata szechuana* and *E. angulata*. The eclosion date was recorded, and the pupal stage and eclosion rate were subsequently calculated.

Survival rate and developmental duration were calculated as follows:

Survival rate (%) = hatching rate × pupation rate × eclosion rate × 100%,

Developmental duration (d) = egg stage + larval stage + pupal stage.

2.3.4 Preference for host plants and leaf consumption

One hundred healthy larvae of the same size for each insect, 2 days after the 5th instar, were chosen to test for the preference for host plants and leaf consumption according to the method used by Lemoine et al. (2013). These larvae was starved for 24 hours and then weighed. Fifty fresh leaves from each host plant were collected and cut into a rectangular shape, 4 cm in length and 3 cm in width, and then were weighed and placed on the carton bottom (1 m in length and 1 m in width) randomly. Then they were settled in darkness, and the quantity of larva on each plant leaf was recorded in the following 24 hours at 3 hour intervals, and the larvae and each of remaining leaves were weighted (LE104E, Switzerland). Additionally, 10 fresh leaves for each plant were collected and weighed, and the weights of these leaves were measured again 24 hours later in the atmosphere for the calculation of the dehydration rate (LE104E, Switzerland).

The feeding preference for each host plant (%) = the number of insects showing a preference for each plant/ number of all the insects × 100%.

The dehydration rate (%) = (the fresh leaf mass – the leaf mass 24 hours later in the atmosphere) /fresh leaf mass × 100%.

The daily consumption of each plant ($g\cdot d^{-1}$) = (leaf mass before breeding − leaf mass after breeding) × (1 − dehydration rate)/d.

Daily consumption ($g\cdot d^{-1}$) = daily consumption by all 5 plants per day.

The feeding preference coefficient (FPC) was introduced to describe the feeding preference to different plants under different temperatures. The bigger FPC value means higher preference for a specific plant.

The feeding preference coefficient (FPC) = standard deviation of the means values of insects choosing different plants / mean of the number of insects choosing different plants.

2.4 Data analysis

The statistical analyses were performed using the SPSS software package (Version 19.0, Chicago, IL, USA). The mean differences in all of the parameters of the survival rate (i.e., hatching rate, pupation rate, and eclosion rate), developmental duration (i.e., egg stage, larval stage, and pupal stage), pupal weight, and feeding preference coefficient among different temperatures were tested by least significant difference (LSD) one-way analysis of variance. The linear regression analysis was carried out to check the correlations between the feeding preference and the daily consumption to each host plant. Data were first tested for a normal distribution. All data that did not fit a normal distribution were standardized. A Spearman rank correlation was used for correlation analysis. Differences in the parameter values were considered to be statistically significant at $P < 0.05$.

3 Results

3.1 Development of three defoliating insects under varying temperatures

The survival rates of the three defoliating insects initially increased and then decreased thereafter with increasing temperature. The maximum values were detected at 25°C. Regarding *O. ebuleata szechuana* and *B. marginata,* the temperature affected their survival rates significantly, and their survival rates declined sharply at 28°C compared to those values observed at 25°C. In contrast, changing temperatures did not affect the survival rate of *E. angulata* significantly, and the differences in the values were not significant among temperatures except at 16°C and 31°C, which were lower compared to those at other temperatures. The three defoliating insects' developmental durations were all shortened with rising temperatures below 25°C, and the differences in developmental duration were not significant when the temperatures were above 25°C. The duration in *O. ebuleata szechuana* and *B. marginata* under 28°C were shortened by 41.3 days and 21.1 days, respectively compared to those values at 19°C. Additionally, the duration of *E. angulata* was 53.8 days shorter at 31°C compared to that at 16°C. Temperature affected the pupal weights of the 3 defoliating insects significantly, which increased with an increasing temperature. However, differences in pupal weight were not significant for *O. ebuleata szechuana* and *B. marginata* among temperatures when the temperature was above 22°C; the same phenomenon was observed for *E. angulata* when the temperature was over 25°C (Fig. 3).

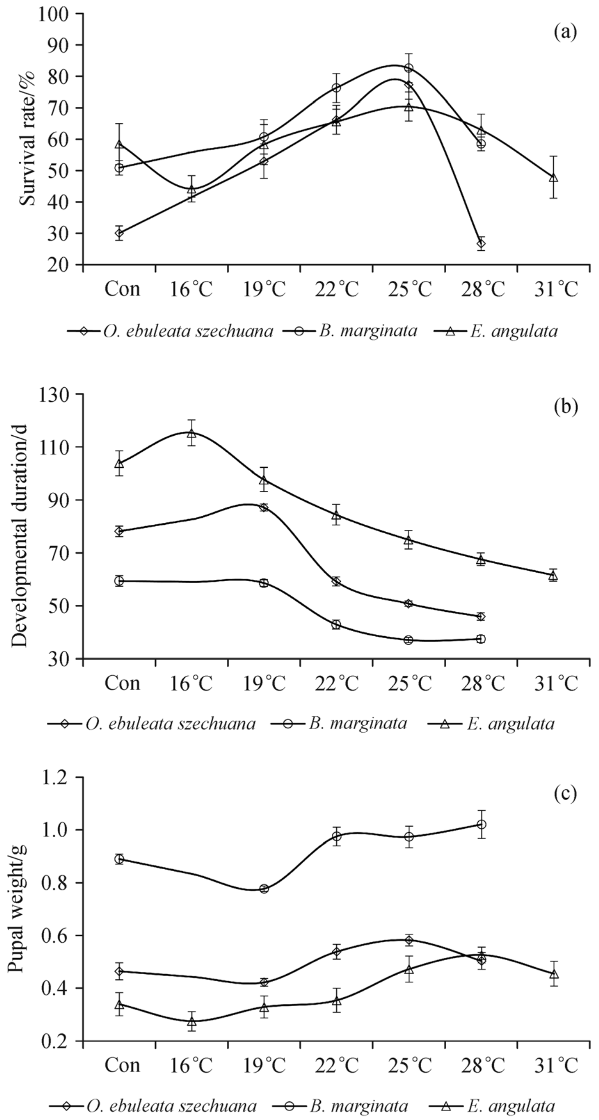

Fig. 3 Mean (±SE, $n=3$) of survival rate, developmental duration, and pupal weight of 3 defoliating insects (*O. ebuleata szechuana*, *B. marginata*, *and E. angulata* under varying temperatures. The 3 figures ((a), (b), and (c)) are for survival rate, developmental duration, and pupal weight of the 3 defoliating insects in order. Con means ambient temperature from March to June in 2014 in the station, and its mean temperature was 17.2°C with a minimum of 4.17°C in March and maximum of 25.68°C in May. In figure 3(a): $F_O=22.123$, $P_O<0.001$; $F_B=11.936$, $P_B<0.001$; $F_E=2.23$, $P_E=0.102$. In figure 3(b): $F_O=51.304$, $P_O<0.001$; $F_B=40.967$, $P_B<0.001$; $F_E=19.898$, $P_E<0.001$. In figure 3(c): $F_O=3.065$, $P_O=0.069$; $F_B=5.658$, $P_B=0.012$; $F_E=3.486$, $P_E=0.025$.

3.2 Feeding preferences for host plants by three defoliating insects under varying temperatures

Under ambient temperatures, 61% of *O. ebuleata szechuana* and 55% of *Euproctis angulata* larvae preferred *Castanopsis sclerophylla* and *Schima superba,* respectively ($F_1=8.489$, $P_1<0.001$; $F_2=6.357$, $P_2<0.001$). In contrast, 52% of *Biston marginata* larvae preferred *Schima superba* and *Cyclobalanopsis sessilifolia* ($F=13.484$, $P<0.001$). A shift in the feeding preference for the three insects was observed with increasing temperatures (Fig. 4). All three insects showed greater preference for *Castanopsis sclerophylla* and *Schima superba* with increasing temperatures, opposite to what was observed in response to the other three plants (Fig. 4). *Ourapteryx ebuleata szechuana* larvae did not feed on *Cyclobalanopsis myrsinaefolia* when the temperatures were above 28°C, *Biston marginata* larvae did not choose *Cyclobalanopsis sessilifolia* under elevated temperature compared to ambient conditions (Fig. 4). Feeding preferences of *O. ebuleata szechuana* and *Biston marginata* were more sensitive to the changing temperature compared to *Euproctis angulata,* as demonstrated by the higher FPC values (Table 1).

3.3 Daily leaf consumption of three defoliating insects under varying temperatures.

The changing temperature affected the daily consumption of the 3 defoliating insects significantly (Fig. 5). The daily leaf consumption of *O. ebuleata szechuana* increased initially and then decreased later; the maximum value (0.478±0.0342 g) was at 25°C ($F=4.454$, $P=0.025$). In contrast, the daily leaf consumption for *B. marginata* and *E. angulata* increased with increasing temperatures, with a maximum value of 0.6869±0.0343 g for *B. marginata* at 28°C and 0.8859±0.0681 g for *E. angulata* at 31°C ($F_1=4.825$, $P_1=0.020$; $F_2=3.348$, $P_2=0.037$) (Fig. 5). The proportion of the daily consumption of *Castanopsis sclerophylla* and *Schima superba* to the total leaf consumption increased with increasing temperatures for these three insects (Fig. 5). The daily leaf consumption showed a close correlation with the feeding preference

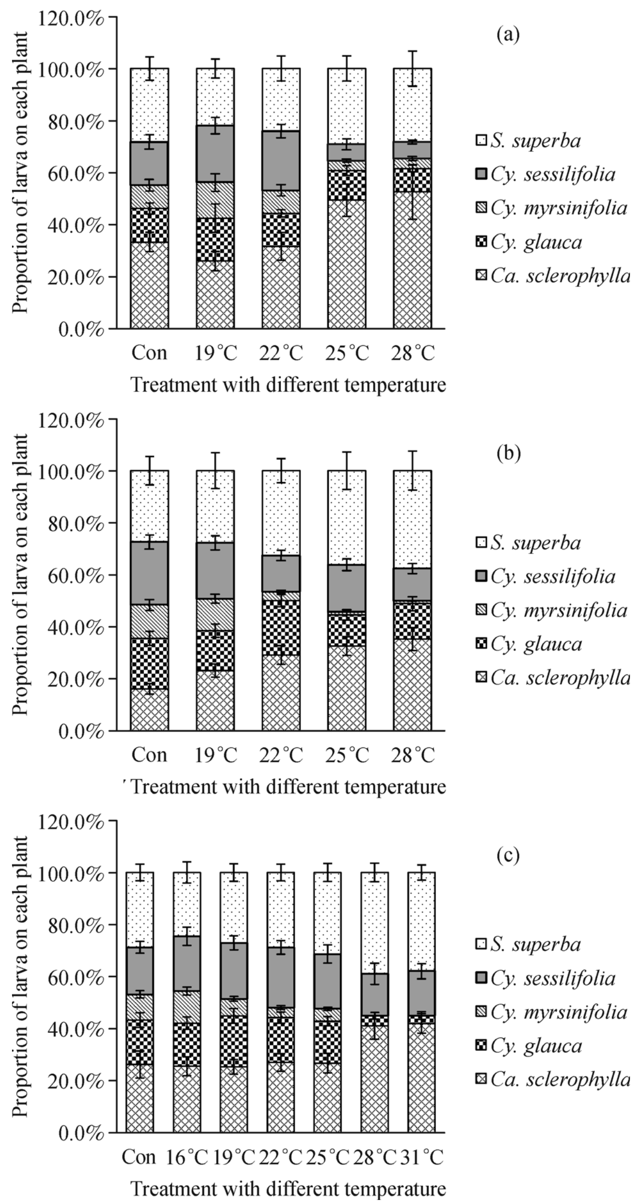

Fig. 4 Means (±SE, $n = 3$) of 3 defoliating insects' feeding preference for five host plants under varying temperatures. (a) *O. ebuleata szechuana*, (b) *B. marginata*, (c) *E. angulata*. Con means ambient temperature from March to June in 2014 in the station, and its mean temperature was 17.2°C with a minimum of 4.17°C in March and maximum of 25.68°C in May.

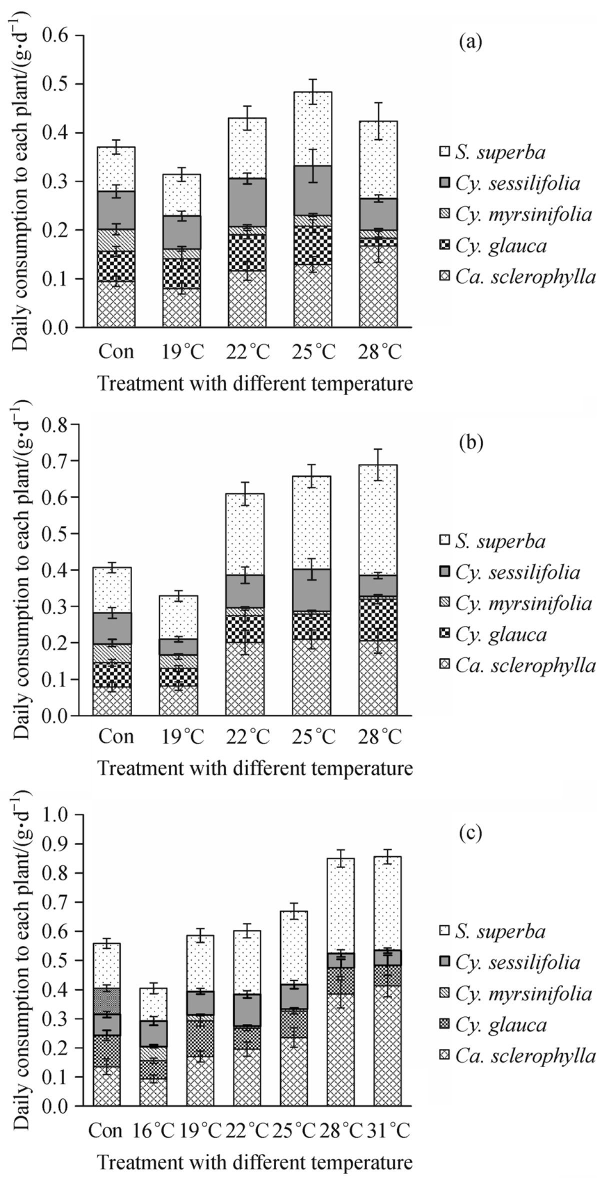

Fig. 5 Means (±SE, $n = 3$) of 3 defoliating insects' daily consumption for five host plants under varying temperatures. (a) *O. ebuleata szechuana*, (b) *B. marginata*, (c) *E. angulata*. Con means ambient temperature from March to June in 2014 in the station, and its mean temperature was 17.2°C with a minimum of 4.17°C in March and maximum of 25.68°C in May.

Table 1 Mean (±SE, $n = 3$) of feeding preference coefficient for 3 defoliating insects under varying temperatures. (*O. ebuleata szechuana*, *B. marginata*, *and E. angulata*) under varying temperatures. Con means ambient temperature from March to June in 2014 in the station, and its mean temperature was 17.2°C with a minimum of 4.17°C in March and maximum of 25.68°C in May. Different letters denote significant differences between means among temperatures within column ($P < 0.05$)

Species	Con	16°C	19°C	22°C	25°C	28°C	31°C	*F* (*P*)
O. ebuleata szechuana	0.59±0.12b	–	0.28±0.09c	0.54±0.10b	0.95±0.14a	1.00±0.11a	–	28.666 (< 0.001)
B. marginata	0.39±0.07c	–	0.44±0.11c	0.92±0.13b	1.00±0.12b	1.14±0.17a	–	30.239 (< 0.001)
E. angulata	0.26±0.09b	0.18±0.09b	0.15±0.07b	0.21±0.09b	0.28±0.10b	0.72±0.14a	0.73±0.17a	21.050 (< 0.001)

coefficient for each plant under varying temperatures: higher feeding preference coefficient with higher daily leaf consumption (Table 2).

4 Discussion

4.1 Effects of changing temperatures on the development of defoliating insects

Elevated temperature shortened the duration of development in the three insects, mainly due to the shortened egg stage, larval stage, and pupal stage (Fig. 6). The timing of hatching and the eclosion of the pupae are strongly driven by temperature (i.e., accumulation of effective temperature), and a rise in temperature is associated with an acceleration in life cycle, with shortened developmental duration (Chen and Ma, 2010). The larval stage, the longest stage in a life cycle, was shortened mainly due to increased energetic enzymatic activity under elevated temperatures; these temperatures also sped up the developmental rate (Su et al., 2013), which is consistent with the findings by Radchuk et al. (2013) and Nyamukondiwa et al. (2013). The rising temperature might disrupt the synchrony between the timing of the insects' development and phenology of their host plants. In this respect, insect emergence may be earlier than leaf emergence, with the newly hatched larvae feeding only on mature leaves with poor nutrition, which results in a relatively lower survival rate (Liu, 2011). On the other hand, Yao and You (2012) reported that the shortened developmental duration reduces the insects' risks of being preyed on by natural enemies, thereby leading to a higher survival rate.

The survival rates of the three defoliating insects increased initially and decreased later under elevated temperatures. The same phenomenon was also observed for the hatching rate, pupation rate, and eclosion rate of the three insects under elevated temperatures (Fig. 7). The egg hatching rate is a key factor determining the survival rate of the insects; therefore, an appropriate rise in temperature would provide an environment that favored egg hatching, leading to a higher hatching rate (Du et al., 2012), but the higher temperature could lead to a higher energy consumption rate of the energy stored in the egg, with energy being depleted during the hatching stage and consequently resulting in a lower hatching rate (Denis et al., 2012). The pupal rate and the eclosion rate were both decreased when the temperatures were above 25°C (Fig. 7), which is in line with other study by Salin et al. (2006); which showed that water metabolism is the key factor affecting the development and survival of insects under high temperatures, and that thermal injury is usually the reason for higher mortality.

4.2 Effects of changing temperatures on the feeding behavior of defoliating insects

In this work, insect feeding behavior is mainly composed of their feeding preference and daily consumption of host plants. We found that these 3 defoliating insects shifted their preference to *Schima superba* and *Castanopsis sclerophylla* compared to the other three host plants.

Rising temperature has been suggested to accelerate the developmental rate of insects, possibly requiring more food resources (i.e., nutrition and water) to satisfy their growth and development. Additionally, insects protect their body from thermal injury by body water evaporation inside and outside (Salin et al., 2006). Leaves rich in nutrition and water should be good choice for insects under high temperatures. In this work, *Schima superba* and *Castanopsis sclerophylla* are rich in leaf nutrition (i.e., leaf nitrogen) and water, and low in tannin content and toughness; therefore, the choice of these two plants is a good strategy for these insects to adapt to a warming climate. In comparison, *Cyclobalanopsis sessilifolia* leaves are rich in leaf nutrition and tannin content, but low in water content and exhibit greater toughness (Table 3). The other two species are rich in water content, but poor in leaf

Table 2 Regression analysis between the feeding preference and consumption to each host plant under treatment with different temperature. Con means ambient temperature from March to June in 2014 in the station, and its mean temperature was 17.2°C with a minimum of 4.17°C in March and maximum of 25.68°C in May

Treatment	*O. ebuleata szechuana*		*B. marginata*		*E. angulata*	
°C	Regression equation	$R^2(P)$	Regression equation	$R^2(P)$	Regression equation	$R^2(P)$
Con	$y=0.0024x+0.0369$	0.886(0.017)	$y=0.0065x$	0.769(0.051)	$y=0.0038x+0.0278$	0.953(0.007)
16°C	–	–	–	–	$y=0.0037x-0.0040$	0.888(0.016)
19°C	$y=0.0060x–0.0249$	0.716(0.071)	$y=0.0073x–0.0290$	0.726(0.067)	$y=0.0073x-0.0395$	0.850(0.026)
22°C	$y=0.0052x+0.0033$	0.773(0.050)	$y=0.0080x–0.0156$	0.876(0.019)	$y=0.0079x-0.0431$	0.890(0.016)
25°C	$y=0.0024x+0.0594$	0.517(0.171)	$y=0.0083x–0.0073$	0.992(< 0.001)	$y=0.0091x-0.0580$	0.877(0.019)
28°C	$y=0.0041x+0.0208$	0.785(0.045)	$y=0.0081x–0.0059$	0.917(0.010)	$y=0.0090x-0.0036$	0.909(0.012)
31°C	–	–	–	–	$y=0.0093x-0.0097$	0.907(0.012)

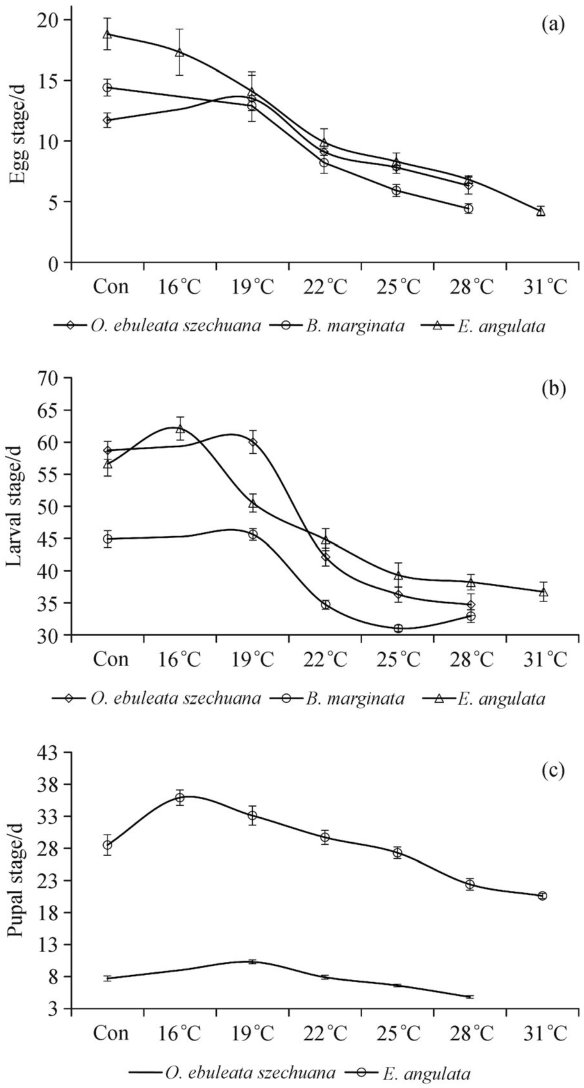

Fig. 6 Mean (±SE, $n = 3$) of egg stage, larval stage and pupal stage of 3 defoliating insects (*O. ebuleata szechuana, B. marginata and E. angulata* under varying temperatures. The 3 figures ((a), (b) and (c)) are for egg stage, larval stage, and pupal stage of the 3 defoliating insects in order. Con means ambient temperature from March to June in 2014 in the station, and its mean temperature was 17.2°C with a minimum of 4.17°C in March and maximum of 25.68°C in May. In figure 6(a): F_O= 6.634, $P_O < 0.001$; F_B= 36.187, $P_B < 0.001$; F_E= 16.435, $P_E < 0.001$. In figure 6(b): F_O= 60.066, $P_O < 0.001$; F_B= 42.256, $P_B < 0.001$; F_E= 16.435, $P_E < 0.001$. In figure 6(c): F_O= 36.009, $P_O < 0.001$; F_E= 16.842, $P_E < 0.001$.

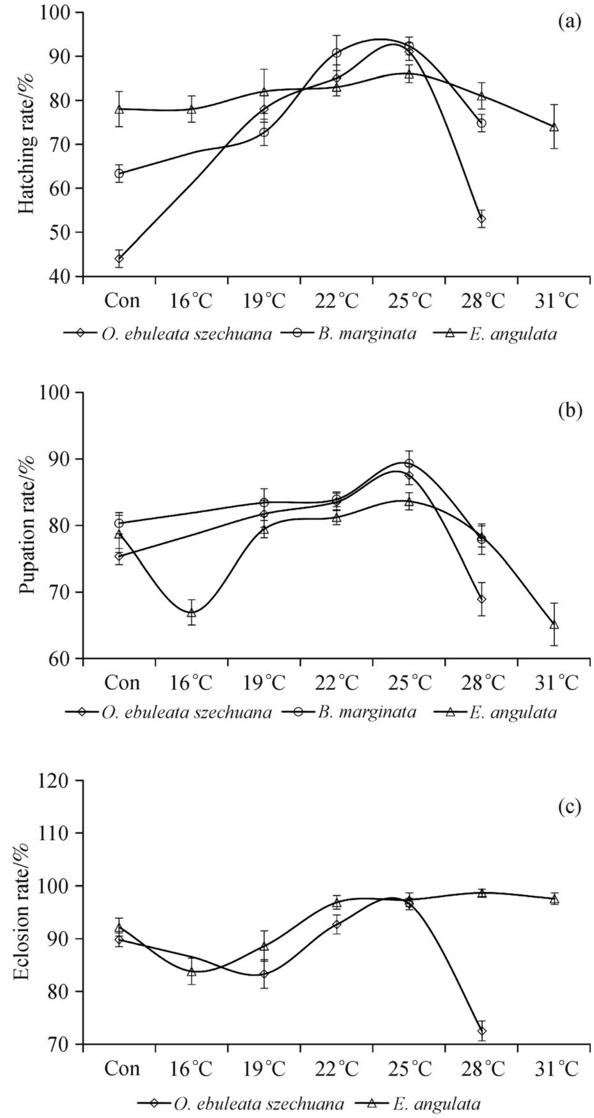

Fig. 7 Mean (±SE, $n = 3$) of hatching rate, pupation rate and eclosion rate of 3 defoliating insects (*O. ebuleata szechuana*, *B. marginata*, *and E. angulata*) under varying temperatures. The 3 figures ((a), (b), and (c)) are for hatching rate, pupation rate, and eclosion rate of the 3 defoliating insects in order. Con means ambient temperature from March to June in 2014 in the station, and its mean temperature was 17.2°C with a minimum of 4.17°C in March and maximum of 25.68°C in May. In figure 7(a): F_O= 52.963, $P_O < 0.001$; F_B= 15.641, $P_B < 0.001$; F_E= 0.763, P_E= 0.573. In figure 7(b): F_O= 10.359, P_O= 0.001; F_B= 4.02, P_B= 0.034; F_E= 11.747, $P_E < 0.001$. In figure 7(c): F_O= 16.476, $P_O < 0.001$; F_E= 3.294, P_E= 0.031.

nutrition (Fig. 7). Our findings were in line with a study by Fleurat-Lessard and Dupuis (2010), who reported that nutrition and water content are the key factors affecting the feeding behavior of *Sitophilus zeamais*.

In general, the daily leaf consumption of the three defoliating insects increased with increasing temperatures (Fig. 5) and had a close correlation with their feeding preference (Fig. 5, Table 3). As observed in this work, the pupal weights increased under elevated temperature (Fig. 3). Additionally, numerous studies found that the approximate digestibility by the insects should decrease with increasing temperatures (Su et al., 2013). Consequently, it is a good strategy for insects to consume more leaves to guarantee growth under the warming climate (Teimouri et al., 2013).

Table 3 Mean (±SE, $n = 3$) of leaf nitrogen concentration (LN), leaf water content (LW), leaf tannin content (LT), and leaf toughness (T) of five host plants. Different letters denote significant differences between means among temperatures within column ($P < 0.05$)

Plant	LN/%	LW/%	LT/%	T/($g \cdot mm^{-2}$)
Castanopsis sclerophylla	3.14±0.15ab	77.72±5.55a	0.38±0.03d	0.542±0.044c
Cyclobalanopsis glauca	2.83±0.16cd	76.1±7.61a	0.54±0.04c	0.628±0.045b
Cyclobalanopsis myrsinifolia	2.72±0.18d	72.69±9.21ab	2.65±0.27b	0.407±0.041d
Cyclobalanopsis sessilifolia	3.08±0.11bc	62.03±3.31b	5.46±0.20a	0.803±0.037a
Schima superba	3.38±0.14a	77.73±4.86a	2.8±0.16b	0.652±0.043b
F	9.131	3.142	464.157	41.9850
(*P*)	(0.002)	(0.065)	(< 0.001)	(< 0.001)

Note: detailed information for the measurement of each parameter was provided as follows: LN: Liu, 2011; LW: Coley and Barone, 1996; LT: Yuan et al., 2009; T: Feeny, 1970.

4.3 Variations in the response of the three defoliating insects to changing temperatures

Variations in insect responses to changing environments have been reported (Visser and Holleman, 2001; Thomson et al., 2010). In this work, the development and feeding preference of *E. angulata* were less sensitive to the changing environment compared to *O. ebuleata szechuana* and *Biston marginata* (Figs. 3 and 4), probably due to physiological differences in the insects: the ecological amplitude in temperatures (i.e., maximum and minimum temperature) is wider for *E. angulata* compared to the other two insects. One distinct difference in the response to changing temperatures among insects was the hatching rate of the eggs (Fig. 7). The reason was probably due to the larger eggs for *E. angulata* compared to *O. ebuleata szechuana* and *Biston marginata.* According to Bergmann's rule, eggs of larger volume are accompanied by smaller superficial area, which can decrease the effective action area with a higher adaptability to the environment (Sun, 2001). Although elevated temperature could shorten the duration of development for the three insects (Fig. 3), voltinism in *O. ebuleata szechuana* and *E. angulata* should be changed due to the shortened life cycle caused by climate warming (Régnière et al., 2012; Radchuk et al., 2013). Regarding *Biston marginata,* voltinism was not affected because the insect experiences a summer and winter diapause.

5 Conclusions

In this work, the development of defoliating insects and their preferences for host plants under varying temperatures in a subtropical evergreen forest were studied. We found that an appropriate rise in temperature would increase the survival rate with an increase in the number of offspring. With increasing temperature, the developmental durations were shortened, possibly allowing for an increase in voltinism, and pupal weight also increased. A shift in the preference for host plants for defoliating insects was observed under elevated temperatures, and the daily leaf consumption of the three insects was positively correlated with their feeding preference under elevated temperatures. Variations existed in the insects' response of the development and feeding preference to the changing temperatures. We concluded that elevated temperature might enhance the fragmentation and stability of the forest communities due to insect feeding. Meanwhile, the variations in the responses of defoliating insects to the changing temperatures should be taken into consideration for pest management in forests adapting to the changing climate.

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