

## **Insect community in *sengon* (*Falcataria moluccana*) stands damaged by stem borers at various altitudes**

**YUSUF ARDIAN SUTRISNO, ANANTO TRIYOGO\*, PRIYONO SURYANTO**

Department of Silviculture, Faculty of Forestry, Universitas Gadjah Mada. Jl. Agro. No 1, Bulaksumur, Sleman 55281, Yogyakarta, Indonesia.  
Tel./fax.: +62-274-512102, \*email: triyogo99@yahoo.com

Manuscript received: 4 January 2022. Revision accepted: 30 May 2022.

**Abstract.** Sutrisno YA, Triyogo A, Suryanto P. 2022. *Insect community in sengon (Falcataria moluccana) stands damaged by stem borers at various altitudes. Biodiversitas 23: 3234-3242.* A healthy ecosystem is characterized by a balanced interaction between its constituent components. Meanwhile, *sengon* or *Falcataria moluccana* stands are one of the ecosystems currently experiencing damage due to stem borer pests. The dominance of pests leads to an imbalance between the constituent components of the ecosystem, especially insects. Therefore, this study aims to examine the characteristics of the community and the role of each insect, as well as the pattern of relationships with the stem borer attack area. It was conducted in a 5-year-old *sengon* stand in the Cangkringan Sub-district, Sleman, Yogyakarta, Indonesia, at altitudes of 500, 600, and 700 m above sea level (asl), while observations and insect collection were carried out from March to August 2018 using pitfall and sticky traps, as well as sweeping nets. Furthermore, direct identification, specimens, and references were used to determine the insects to the morphospecies level, while the diversity (H'), evenness (E), and similarity (S) indexes were calculated to describe the community. The two-way ANOVA analysis was conducted to determine the effect of altitude and observation month on insects at the family level, while a correlation analysis was performed to determine the relationship between insect diversity and the stem borer attack area. The results showed that the insect community in the *sengon* stands consisted of 14 orders, 49 families, with 104 morphospecies. The most abundant was Family Formicidae (Hymenoptera) and the classification was based on the respective roles obtained in five groups, namely herbivores, predators, pollinators, parasitoids, and decomposers. The observation month, altitude, and interaction have different effects on insects at the family level, which includes Eucharitidae, Tephritidae, and Cicadellidae. Moreover, the abundance of Eucharitidae parasitoids decreased with an increase in altitude, while the herbivores with the highest abundance were Tephritidae at an altitude of 500, 700, and 600 m, as well as Cicadellidae at an altitude of 500, 600, and 700 m above soil level, respectively. Natural predators dominated by Formicidae (Hymenoptera) showed a similar tendency at every altitude and observation month. Based on the results, the higher the level of insect diversity in the form of population and species, the lower the stem borer attack area. Therefore, further observations need to be carried out on the natural predator found, including specialists or generalists, to obtain the most suitable for controlling stem borers.

**Keywords:** Biodiversity, insect predator, *sengon*, stem borers

### **INTRODUCTION**

One of the characteristics of an ecosystem, including terrestrial and aquatic, is the interaction between the constituent components or trophic levels (Lynam et al. 2017; Tadesse 2017). The ecosystem is simply composed of three trophic levels, including producers, which are plants, herbivores as primary consumers, and natural enemies or secondary consumers (Van Nouhuys 2005). Equilibrium is achieved when there is a balanced interaction between these three components, this is known as multitrophic interaction (Shikano 2017; Barnes et al. 2018). In the context of forest studies, a healthy condition of the ecosystem is achieved when the interaction between the components is balanced and allows the ecosystem to self-recovery against damage. One of the interactions that affect forest balance is between fauna components, especially insects (Triyogo et al. 2017; Schowalter et al. 2018).

The study of plant-insect interactions identifies the role of insects in trophic levels two (insect herbivores) and three (natural enemies), although in development, the grouping can be wider even across kingdoms (Price et al. 1980;

Abdala et al. 2019; Chen et al. 2019). Ecologically, insects in the ecosystem act as herbivores, pollinators, predators, parasitoids, and decomposers, thereby supporting the formation of interactions and food web stability (Didham et al. 1996). In general, stability should decrease as the number of connecting links in the food web increases, for example, the interaction between herbivores and their natural enemies, individual plants may modify interaction between herbivores and their natural enemies, the enemy, or both (Price et al. 1980).

Several studies on the role of insects have been widely carried out, but majorly at an individual level (Denno et al. 2017; Triyogo et al. 2020). Meanwhile, at the community level, insect presence, including composition, species, density, and diversity, as well as interactions between the tropics, are still very limited (Reece et al. 2014). All terrestrial communities based on live plants, according to studies on plant and insect interactions, are composed of at least three interacting trophic levels: plants, herbivores, and natural enemies of herbivores (Price et al. 1980). Information on the presence and interaction of insects at the community level is very important as it significantly

affects plant structure and vice versa (Nakamura et al. 2006; Ogushi et al. 2007; Triyogo et al. 2017; Mensah et al. 2018).

*Sengon* or *Falcataria moluccana* (Miq.) Barneby & J.W.Grimes (syn. *Albizia falcata* (L.) Backer, *Falcataria falcata* (L.) Greuter & R.Rankin or *Paraserianthes falcataria* (L.) I.C.Nielsen) is a fast-growing woody plant species with high economic value. After the eruption of Mount Merapi in 2010, one of the rehabilitation efforts carried out was the planting of *sengon* on community land at different altitudes on the slopes of the mountain in Cangkringan Sub-district, Sleman, Yogyakarta. Meanwhile, monoculture and large-scale planting are potentially at risk of insect pest attack (Kumar et al. 2017; Jactel et al. 2021). Previous observations showed that the *sengon* stands on the slopes of Mount Merapi are in danger of extinction due to frequent attacks by the stem borer, *Xystrocera festiva* (Triyogo et al. 2016).

Several studies reported the factors that influence the differences in the presence of insects in the ecosystem include the diversity of vegetation and altitude (Triyogo et al. 2017; Poggetti et al. 2019). Furthermore, varying altitudes and micro-environmental conditions affect the presence of insects in general (Poggetti et al. 2019). Meanwhile, for herbivores and pollinators, altitude indirectly affects the diversity of vegetation that grows in the location (Pi et al. 2020).

Currently, data on pests that destroy *sengon* plants is sufficient (Nair 2000; Rahayu et al. 2021), but information on the insect community based on trophic levels is still limited. Therefore, this study aims to examine the characteristics of the community and the role of each insect, as well as the pattern of relationships with the stem borer attack area on *sengon* stands.

## MATERIALS AND METHODS

### Study area

This study was conducted in a 5-year-old *sengon* stand located in Cangkringan Sub-district, Sleman District, Yogyakarta, Indonesia, with three different growing altitudes of 500, 600, and 700 m above sea level (Figure 1). The plant used was *sengon* planted monoculturally in community forest areas with irregular spacing, while data

collection was carried out for six months, from March to August 2018.

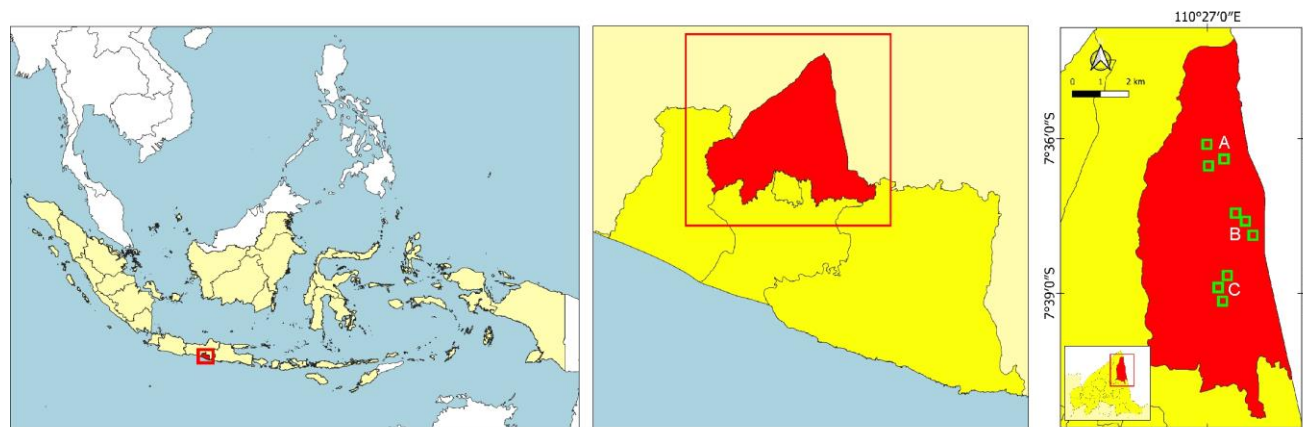
### Observation plot

The observation plot was a square measuring plot with a size of 20 x 20 m<sup>2</sup> made at each altitude, while the distance between the altitudes was at least 5 km with rivers, roads, and residential areas at intervals. The number of plots based on the altitude was 3 respectively, hence, the total was 9 observation plots (Figure 1). The measuring plots were placed purposively by considering the condition and number of the *sengon* trees, topography, and a minimum distance of 10 meters between the plots.

### Insect community observation

Insect collection was carried out in each observation plot using two different of traps, pitfall and sticky traps, as well as a sweeping net. A total of 9 pitfalls and 5 sticky traps were respectively installed following the grid and diagonal method on each plot for a maximum of 2 x 24 hours (Triyogo et al. 2017). Several previous references used various pitfall diameter sizes to obtain terrestrial insects (Gomes et al. 2014; Pehle and Schirmel 2015), while the depth of the pitfall did not significantly affect the insects obtained (Pendola and New 2007).

The pitfall used in this study is 11 cm in diameter with a depth of 20 cm. We prepared sticky traps by using yellow-colored sticky paper. The yellow sticky paper was adjusted to a board 30 cm x 10 cm on both sides using double-sided tape. Finally, the boards are attached on 200 m sticks and then planted 50 cm below the soil surface and 150 cm above it (the top edge of the sticky board is 150 cm from the ground). Nine pitfall traps and five sticky traps were placed in the center of the observation plot by using a grid and diagonal method for pitfall and sticky, respectively (Triyogo et al. 2020), hence a total 81 pitfalls and 45 sticky traps. Furthermore, the sweeping net was used in line with the grid path of laying pitfall traps and swinging ten double swings for each observation plot. A total of 90 swings were made for the entire plot. The insect collection process was performed two times a month (once per two weeks), summing up to 6 observations during three-month observation.



**Figure 1.** The location of data collection conducted on 9 square (20x20 m<sup>2</sup>) plots in Cangkringan Sub-district, Sleman district, Yogyakarta province, Indonesia, at three different altitudes. A. 700 m asl in Kepuharjo village; B. 600 m asl in Kepuharjo village; and C. 500 m asl in Wukirsari village (Source of map: Sleman District Government)

The insects obtained were then collected and identified to the morphospecies level. Insects are grouped into two trophic level groups based on their interaction with plants: (i) herbivores as second trophic and (ii) natural enemies of herbivores (predator and parasitoid) as third trophic (Price et al. 1980; Ohgushi 2005; Triplehorn et al. 2005; Van Nouhuys 2005).

### Factors affecting insect community

The collected insects were grouped by order, family, and morphospecies, while the identification results up to the morphospecies level were used to calculate the Shannon-Wiener Diversity Index ( $H'$ ) (Shannon and Weaver 1948) with the following criteria:  $H' > 3$  = high diversity;  $1 < H' < 3$  = moderate diversity; and  $H' < 1$  = low diversity). Furthermore, the Evenness Index ( $E'$ ) was calculated with the criteria from 0 -1, the closer the  $E'$  value to 1, the higher the difficulty for insect species to dominate (Krebs and Davies 2009). The next ecological index used was Sorensen Similarity ( $S'$ ), with indicator values from 0 -1. The value 1 means that the two habitats compared have identical similarities in terms of insect species found (Magurran 1988; Krebs and Davies 2009).

Because assumptions of normality were not met, thus, we used a data transformation to analyze all data from the field observations and experiments. We first perform transformations to improve the additivity and homoscedasticity of the time series. Various forms of transformation could be used, including a square root transformation, a logarithmic transformation (Box and Cox 1964; Yamamura et al. 2006). To solve the problem that arises from the discreteness of the number of individuals, we use a common logarithm  $\log(x+1)$ , where  $x$  is the number of individuals, so that we are able to easily back-transform the variable (modification of Yamamura 1999; Swarnali et al. 2019). Furthermore, transformed data at the family level was used to determine the effect of altitude and observation month on insect abundance using ANOVA analysis. Observation of field conditions, including temperature and humidity for each observation plot, was measured during installation and harvesting of insect traps, while the environmental data were measured in the middle of the observation plot at the height of 1.3 m above ground level using a thermometer hygrometer HTC-1 (Table 1).

### Relationship of diversity and stem borer incidence

Data on *semon* stand damage caused by stem borer were obtained from each PU and measured using the calculation of stem borer incidence (Cooke et al. 2006):

$$\text{Stem Borer Incidence (SBI)} = \frac{\text{Number of semon showing damage}}{\text{Total number of semon}} \times 100\%$$

The observation results of SBI of *semon* stands in each plot were grouped based on each altitude. Furthermore, a simple regression analysis was performed using Excel software to obtain the Pearson Value ( $R$ ) between SBI and the insect Diversity Index obtained.

## RESULTS AND DISCUSSION

### Insect community

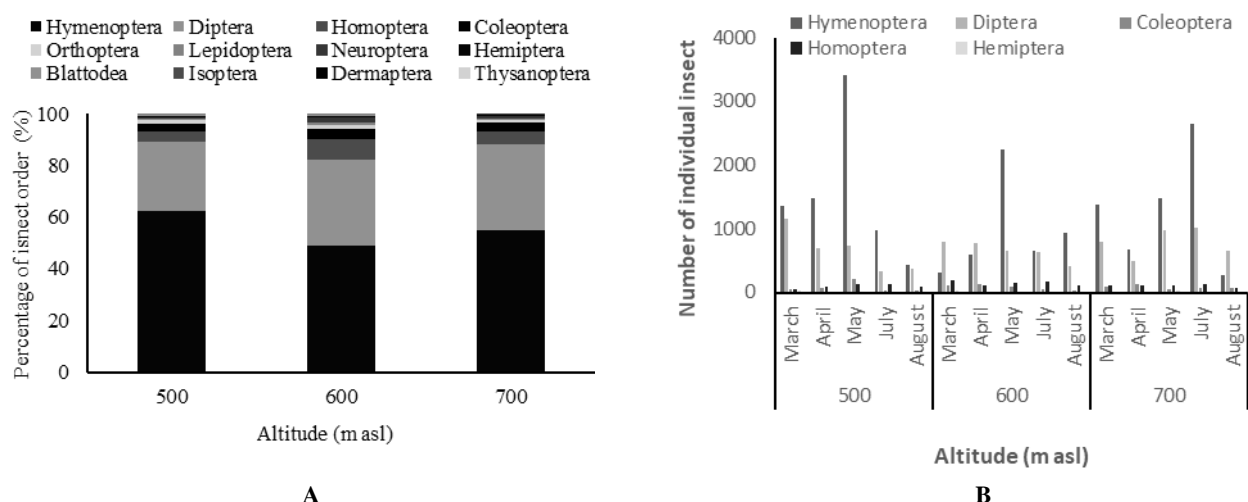
Observations of insect community in the *semon* stand obtained 14 orders with various abundance. The most abundant was the order Hymenoptera, followed by Diptera, Homoptera, Coleoptera, and Hemiptera, respectively (Figure 2A). Furthermore, the number of individual insects among those five orders was varied by differences in the observation month and altitude (Figure 2B).

In this study, the insect community based on the trophic levels showed different results at each altitude (Tables 2 and 3). The third trophic was natural enemies of herbivores consisting of predators and parasitoids consisting of 8 orders, 21 families (Table 2), while in the second trophic was herbivorous insect consisting of 9 orders and 30 families (Table 3).

Based on the respective roles, the population of herbivorous insects was balanced by the large population of natural enemies, including predators and parasitoids at each altitude (Figure 3.A). The most abundant of herbivorous insects include Tephritidae, Drosophilidae, and Cicadellidae, respectively, at each altitude (Figure 3.B). Observations on the relative abundance of predatory insects showed that Formicidae dominated at every altitude (Figure 3.C). Meanwhile, observations of parasitic wasps showed that the presence of Eucharitidae dominated at an altitude of 500 and 600 m asl, while Dolichopodidae at 700 m asl (Figure 3.D).

**Table 1.** Environmental conditions of *semon* stands on three different altitudes

Moon (2018)	Air temperature (°C)				Humidity (%)				Lux (100x)			
	Altitude (m asl)											
	500	600	700	Average	500	600	700	Average	500	600	700	Average
March	26.5	26.1	26.2	<b>26.3</b>	71.0	70.0	70.0	<b>70.3</b>	366.7	331.0	359.3	<b>352.3</b>
April	26.1	25.9	25.7	<b>25.9</b>	65.7	69.3	68.3	<b>67.8</b>	356.3	291.3	336.0	<b>327.9</b>
May	27.2	26.8	26.2	<b>26.7</b>	68.3	68.7	71.0	<b>69.3</b>	367.3	321.0	344.3	<b>344.2</b>
July	27.4	27.0	26.8	<b>27.1</b>	67.7	68.0	67.7	<b>67.8</b>	407.0	368.7	390.7	<b>388.8</b>
August	27.1	26.9	26.8	<b>26.9</b>	66.0	65.3	67.3	<b>66.2</b>	390.0	371.7	382.7	<b>381.4</b>
<b>Average</b>	<b>26.9</b>	<b>26.5</b>	<b>26.3</b>	<b>26.6</b>	<b>67.7</b>	<b>68.3</b>	<b>68.9</b>	<b>68.3</b>	<b>377.5</b>	<b>336.7</b>	<b>362.6</b>	<b>358.9</b>



**Figure 2.** The abundance of individual insects in each observation month at different altitudes. A. Percentage of 14 insect orders obtained; B. Number of individual insects for 5 dominant orders

**Table 2.** Insect community structure based on trophic level 3 on *sengon* stands at three different altitudes (500 m asl, 600 m asl, and 700 m asl). The table shows insect orders, families, and number of morphospecies

Ordo	Family	Number of morphospecies at (m asl)		
		500	600	700
Odonata	Libellulidae	1	1	1
Hemiptera	Nabidae	1	1	1
Coleoptera	Ostomatidae	1	-	1
	Cicindelidae	2	2	2
Diptera	Coccinellidae	1	1	2
	Staphylinidae	2	2	2
	Drosophilidae	1	1	1
	Tachinidae	1	1	1
	Asilidae	1	1	1
Hymenoptera	Stratiomyidae	1	1	1
	Cecidomyiidae	2	1	1
	Dolichopodidae	1	1	1
	Formicidae	17	15	18
	Eucharitidae	1	1	1
Neuroptera	Scelionidae	1	1	1
	Braconidae	1	1	1
	Evaniidae	1	-	1
Thysanoptera	Chrysopidae	1	1	1
	Corydalidae	1	1	1
Mantodea	Phlaeothripidae	1	-	-
	Mantidae	-	-	1

**Table 3.** Insect community structure based on trophic level 2 on *sengon* stands at three different altitudes (500 m asl, 600 m asl, and 700 m asl). The table shows insect orders, families, and number of morphospecies

Ordo	Family	Number of morphospecies at ... (m asl)		
		500	600	700
Orthoptera	Acrididae	3	4	3
	Gryllidae	1	1	1
Hemiptera	Pentatomidae	1	-	-
	Largidae	1	1	-
	Reduviidae	-	1	1
	Nabidae	-	2	1
	Tingidae	-	1	1
Blattodea	Blattidae	2	3	3
Coleoptera	Scarabaeidae	3	3	3
	Nitidulidae	2	2	2
Diptera	Elateridae	1	1	1
	Muscidae	2	2	2
	Drosophilidae	1	1	1
	Tephritidae	1	1	1
	Cecidomyiidae	2	1	1
Lepidoptera	Tipulidae	1	2	2
	Papilionidae	2	2	2
	Pieridae	5	5	5
	Nymphalidae	4	4	4
	Lycaenidae	2	2	2
Isoptera	Geometridae	2	1	1
	Nepticulidae	2	1	1
	Rhinotermitidae	1	1	-
	Tripidae	1	-	1
	Phlaeothripidae	1	-	1

### Factors affecting insect community

In the present study, significant differences in insect abundance were found on several families for the effects of month and altitude (Table 4).

In each month of observation, the average abundance of individuals in each family varied, with Formicidae (20.6-27.3), Tephritidae (19.0-21.5), Drosophilidae (15.2-18.3), Cicadellidae (11.8-13.6), Scarabaeidae (2.0-14.2), Cicadidae (7.88-13.5), Cecidomyiidae (5.3-13.4), Eucharitidae (5.3-13.4) (2.7-10.5) (Table 5).

The effect of altitude appears in the families Drosophilidae (16.4-18.0), Cicadidae (8.6-12.2), and Eucharitidae (4.2-8.2) based on mean value of individual insect data (Table 6).

The calculation results of the moderate  $H'$  value at the three altitudes showed that the number of species and the relative abundance of insects at each altitude was not significantly different. This is supported by moderate  $E'$  and  $S'$ , which are close to 1 as shown in Tables 7 and 8.

### Relationship of insect diversity with stem borer attack area on *sengon* stand

The calculation results show that the level of stem borer attack and insect diversity has a negative relationship with  $y = -18.468x + 73.167$ ;  $R^2: 0.6739$  as shown in Figure 4.

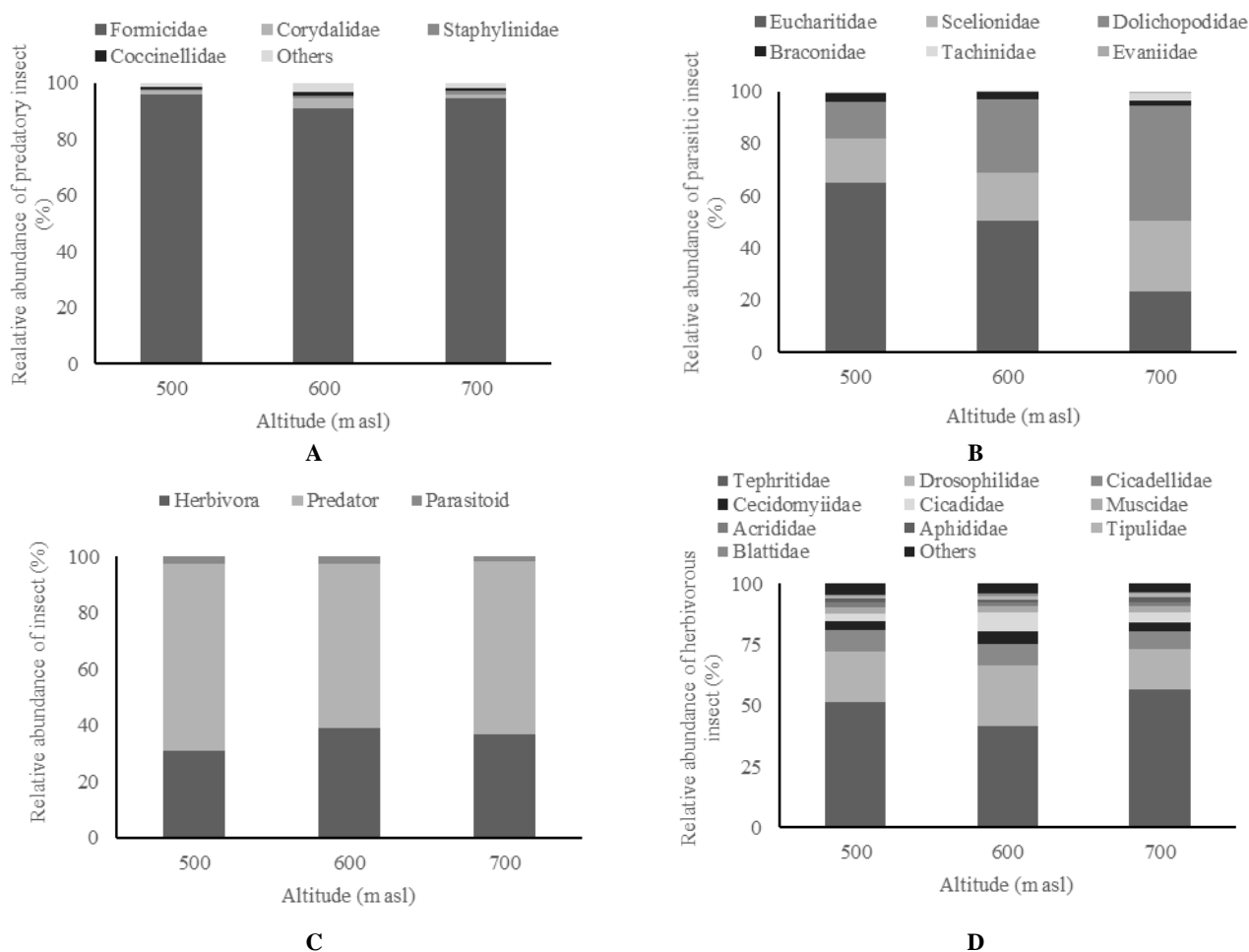
### Discussion

#### *Insect community*

Observations of insect community in the *sengon* stand obtained 14 orders, 49 families, and 104 morphospecies. The insect population was influenced by differences in the observation month and altitude. The most abundant was the order Hymenoptera, Diptera, Coleoptera, Homoptera, and Hemiptera, respectively (Figure 2A). Furthermore, among

the total of 14 orders, Hymenoptera and Mantodea had the largest and smallest percentages, respectively (Figure 2B).

The Formicidae are a very common group of insects due to the large habitat and a variety of food sources (Del Toro et al. 2012; Triyogo et al. 2017), followed by Diptera, including Tephritidae and Drosophilidae, as well as Homoptera (Cicadellidae). The presence of fruit plants such as bananas, jackfruit, and coffee planted with *sengon* acts as hosts and triggers the presence of fruit flies such as Tephritidae and Drosophilidae (Morais et al. 2021). Meanwhile, leafhoppers (Cicadellidae) are commonly found scattered in a wide range of hosts and tend to survive under varying habitats and environmental conditions (Dietrich 2004).



**Figure 3.** Percentage of insect abundance by role at three different altitudes. A. Relative abundance of herbivores, predators, and parasitoids; and relative abundance for each insect rules at family level (B) herbivorous insects; (C) predatory insects; (D) parasitic insects

**Table 4.** Results of F ANOVA values for the effect of observation month, altitude, and the interaction on insect abundance at the family level (data of insect abundance was transformed by using  $\log(x+1)$ )

Variation Source	Form.	Teph.	Drosop.	Cicadell.	Scarab.	Cicad.	Cecidomyiid.	Eucharit.
Month	5.19*	0.34	4.29*	1.89	27.71*	10.77*	6.53*	19.24*
Altitude	0.87	0.09	3.12	0.39	1.16	12.99*	0.03	10.75*
Moon x Altitude	2.57*	3.60*	2.15	0.81	0.28*	1.41	3.09*	20.21*

Note: \*: significance level at  $P < 0.05$ . Form.: Formicidae; Teph.: Tephritidae; Drosop.: Drosophilidae; Cicadell.: Cicadellidae; Scarab.: Scarabidae; Cicad.: Cicadidae; Cecidomyiid.: Cecidomyiidae; Eucharit.: Eucharitidae

**Table 5.** Mean values of insect abundance on family level on five months observation

Month	Form.	Teph.	Drosop.	Cicadell.	Scarab.	Cicad.	Cecidomyiid.	Eucharit.
March	23.88 <sup>ab</sup>	20.22 <sup>a</sup>	18.33 <sup>b</sup>	12.55 <sup>a</sup>	12.22 <sup>c</sup>	11.33 <sup>bc</sup>	13.44 <sup>b</sup>	4 <sup>a</sup>
April	23.33 <sup>ab</sup>	20.55 <sup>a</sup>	17.33 <sup>ab</sup>	13.66 <sup>a</sup>	14.22 <sup>c</sup>	7.88 <sup>a</sup>	7.66 <sup>a</sup>	2.77 <sup>a</sup>
May	27.33 <sup>b</sup>	21.55 <sup>a</sup>	18.22 <sup>b</sup>	15.11 <sup>a</sup>	13.11 <sup>c</sup>	9.33 <sup>ab</sup>	9.77 <sup>ab</sup>	5.22 <sup>a</sup>
July	25.22 <sup>b</sup>	21 <sup>a</sup>	16.67 <sup>ab</sup>	12.77 <sup>a</sup>	7.77 <sup>b</sup>	13.55 <sup>c</sup>	6.55 <sup>a</sup>	10.33 <sup>b</sup>
August	20.66 <sup>a</sup>	19.88 <sup>a</sup>	15.22 <sup>a</sup>	11.88 <sup>a</sup>	2 <sup>a</sup>	11.33 <sup>bc</sup>	5.33 <sup>a</sup>	10.55 <sup>b</sup>

Note: Form.: Formicidae; Teph.: Tephritidae; Drosop.: Drosophilidae; Cicadell.: Cicadellidae; Scarab.: Scarabidae; Cicad.: Cicadidae; Cecidomyiid.: Cecidomyiidae; Eucharit.: Eucharitidae. Means followed by different letters are significant at the 5% level

**Table 6.** Mean values of insect abundance on family level on three different land altitudes

Altitude (m asl)	Form.	Teph.	Drosop.	Cicadell.	Scarab.	Cicad.	Cecidomyiid.	Eucharit.
500	24.66 <sup>a</sup>	20.6 <sup>a</sup>	17 <sup>ab</sup>	13.25 <sup>a</sup>	9.06 <sup>a</sup>	8.66 <sup>a</sup>	8.53 <sup>a</sup>	8.2 <sup>b</sup>
600	23.2 <sup>a</sup>	20.4 <sup>a</sup>	18.06 <sup>b</sup>	13.6 <sup>a</sup>	9.86 <sup>a</sup>	12.2 <sup>b</sup>	8.73 <sup>a</sup>	7.33 <sup>b</sup>
700	24.4 <sup>a</sup>	20.93 <sup>a</sup>	16.4 <sup>a</sup>	12.73 <sup>a</sup>	10.66 <sup>a</sup>	11.13 <sup>b</sup>	8.4 <sup>a</sup>	4.2 <sup>a</sup>

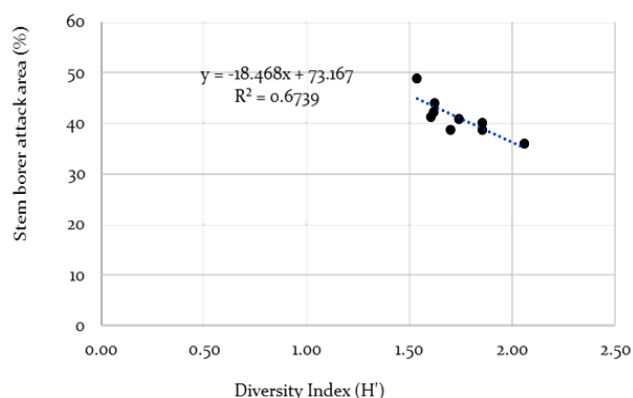
Note: Form.: Formicidae; Teph.: Tephritidae; Drosop.: Drosophilidae; Cicadell.: Cicadellidae; Scarab.: Scarabidae; Cicad.: Cicadidae; Cecidomyiid.: Cecidomyiidae; Eucharit.: Eucharitidae. Means followed by different letters are significant at the 5% level

**Table 7.** Diversity (H') and Evenness (E') indexes of insects on three different altitudes

Altitude (m asl)	Diversity(H')	Evenness(E')
500	1.58	0.35
600	1.98	0.44
700	1.68	0.37

**Table 8.** Insect similarity index on three different altitudes

Altitude (m asl)	500	600	700
500	-	0.89	0.82
600		-	0.88
700			-

**Figure 4.** The relationship between insect diversity and the stem borer attack area

In this study, the insect community based on the trophic levels showed different results at each altitude (Tables 2 and 3). The third trophic, predators and parasitoids,

consisted of 8 orders, 21 families (Table 2), while the second (herbivores) consisted of 9 orders and 30 families (Table 3). Insect community indicated by the presence of taxa at each trophic level is influenced by habitat conditions and interactions (Matthews and Matthews 2010). Insect observations at the order level at three different altitudes revealed only little changes (less than 1%), particularly in tropics 2 (Isoptera) and 3 (Mantodea and Thysanoptera). Host plants enhance the second trophic of insects by providing food, volatile compounds, architecture, and a place of refuge (Damman 1993; Schoonhoven et al. 1998). Termites appear to be associated to the presence of *sengon* trunks on the ground at 500 and 600 m asl. The abundance and homogeneity of *sengon* species planted at different altitudes tend to correlate with the number and types of insects at the order level. On the other hand, insect responses at the family and species levels can reveal significant differences in abundance. The herbivores are relatively abundant due to the high number of host plants that support life and development (Matthews and Matthews 2010). Furthermore, all members of Homoptera are herbivorous and have the potential to cause damage to annual and perennial plants (Denno et al. 1991; Kumar et al. 2019).

Based on the respective roles, the population of herbivorous insects was balanced by the large population of natural enemies, including predators and parasitoids at each altitude (Figure 3A). The most abundant insects include Tephritidae, Drosophilidae, and Cicadellidae, respectively, at each altitude (Figure 3B). The results showed that there were no differences in insects at the family level that dominate at each altitude for herbivores, predators, and parasitoids (Figures 3B-D).

The observations also showed a higher percentage of natural enemies compared to herbivores, this is consistent with a previous study that stated that the abundance of natural enemies in certain ecosystems is influenced by the

presence of prey (Triyogo et al. 2017). However, the existence, including survival and reproduction of an insect species, is ultimately determined by its behavior, roles, and interactions (Matthews and Matthews 2010).

#### *Factors affecting insect community*

The insect population in a location is usually influenced by environmental conditions that support the development and growth (Ciesla 2011), as shown in this study, the observation month affects almost all insects at the family level (Table 4). A previous study stated that insect abundance is influenced by two main factors: (1) biotic in the form of reproductive power and (2) environmental resistance (Odum 1993; Pureswaran et al. 2018). One of the environmental resistance factors observed in this study was air temperature with monthly variations and altitudes. The difference in the monthly air temperature was  $\pm 1.2^{\circ}\text{C}$  and humidity was  $\pm 4.1\%$ , as shown in Table 1. Meanwhile, previous studies reported that the differences in temperature and humidity potentially influence insect abundance (Odum 1993; Triyogo et al. 2017). This study showed that not all insects at the family level produced the same response to the range of temperature and humidity obtained with variations in observation months. For example, Cicadellidae (leafhoppers) were not affected by altitude or observation month, as shown in Table 5. This is presumably because these insects have active migratory and polyphagous characters, which tend to facilitate adaptation to changing environmental conditions.

Previous studies reported that differences in altitude affect insect diversity (Acharya and Vijayan 2015; Sohn et al. 2019). In this study, differences in altitude influenced mean number of Drosophilidae, Cicadidae, and Eucharitidae with different patterns, while other families were not affected (Table 6). Our results were consistent with a study that stated that each insect has the various ability to adapt to temperature in the form of environmental resistance and different reproductive power (Odum 1993). The abundance of Drosophilidae and Eucharitidae was lower at 700 m asl compared to 500 and 600 m asl (Table 6). As shown in this study, differences in altitude tend to be followed by variations in climatic variables, particularly temperature and humidity ( $\pm 0.6^{\circ}\text{C}$  and  $\pm 1.2\%$ , respectively) (Table 1). *Drosophila* can live at a temperature of  $24\text{--}26^{\circ}\text{C}$  in general, according to a previous study; however, at the species level, *Drosophila* responds to changes in temperature differently (Gibert et al. 2001; Garrity et al. 2010). Previous research has stated that several species of *Drosophila*, including *D. funebris*, *D. paulistorum*, *D. bipectinata* have a narrow optimum temperature range so that its distribution is limited, while *D. melanogaster*, *D. repleta* show a high degree of variability and evolutionary capacity to cope with drought and heat stress (Kellermann et al. 2009; Garrity et al. 2010; Hoffmann 2010). Meanwhile, the Eucharitidae population tends to be influenced by the increase in air temperature (lower altitude) and the presence of parasitic hosts (Hagstrum and Subrananyam 2010; Barrantes and Castelo 2014). In this study, the abundance of parasitic hosts was one of the factors that caused the high population of Eucharitidae as

shown in Figure 4D. Based on the results, ants are suspected to act as parasitic hosts. Moreover, the understorey harvested by the community affects the abundance of Eucharitidae, hence, frequent harvesting hampers its development.

The fruit fly group (*Tephritidae*) is indirectly affected by differences in temperature and humidity through mating behavior and egg-laying, in addition, these factors affect the birth, death, and spread rates (Duyck et al. 2004; Zeng et al. 2019). A previous study by using *Bactrocera dorsalis* (*Tephritidae*) explained that the ideal temperature to thrive ranges from  $20^{\circ}\text{--}28^{\circ}\text{C}$  (Ye and Liu 2005). Meanwhile, another species, *B. cucurbitae*, has a population tendency to increase exponentially during high temperature (Zhou et al. 2016; Zeng et al. 2018).

The calculation results of the moderate  $H'$  value at the three altitudes showed that the number of species and the relative abundance of insects at each altitude was not significantly different. This is supported by moderate  $E'$  and  $S'$ , which are close to 1 as shown in Tables 3 and 4. A low  $E'$  in an ecosystem indicates the presence of a dominant individual species (insect) (Magurran 1988). Based on the results, the dominant insects at each altitude were ants, namely Formicidae; Hymenoptera, which constitute more than 50% of the total families obtained. Besides, ant activity is strongly influenced by habitat characteristics (Majeed et al. 2021) and climatic parameters, such as temperature with an optimal range of  $25\text{--}37^{\circ}\text{C}$  (Silva et al. 2015), this is consistent with the average temperature in *sengon* stands at each altitude which ranged from  $26\text{--}27^{\circ}\text{C}$  (Table 1). Furthermore, the  $S'$  value between altitudes was close to 1, indicating the tendency of the same insect community between altitudes. These results indicate that the environmental conditions at the three altitudes have no significant difference and do not have varying effects on insects at the community level. The predominance of *sengon* monoculture at each altitude causes the formed microclimate to be similar.

#### *Relationship of insect diversity with stem borer attack area*

The study was carried out in *sengon* stands often attacked by stem borer pests with a fairly high attack area and severity  $>70\%$  (Triyogo et al. 2016). Stem borer attacks begin when the female beetle lays eggs in holes or cracks in the bark of tree trunks. The newly hatched larvae feed in groups on the bark as well as sapwood inside and outside the tree respectively and push out the dirt (frass) mixed with sawdust that falls on the forest floor. At further attack, this pest could cause the death of trees and reduces the productivity and quality of the wood produced (Haneda et al. 2021). Furthermore, aside from the abundance of hosts, another cause of high stem borer attack is the absence of natural enemy insect species. The calculation results show that the level of stem borer attack and insect diversity has a negative relationship with  $y = -18.468x + 73.167$ ;  $R^2: 0.6739$  as shown in Figure 5.

According to the equation, an increase in insect diversity is typically followed by a decrease in the attack of stem borer insects. However, because this study merely used a limited number of regression points, more research



on the relationship between increased insect diversity and stem borer attack area is essential. According to a previous study, the higher the diversity, the more complicated the interactions, and the less damage to ecosystems (Lundgren and Fausti 2015).

The H' value of the insect community at each altitude showed that the diversity condition was in the medium category. Moreover, the dominant insects at each altitude were from the Formicidae (ants) group, as indicated by the E' and S' values. Ants play an important ecological role in the ecosystem as a natural enemy (predator) (Dassou et al. 2015; Dassou and Tixier 2016). Based on the biodiversity value and the availability of predators, insect pest populations tend to be suppressed.

However, the conditions in the field show that most *sengon* plants are damaged by stem borer attacks. Several possibilities are proposed, first, the cropping pattern tends to be monoculture on a large scale, hence, the availability of hosts, including housing and food for stem borer, is very abundant. A previous study stated that *sengon* plants are very susceptible to stem borer (*Xystrocera festiva*) attacks on both mixed and monoculture planting systems (Endang and Farikhah 2010). Therefore, monoculture cropping conditions support an increase in stem borer insect populations. Furthermore, there is a mismatch of interactions (asynchronous) between stem borer insects and natural enemies. Several studies suggested the grouping of ants into specialist and generalist predators based on respective prey (Dassou and Tixier 2016; Triyogo et al. 2020).

The dominance at each altitude did not suppress the insect pest population because the predators obtained were presumably not specialist stem borers. Furthermore, the population and effectiveness of generalist predatory ants as biological controllers are influenced by the presence of prey of different species (Dassou and Tixier 2016). The two possibilities above lead to a high population of stem borer insects in the *sengon* forest ecosystem despite the low population of natural enemies.

In conclusion, the *sengon* monoculture system on the slopes of Mount Merapi with varying altitudes has biodiversity values (H') and insect similarity (S'), which indicates that the environmental conditions at each altitude are not significantly different. The insect communities are found in the third trophic level consisting of predators and parasitoids. Furthermore, the similarity index value (E') indicates the dominant tendency of insects, especially ants, which have the potential to reduce stem borer populations. However, this study found that the presence of natural enemies is not accompanied by a decrease in the population of stem borer insects. Two factors that reduce the effectiveness of natural enemies in suppressing stem borer insect populations are (1) the availability of abundant *sengon* (2) a mismatch of interactions (asynchronous) between stem borer insects and natural enemies. The relationship between insect diversity and stem borer attack area shows that the higher the level of diversity, including population and species, the lower the attack area. Further studies are needed to identify the most suitable natural

enemies among Formicidae, Ostomatidae, Braconidae, and Evanidae for controlling stem borer insects.

## REFERENCES

- Abdala-Roberts L, Puentes A, Finke DL, Marquis, RJ, Montserrat M, Poelman EH, Rasmann S, Sentis A, van Dam NM, Wimp G, Mooney K. 2019. Tri-trophic interactions: Bridging species, communities and ecosystems. *Ecol Lett* 22 (12): 2151-2167. DOI: 10.1111/ele.13392.
- Acharya BK, Vijayan L. 2015. Butterfly diversity along the elevation gradient of eastern Himalaya, India. *Ecol Res* 30: 909-919. DOI: 10.1007/s11284-015-1292-0.
- Barnes AD, Jochum M, Lefcheck JS, Eisenhauer N, Scherber C, O'Connor MI, de Ruiter P, Brose U. 2018. Energy flux: The link between multitrophic biodiversity and ecosystem functioning. *Trends Ecol Evol* 33 (3): 186-197. DOI: 10.1016/j.tree.2017.12.007.
- Barrantes ME, Castelo MK. 2014. Host specificity in the host-seeking larva of the dipteran parasitoid *Mallophora ruficauda* and the influence of age on parasitism decisions. *Bull Entomol Res* 104 (3): 295-306. DOI: 10.1017/S0007485314000029.
- Box GE, Cox DR. 1964. An analysis of transformations. *J Roy Stat Soc B* 26: 211-252. DOI: 10.1111/j.2517-6161.1964.tb00553.x.
- Chen C, Gols R, Biere A, Harvey JA. 2019. Differential effects of climate warming on reproduction and functional responses on insects in the fourth trophic level. *Func Ecol* 33 (4): 693-702 DOI: 10.1111/1365-2435.13277
- Ciesla W. 2011. *Forest Entomology: A Global Perspective*. John Wiley & Sons, New Jersey.
- Cooke BM, Jones DG, Kaye B. 2006. *The Epidemiology of Plant Diseases*. 2nd Edition. Springer, Berlin.
- Damman H. 1993. Patterns of herbivore interaction among herbivore species. In: Stamp NE, Casey TM (eds). *Caterpillars: Ecological and Evolutionary Constraints on Foraging*. Chapman and Hall, New York.
- Dassou AG, Carval D, Dépigny S, Fansi G, Tixier P. 2015. Ant abundance and cosmopolites sordidus damage in plantain fields as affected by intercropping. *Biol Control* 81: 51-57. DOI: 10.1016/j.biocontrol.2014.11.008.
- Dassou AG, Tixier P. 2016. Response of pest control by generalist predators to local-scale plant diversity: A meta-analysis. *Ecol Evol* 6 (4): 1143-1153. DOI: 10.1002/ece3.1917.
- Del Toro I, Ribbons RR, Pelini SL. 2012. The little things that run the world revisited: A review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). *Myrmecol News* 17: 133-46.
- Denno RF, Roderick GK, Olmstead KL, Dobel HG. 1991. Density-related migration in planthoppers (Homoptera: Delphacidae): The role of habitat persistence. *Am Nat* 138 (6): 1513-1541.
- Denno RF, Kaplan I, Price PW, Eubanks MD, Finke DL. 2017. *Insect Ecology: Behavior, Population and Communities*. Cambridge University Press, Cambridge.
- Didham RK, Ghazoul J, Stork NE, Davis AJ. 1996. Insects in fragmented forests: A functional approach. *Trends Ecol Evol* 11 (6): 255-260. DOI: 10.1016/0169-5347(96)20047-3.
- Duyck PF, David P, Quilici S. 2004. A review of relationships between interspecific competition and invasions in fruit flies (Diptera: Tephritidae). *Ecol Entomol* 29 (5): 511-520. DOI: 10.1111/j.0307-6946.2004.00638.x.
- Dietrich CH. 2004. *Encyclopedia of Entomology: Leafhopper (Hemiptera: Cicadellidae)*. Springer, Dordrecht.
- Endang AH, Farikhah HN. 2010. Infestation of *Xystrocera festiva* in *Paraserianthes falcataria* plantation in East Java, Indonesia. *J Trop For Sci*: 397-402.
- Garrity PA, Goodman MB, Samuel AD, Sengupta P. 2010. Running hot and cold: Behavioral strategies, neural circuits, and the molecular machinery for thermotaxis in *C. elegans* and *Drosophila*. *Genes Dev* 24 (21): 2365-2382. DOI: 10.1101/gad.1953710.
- Gibert P, Huey RB, Gilchrist GW. 2001. Locomotor performance of *Drosophila melanogaster*: Interactions among developmental and adult temperatures, age, and geography. *Evolution* 55 (1): 205-209. DOI: 10.1111/j.0014-3820.2001.tb01286.x.
- Gomes ECF, Ribeiro GT, Souza TMS, Sousa-Souto L. 2014. Ant assemblages (Hymenoptera: Formicidae) in three different stages of forest regeneration in a fragment of Atlantic Forest in Sergipe, Brazil. *Sociobiol* 61: 250-57. DOI: 10.13102/sociobiology.v61i3.250-257.



- Hagstrum DW, Subramanyam B. 2010. Immature insects: Ecological roles of mobility. *Am Entomol* 56 (4): 230-241. DOI: 10.1093/ae/56.4.230.
- Haneda NF, Supriatna AH, Shabrina H, Istikorini Y, Siregar UJ, Wahyudi I. 2021. Chemical characteristics of *Falcataria moluccana* wood infested by Boktor stem borer (*Xystrocera festiva*). *Biodiversitas* 22 (10): 4203-4208. DOI: 10.13057/biodiv/d221010.
- Hoffmann AA. 2010. Physiological climatic limits in *Drosophila*: Patterns and implications. *J Exp Biol* 213: 870-880. DOI: 10.1242/jeb.037630.
- Jactel H, Moreira X, Castagneyrol B. 2021. Tree diversity and forest resistance to insect pests: Patterns, Mechanisms, and Prospects. *Ann Rev Entomol* 66: 277-296. DOI: 10.1146/annurev-ento-041720-075234.
- Kellermann V, van Heerwaarden B, Sgrò CM, Hoffmann AA. 2009. Fundamental evolutionary limits in ecological traits drive *Drosophila* species distributions. *Science* 325 (5945): 1244-1246. DOI: 10.1126/science.
- Krebs JR, Davies NB. 2009. Behavioural Ecology: An Evolutionary Approach. John Wiley & Sons, New Jersey.
- Kumar V, Uthappa AR, Srivastava M, Alam B, Handa AK, Chaturvedi OP. 2017. Incidence pattern of wood borer (*Sinoxylon anale* Lesne) on *Dalbergia sissoo* Roxb. *Range Manag Agrofor* 38 (2): 285-288.
- Kumar K, Kamboj R, Rao NJ. 2019. Status and Role of Coccinellids in Insect Pest Management. AkiNik Publications, India.
- Lundgren JG, Fausti SW. 2015. Trading biodiversity for pest problems. *Sci Adv* Jul 1 (6): e1500558. DOI: 10.1126/sciadv.1500558.
- Lynam CP, Llope M, Möllmann C, Helaouët P, Bayliss-Brown GA, Stenseth NC. 2017. Interaction between top-down and bottom-up control in marine food webs. *Proc Natl Acad Sci* 114 (8): 1952-1957. DOI: 10.1073/pnas.1621037114.
- Magurran A. 1988. Ecological Diversity and Its Measurement. Chapman & Hall, London.
- Majeed W, Khawaja M, Rana N. 2021. Assessing fluctuation of ant populations in a distinct ecological habitat to track climate change effects. *Biodiversitas* 22 (5): 2722-2727. DOI: 10.13057/biodiv/d220533.
- Matthews RW, Matthews JR. 2010. Insect Behavior, Second Edition. Springer Science and Business Media B.V. London, New York.
- Mensah BA, Kyerematen R, Annang T, Adu-Acheampong S. 2018. Influence of human activity on diversity and abundance of insects in three wetland environments in Ghana. *Bonorowo Wetl* 8: 33-41. DOI: 10.13057/bonorowo/w080104.
- Morais MC, Rakes M, Padilha AC, Grützmacher AD, Nava DE, Bernardi O, Bernardi D. 2021. Susceptibility of Brazilian populations of *Anastrepha fraterculus*, *Ceratitis capitata* (Diptera: Tephritidae), and *Drosophila suzukii* (Diptera: Drosophilidae) to selected insecticides. *J Econ Entomol* 114 (3): 1291-1297. DOI: 10.1093/jee/toab050.
- Nair KSS. 2000. Insect Pests and Diseases in Indonesian Forest: An Assessment of the Major Threats, Research Efforts and Literature. Cifor, Bogor.
- Nakamura MH, Kagata, Ogushi T. 2006. Trunk cutting initiates bottom-up cascades in a tri-trophic system: Sprouting increases biodiversity of herbivorous and predaceous arthropods on willows. *Oikos* 113: 259-268. DOI: 10.1111/j.2006.0030-129914251.x.
- Odum 1993. Fundamental of ecology. Gajah Mada University Press, Yogyakarta.
- Ogushi T, Craig TP, Price PW. 2007. Ecological Communities. Cambridge University Press, Cambridge.
- Ogushi T. 2005. Indirect interaction webs: Herbivore-induced effects through trait change in plants. *Ann Rev Ecol Evol Syst* 36: 81-105. DOI: 10.1146/annurev.ecolsys.36.091704.175523.
- Pehle A, Schirmel J. 2015. Moss invasion in a dune ecosystem influences ground-dwelling arthropod community structure and reduces soil biological activity. *Biol Invasions* 17: 3467-77. DOI: 10.1007/s10530-015-0971-7.
- Pendola A, New TR. 2007. Depth of pitfall traps - does it affect interpretation of ant (Hymenoptera: Formicidae) assemblages?. *J Insect Conserv* 11: 199-201. DOI: 10.1007/s10841-006-9028-7.
- Pi HQ, Quan QM, Wu B, Lv XW, Shen LM, Huang SQ. 2020. Altitude-related shift of relative abundance from insect to sunbird pollination in *Elaeagnus umbellata* (Elaeagnaceae). *J Syst Evol* 59 (6): 1266-1275. DOI: 10.1111/jse.12685.
- Poggetti L, Rarancius S, Chiabà C, Vischi M, Zandigiacomo P. 2019. Altitude affects the distribution and abundance of two non-native insect pests of the common walnut. *J Appl Entomol* 143 (5): 527-534. DOI: 10.1111/jen.12609.
- Price PW, Bouton CE, Gross P, McPherson BA, Thompson JN, Weis AE. 1980. Interactions among three trophic levels: Influence of plants on interactions between insect herbivores and natural enemies. *Ann Rev Ecol Evol Syst* 11 (1): 41-65. DOI: 10.1146/annurev.es.11.110180.000353.
- Pureswaran D, Roques A, Battisti A. 2018. Forest insects and climate change. *Curr For Rep* 4 (2): 35-50. DOI: 10.1007/s40725-018-0075-6.
- Rahayu S, Triyogo A, Widyastuti SM, Musyafa, Ardianyah F. 2021. Pests and diseases on *Falcataria moluccana* trees in agroforestry systems with pineapple in East Java, Indonesia. *Biodiversitas* 22 (5): 2779-2788. DOI: 10.13057/biodiv/d220541.
- Reece JB, Urry LA, Cain ML, Wasserman SA, Minorsky PV, Jackson RB. 2014. Campbell Biology, Tenth Edition. Macmillan, Boston.
- Schoonhoven LM, Jermy T, Van Loon JJA. 1998. Insect-Plant Biology, From Physiology to Evolution, 1st edn. Chapman & Hall, United Kingdom.
- Schowalter TD, Noriega JA, Tschirntke T. 2018. Insect effects on ecosystem services-Introduction. *Basic Appl Ecol* 26: 1-7. DOI: 10.1016/j.baae.2017.09.011.
- Shannon CE, Weaver W. 1948. Mathematical Theory Communication: Biodiversity Measurements. University of Illinois Press, Urbana.
- Shikano I. 2017. Evolutionary ecology of multitrophic interactions between plants, insect herbivores and entomopathogens. *J Chem Ecol* 43 (6): 586-598. DOI: 10.1007/s10886-017-0850-z.
- Silva MF, Mota CM, Miranda VDS, Oliveira CAD, Silva MC, Naves KSC, Oliveira FD, Silva DADO, Mineo TWP, Santiago FM. 2015. Biological and enzymatic characterization of proteases from crude venom of the ant *Odontomachus bauri*. *Toxins* 7 (12): 5114-5128. DOI: 10.3390/toxins7124869.
- Sohn JC, Kim NH, Choi SW. 2019. Effect of elevation on the insect herbivory of Mongolian oaks in the high mountains of southern South Korea. *J Asia-Pac Entomol* 22 (3): 957-962. DOI: 10.1016/j.aspen.2019.08.004.
- Swarnali M, Rudra DP, Soumyajit B, Pathiba B, Goutam SK, Gautam A. 2019. Correspondence of butterfly and host plant diversity: Foundation for habitat restoration and conservation. *Eur J Ecol* 5 (1): 49-66. DOI: 10.2478/eje-2019-0007.
- Tadesse S. 2017. Community structure and trophic level interactions in the terrestrial ecosystems: A Review. *IJWB* 2 (6): 1-9. DOI: 10.15406/ijawb.2017.02.00040.
- Triplehorn CA, Johnson NF, Borror DJ. 2005. Borror and DeLong's Introduction to the Study of Insects (No. QL463 B69 2005). Cengage Learning, United States.
- Triyogo A, Rahayu S, Widyastuti SM, Musyafa. 2016. The Existence of the *Sengon* Stem Borer and Its Attack Pattern. Gadjah Mada University, Yogyakarta. [Indonesian]
- Triyogo A, Suryanto P, Widyastuti SM, Baresi AD, Zughro IF. 2017. The abundance and trophic level structure of insects at different stages of teak agroforestry development in Nglangeran, Gunungkidul, Yogyakarta. *Jurnal Ilmu Kehutanan* 11: 239-248. DOI: 10.22146/jik.28287. [Indonesian]
- Triyogo A, Budiadi, Widyastuti SM, Subrata SA, Budi SS. 2020. Abundance of ants (Hymenoptera: Formicidae) and the functional groups in two different habitats. *Biodiversitas* 21 (5): 2079-2087. DOI: 10.13057/biodiv/d210535.
- Van Nouhuys S. 2005. Effects of habitat fragmentation at different trophic levels in insect communities. *Ann Zool Fennici* 42: 433-447.
- Yamamura K. 1999. Transformation using (x+0.5) to stabilize the variance of populations. *Res Popul Ecol* 41: 229-234. DOI: 10.1007/s101440050026.
- Yamamura K, Yokozawa M, Nishimori M, Ueda Y, Yokosuka T. 2006. How to analyze long-term insect population dynamics under climate change: 50-year data of three insect pests in paddy fields. *Popul Ecol* 48 (1): 31-48. DOI: 10.1007/s10144-005-0239-7.
- Ye H, Liu JH. 2005. Population dynamics of the oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae) in the Kunming area, southwestern China. *Insect Sci* 12 (5): 387-392. DOI: 10.1111/j.1005-295X.2005.00048.x.
- Zeng B, Zhu W, Fu Y, Zhou S. 2018. Influence of high-temperature exposure on the mating, oviposition and thermotaxis of *Bactrocera cucurbitae* (Coquillett) (Diptera:Tephritidae). *Plos One* 13 (9): e0204065. DOI: 10.1371/journal.pone.0204065.
- Zeng Y, Reddy GV, Li Z, Qin Y, Wang Y, Pan X, Jiang F, Gao F, Zhao ZH. 2019. Global distribution and invasion pattern of oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae). *J Appl Entomol* 143 (3): 165-176. DOI: 10.1111/jen.12582.
- Zhou S, Zhang F, Fu Y. 2016. Impact of high temperature on the growth and development of melon fly. *Oxid Commun* 39 (1A): 977-984.