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Flower-visiting Arthropods of the Invasive Weed, *Lantana camara* L.

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ABSTRACT.– *Lantana camara* L. is an important invasive plant species in many regions around the world including Thailand. Efficient reproductive characteristics and pollination by insects seems to be of major importance to its spread into new areas. Therefore, this study aims to explore diversity of flower-visiting arthropods of *L. camara* in Thailand. Field work was conducted bimonthly throughout a year (Nov 2013-Dec 2014) at Mahidol University, Kanchanaburi Campus, Sai Yok District, Kanchanaburi Province, Thailand. In total, 27 taxonomic groups of arthropods were recorded visiting and living on flowers/inflorescences of *L. camara*. Bees and adult butterflies showed the highest frequencies of visits, 32% and 28% respectively. While, lace bugs spent the longest time on flowers of *L. camara* for both total visiting time and length of time per visit. For small arthropods extracted from the inflorescences, thrips and mites were the most frequently found animals in all surveys. Moreover, thrips were found in large numbers and in significantly higher numbers during dry season (Nov-Dec 2013, and 2014) than wet season. Several groups of associated animals found here were noted as potential pollinators, such as bees, butterflies, and thrips. Whereas, other phytophagous groups, such as hemipterans and mites, could possibly be used as biological control agents of *L. camara*.

KEY WORDS: Biological control agents, diversity, invasive species, potential pollinators, Thailand

INTRODUCTION

Lantana, *Lantana camara* L., is a flowering plant species in the family Verbenaceae. It was originally native to tropical and subtropical America (Sanders, 2012), but now has spread into more than 60 countries around the world, especially in tropical Asia, Africa, and Australia (Ghisalberti, 2000; Day et al., 2003; GISD, 2006). The plant is aggressive and often invades pastures, orchards, and previously disturbed areas such as logged forests, areas cleared for agriculture, and unutilized lands (Gentle and Duggin, 1997b). It has negative impacts on natural ecosystems, agricultural productivity and livestock, and also human health (Morton, 1994; Gentle and Duggin, 1997a; Aravind et al., 2010). It is thus considered as one of the 100 worst invasive alien species in the world (Lowe et al., 2000). Lantana has been reported to have become an important invasive weed in many countries, such as India (Aravind et al., 2010), Australia (Gentle and Duggin, 1997a), South Africa (Wells and Stirton, 1988), Hawaii (Davis et al., 1992), and the Galapagos Islands (Tye, 2001). There is no evidence of when lantana arrived in Thailand, but it probably arrived during the 17th century after it was introduced to Hawaii as an ornamental plant from where it soon spread to pacific islands, Australia, and southern Asia (Ghisalberti, 2000). Lantana has been reported as one of the main weed species in oil palm plantations in southern Thailand (Krasaesindhu, 1998), and also in dipterocarp–pine forest in Thung Salaeng Luang National Park, lower northern part of Thailand, Phitsanulok and Phetchabun provinces (Jongjitvimol and Petchsri, 2015).

The distribution range of lantana is still increasing. The reproductive characteristics of the plant may contribute to its ability to invade new areas, in addition to fire and grazing by herbivores (Sharma et al., 2005). The plant can produce flowers throughout the year (Duggin and Gentle, 1998), and has a high fruit set and can self-pollinate if necessary (Sharma et al., 2005). Carrión-Tacuri et al. (2014) found that lantana can produce fruits by autonomous self-pollination within bagged inflorescences. Although individual lantana flowers are capable of self-pollination, pollination by insects seems to be of major importance to its spread. Conflicting reports occur of what are the major pollinator taxa of lantana. Insects as diverse as butterflies (Lepidoptera: Central America, Kunte, 2007; Galapagos, Carrión-Tacuri et al., 2014), thrips (Thysanoptera: India, Mathur and Mohan Ram, 1978), and honeybees (Hymenoptera: Australia, Goulson and Derwent, 2004) have been reported so far.

Lantana can be controlled by using chemicals, mechanical removal, fire, and planting of competitive species (Day et al., 2003). However, these methods are not practicable in many situations. Therefore, biological control would appear to be the only likely solution for long-term control of this plant. Biological control of lantana started in 1902 and since then up to 41 biological control agents have been released worldwide (Day et al., 2003). In Thailand, three biological control agents have been used in lantana control programs, namely *Uroplata girardi* Pic, 1934 (Coleoptera), *Teleonemia scrupulosa* Stål, 1873 (Hemiptera), and *Calycomyza lantanae* (Frick, 1956) (Diptera) (Day et al., 2003; Napompeth, 2004). The first two species were directly introduced from Brazil and Mexico for lantana control purposes, whereas *C. lantanae* was detected naturally without intentional introduction (Napompeth, 2004).

In order to acquire further information on reproduction, pollination and the invasive ability of lantana, animal-flower associations must first be explored. Each visiting animal may play a different role on an inflorescence or individual flower during interactions with lantana. Nectarivorous insects are potential pollinators due to their regular visiting and transfer of pollen from one flower to the stigmas of other flowers, whereas herbivorous insects and seed predators are utilized as weed biological control agents. According to our knowledge, animal-flower associations of lantana have never been fully studied in Thailand so far. This study thus aims to determine the lantana flower-visiting animals and their activities during flower visits, with emphasis on arthropod species.

MATERIALS AND METHODS

Study sites

Field work was conducted at Mahidol University, Kanchanaburi Campus (MUKA), Sai Yok District, Kanchanaburi Province (14°07'N 99°09'E; ca. 257 m above sea level). The physical geography of this region consists of mainly limestone mountains with a mixed deciduous forest type. The major vegetation types are secondary forests and bamboo forests. The study site was an unutilized area along an asphalt road, located approximately 1000 m away from buildings. Grasses and shrubs were the main vegetative component.

Observations of flower-visiting arthropods

Field work was conducted bimonthly throughout one year from November 2013 to December 2014, seven times in total. The field observation site was prepared by clearing a transect path and tagging plants on the first day. Lantana plants were sampled using a zigzag technique. Only plants with numerous flowers were chosen and tagged. The tag number was printed on paper card and wrapped with plastic tape. Tagging was started in the first 10 meters and omitted for the next 10 meters and then crossed the road for the next 10 meters, until a total of 400 meters was reached at the end of the transect.

On the second day, flower-visiting animals were observed. Observation time was roughly divided into four periods, three hours each, as follows: early morning (06:00–09:00), late morning (09:00–12:00), early afternoon (12:00–15:00), and late afternoon (15:00–18:00). Four plants were randomly chosen for observation during each time period. In each period, observations were conducted for 30 minutes for each lantana plant, and intercepted by a 15 minute break, which allowed for walking to the next plant. The order of plant observations was random among four plants. The data were recorded for each flower or inflorescence onto a datasheet, including: categories of flower-visiting arthropods; the visiting times (starting from the animals first being present and displaying interactions with lantana flowers until leaving); behaviors on the flower (or inflorescence), such as probing, feeding, ambushing, resting etc. For convenience in field observation, the flower-visiting arthropods were grouped into the following categories: 1) spiders, 2) flies, 3) stink bugs, 4) mealybugs, 5) lace bugs, 6) ants, 7) bees, 8) wasps, 9) adult butterflies, 10) caterpillars, and 11) crickets. Minute insects, such as thrips and mites, were not included in this observation because of their small sizes which made them difficult to observe.

To sample small arthropods, one inflorescence from each plant was cut and put directly into a bottle with alcohol-glycerin-acetic acid (AGA) solution at the end of each 30-min period, four inflorescences per plant. These inflorescences were brought back to the laboratory. Animal extraction was done under a stereo microscope. Arthropod specimens were preserved and prepared for further identification using standard taxonomic methods specific to each animal group. Animal identifications were taken to family level following CSIRO (1970) for insects, Palmer et al. (1989) for thrips, Krantz and Walter (2009) for mites, and Barrion and Litsinger (1995) for spiders. Due to insufficient taxonomic knowledge in identification and classification, centipedes was identified only to the class level, springtails to order level, bees to superfamily level, and wasps to suborder level.

Statistical analysis

In order to compare arthropod communities between surveys, relative abundance and taxonomic group richness were calculated. We used the dataset of small arthropods from inflorescence extractions only. The taxonomic groups were classified into order level, including 1) Mesostigmata, 2) Trombidiformes, 3) Araneae, 4) Collembola, 5) Hemiptera, 6) Hymenoptera, 7) Lepidoptera, and 8) Thysanoptera. Relative abundance of taxonomic groups was followed Pielou’s index of evenness (Pielou, 1969), which is the ratio of observed diversity to the maximum possible diversity of a community with the same taxonomic group richness, as in the following equation:

$$E = \frac{H'}{H'_{max}} = \frac{-\sum_i p_i \ln p_i}{\ln S}$$

Where: H' = Shannon's diversity index

p_i = proportion of individual numbers of arthropods within the *ith* group per total number of all groups

S = total number of taxonomic groups in a community (richness)

In addition, taxonomic group richness was also calculated following Margalef's index (Margalef, 1968). This index is the ratio of the number of groups to the total number of observed individuals, as in the equation below:

$$D = \frac{(S-1)}{\ln N}$$

Where: S = the number of taxonomic groups

N = the number of observed individuals

One-way ANOVA was also used to compare the means of the number of animal individuals per survey. Data transformations were performed in case of non-normally distributed data. If significant differences between surveys were detected, treatment means were then compared using Tukey's HSD multiple comparisons. The significance level used for this test was 5%. One-way ANOVA was performed with PASW Statistics version 18.0 (SPSS, 2009).

RESULTS

Seven surveys were conducted during November 2013 to December 2014 in total. However, two surveys did not successfully obtain adequate data. At the time of Survey II (Jan–Feb 2014), all plants in the study area were damaged by wildfire, and in Survey V (Jul–Aug 2014), lantana plants did not flower. Therefore, only five surveys were included in subsequent analyses.

A list of flower-visiting arthropods and some behaviors recorded during field observation are shown in Table 1. The spectrum of flower-visiting arthropods of lantana from both field observation and inflorescence extraction comprised 27 taxonomic groups (23 taxa at family level and 4 higher level taxa), including members from several classes/subclasses, as diverse as Arachnida, Chilopoda, Collembola, and Insecta. Among taxonomic groups, mites and hemipterans showed the highest family-richness consisting of six families in each taxonomic group, whereas lepidopterans were the second most diverse group including five families.

Eleven temporary visiting groups were observed for frequency of visit and visiting time. The results are summarized and shown in Table 2 and Fig. 1. Visitors to lantana flowers were composed mainly of bees, adult butterflies, spiders, and lace bugs. Bees showed the highest frequency of visits (32%), while adult butterflies were the second (28%). The lowest frequency of visiting animals were stink bugs, mealybugs, and wasps. They visited only two times over all field observations (less than 1% of all visits). When considering the visiting time, lace bugs were the flower-visiting group that spent the longest time in terms of both total visiting time (671 minutes) and length of time per visit (23.96

TABLE 1. Flower-visiting arthropods on *Lantana camara* with observed behavior.

Taxa	Common name	Observed behavior
Mesostigmata		
Phytoseiidae	mites	found in inflorescence extraction
Trombidiformes		
Cheyletidae	mites	found in inflorescence extraction
Stigmaeidae	mites	found in inflorescence extraction
Tarsonemidae	thread-footed mites	found in inflorescence extraction
Tenuipalpidae	false spider mites	found in inflorescence extraction
Tetranychidae	spider mites	found in inflorescence extraction
Araneae		
Oxyopidae	lynx spiders	sit and wait for their prey on inflorescences
Thomisidae	crab spiders	sit and wait for their prey on inflorescences
Chilopoda	centipedes	rest on flower buds
Collembola	springtails	found in inflorescence extraction
Diptera		
Muscidae	house flies	rest on corolla lobes
Hemiptera		
Aleyrodidae	whiteflies	rest on corolla lobes
Miridae	plant bugs	found in inflorescence extraction
Pentatomidae	stink bugs	rest on pedicels of inflorescences and infructescences
Pseudococcidae	mealybugs	rest on pedicels and receptacles of inflorescences
Reduviidae	assassin bugs	stab their prey with beak on flower buds
Tingidae	lace bugs	rest and suck the sap from inflorescences
Hymenoptera		
Formicidae	ants	probe corolla tubes/ some bite the bases of corolla tubes
Apoidea	bees	probe corolla tubes/ collect pollen
Apocrita	wasps	probe corolla tubes
Lepidoptera		
Lycaenidae	blue butterflies	probe corolla tubes/ feed on nectar
Lymantriidae	tussock moths	caterpillar bite flower buds, blooms, and fruits
Nymphalidae	brush-footed butterflies	probe corolla tubes/ feed on nectar
Papilionidae	swallowtail butterflies	probe corolla tubes/ feed on nectar
Pieridae	pierid butterflies	probe corolla tubes/ feed on nectar
Orthoptera		
Gryllidae	crickets	rest on top of inflorescences
Thysanoptera		
Thripidae	thrips	live inside the corolla tubes/ walk to the top of corolla tubes and also fly a short distance

± 4.34 minutes). Wasps spent less than two minutes which was the shortest among the observed total visiting times of all animals. When considering the length of time per visit, bees, adult butterflies, and wasps spent the shortest time among visiting animals (less than 1 min per visit). In addition, the accumulation curve of numbers of visits in a

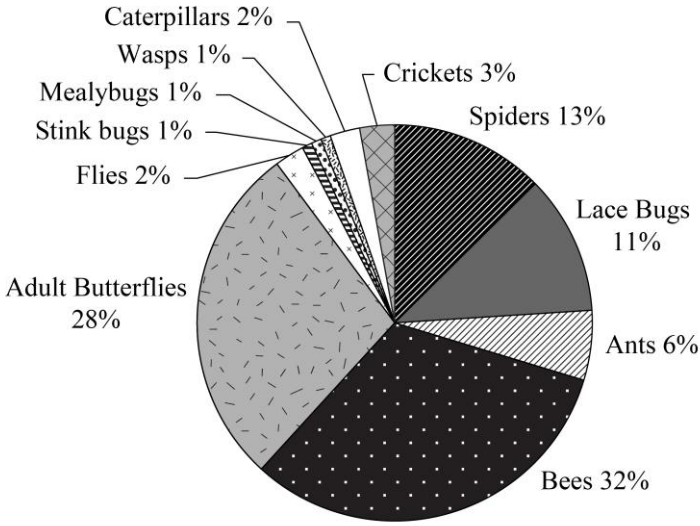

FIGURE 1. Percentages of each flower-visiting arthropod on *Lantana camara* flowers in all field surveys combined.

year of flower-visiting group in relation to accumulation of observation time, as shown in Fig. 2, revealed that all groups made more visits as observation progressed. However, spiders and ants had the rate of increase less than in bees and adult butterflies; while lace bugs more or less stopped their visits after about 1,300 minutes of observation.

In total, 316 individuals of small arthropods were extracted from lantana inflorescences over all field surveys. The percentage of individuals of each arthropod group for each survey is shown in Fig. 3. Thrips (Thysanoptera) and mites (Trombidiformes) were the most frequently

TABLE 2. Total number of visits, total visiting time, and length of time per visit of each arthropod group on *Lantana camara* flowers.

Flower associates	Total number of visits	Total visiting time (min.)	Length of time per visit (min. ± SD)
Spiders	31	596	19.23 ± 9.43
Lace bugs	28	671	23.96 ± 4.34
Ants	14	29	2.07 ± 1.77
Bees	79	<79	<1
Adult butterflies	69	<69	<1
Flies	6	59	9.83 ± 5.71
Stink bugs	2	26	13
Mealybugs	2	45	22.50 ± 4.95
Wasps	2	<2	<1
Caterpillars	6	121	20.17 ± 9.60
Crickets	7	133	19 ± 8.56

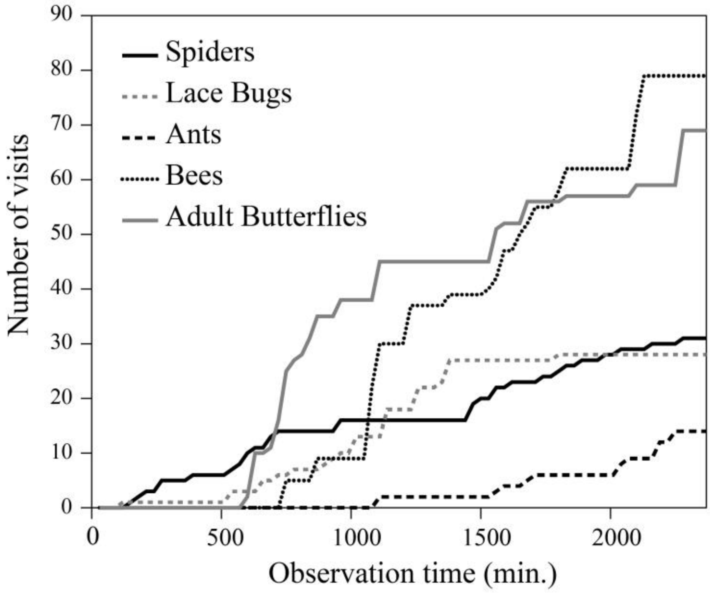

FIGURE 2. Cumulative numbers of visits in a year of flower-visiting arthropods on *Lantana camara* flower, in relation with observation time.

found animals from five surveys. Thrips showed the highest abundance in Survey I (75.66%) and Survey VII (52.17%). For the other three surveys, mites in the order Trombidiformes were the most abundant group in Survey III (39.39%), Survey IV (45.24%), and Survey VI (35.00%). In Survey VII, eight different animal orders were found, which was the highest group richness among the five surveys. Whereas in Survey I and IV, only five animal orders were recorded. The Pielou's evenness (*E*) index and Margalef's richness index (*D*) were calculated for each survey, and are shown in Fig. 3. The highest *E* was 0.767 for Survey VI and the lowest *E* was 0.348 for Survey I; while the highest *D* was 1.669 for Survey VI and the lowest *D* was 0.796 for Survey I.

Because they were the most abundant group, the mean number of thrips individuals was compared among five surveys. One-way ANOVA revealed that the individual numbers of thrips, transformed to $\text{logarithm}_{10}(x+1)$, were significantly different among five pairs of surveys (F = 14.606, df = 4, 15, $P < 0.05$; Table 3). Among the surveys, Tukey's HSD multiple comparisons revealed that the average number of thrips in Survey I was significantly higher than those of Surveys III, IV and VI (Fig. 4). Whereas, Survey III, Survey IV, and Survey VI were not different from each other, and showed relatively low mean values of thrips numbers when compared to Survey I and Survey VII.

DISCUSSION

In this study, the flower-visiting arthropods of lantana were investigated. They were quite diverse, and included members from several classes/subclasses, namely Arachnida, Chilopoda, Collembola,

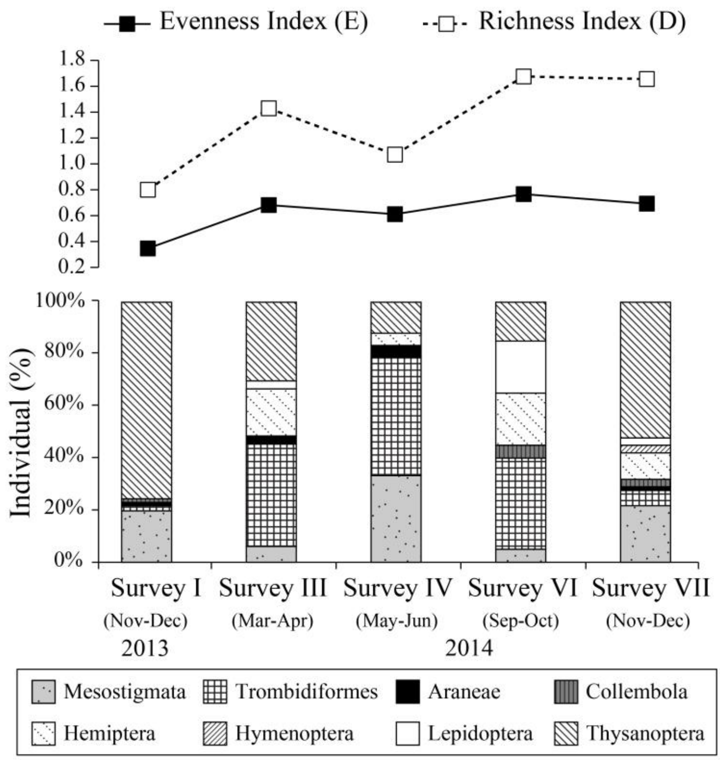

FIGURE 3. Percentages of individuals and Pielou's evenness and Margalef's richness indices of small arthropods extracted from *Lantana camara* inflorescences for each survey.

and Insecta. This result is consistent with other surveys of the flower-visiting insects of *L. camara* in other countries that also revealed a variety of taxonomic groups and indicated that lantana was one of the insect-attracting plants (Mathur and Mohan Ram, 1978; Goulson and Derwent, 2004; Carrión-Tacuri et al., 2014). In order to attract and have interactions with diverse animal groups, flower and inflorescence structures of lantana are probably the most important components which are linked to pollination syndromes (Carrión-Tacuri et al., 2014). Flowers of *L. camara* are characterized by being brightly colored, having high floret numbers per inflorescence (20-35 florets; field observation), and having narrow tubular flowers with spreading lobes grouped in inflorescences (Schemske, 1976). This structure facilitates easy landing by pollinators on the inflorescences. Flowers of *L. camara* also have high nectar volumes and sugar contents (Carrión-Tacuri et al., 2012), which may attract pollinators to visit them. In addition, flowers of *L. camara* undergo dramatic localized color changes, turning from yellow to orange, scarlet, and magenta, which are perhaps stimulated by pollination (Mohan Ram and Mathur, 1984). Nectar-containing flowers are always indicated by yellow color, while empty flowers are magenta or red (Carrión-Tacuri et al., 2012). A wide variety of insect pollinators can perceive this color change

TABLE 3. One-way ANOVA on the number of thrips in five surveys. SS, sum of squares; df, degrees of freedom; MS, mean squares; F, F statistic; and p, statistical significance.

	SS	df	MS	F	Sig.
Between Surveys	4.212	4	1.053	14.606	0.000
Within Surveys	1.081	15	0.072		
Total	5.293	19			

and thus may discriminate between rewarding flowers filled with nectar and non-rewarding empty flowers. The pollinator is accurately directed to rewarding flowers, which provide benefits to the plant by receiving an efficient pollination service (Weiss, 1991). All of these advantages in characters listed above may contribute to the invasive ability of *L. camara* over endemic species, in terms of being more attractive to pollinators and resulting in more successful reproduction regarding the number of fruit set (Carrión-Tacuri et al., 2014).

Three groups of flower-visiting insects, namely bees, adult butterflies, and thrips, seem to be potential pollinators of *L. camara* according to their behaviors, abundance, and handling time, as revealed in the present study. Bees spent very short periods, less than one minute per visit, for collecting pollen and hovering back and forth on the inflorescence. This is consistent with a previous report on the mean time spent by the honeybee, *Apis mellifera* Linnaeus, 1758, on inflorescences of biofuel tree species (8±1 second; Negussie et al., 2013). Several families of adult butterflies were found feeding on lantana nectar, including Lycaenidae, Nymphalidae, Papilionidae, and Pieridae. These butterfly families were also reported as major flower-visiting insects on lantana in Australia (Goulson and Derwent, 2004). In addition, the total numbers of visits by butterflies was second only to bees, which was similar to the work of Goulson and Derwent (2004). Many studies have claimed that butterflies were the major pollinator taxa of lantana (Schemske, 1976; Kunte, 2007; Carrión-Tacuri et al., 2014).

There is no doubt that bees and adult butterflies are well known for flower visiting behavior and probably are the most important pollinator for flowering plants (Corbet et al., 1992). However, in this study, we found that thrips also showed interesting behavior and thus could be considered as a potential pollinator of *L. camara*. They were found living inside the corolla tube of the flower, sometimes walking to the top of the corolla tube and then moving back inside the flower, as well as flying short distances between flowers and inflorescences. Thrips have been previously reported as regular pollinators of lantana plants, especially for self-pollination. (Mathur and Mohan Ram, 1978; Mohan Ram and Mathur, 1984). Mathur and Mohan Ram (1978) reported that thrips have been found with pollen loads on their legs and some parts of their abdomen. They were also claimed to be more effective pollinators than butterflies, based on them producing higher fruit set (Mathur and Mohan Ram, 1986).

Hemipterans are noted as important herbivores in many plants (e.g. Takagi, 2014). In the present study, various families of hemipterans were found to have interactions with lantana flowers, namely

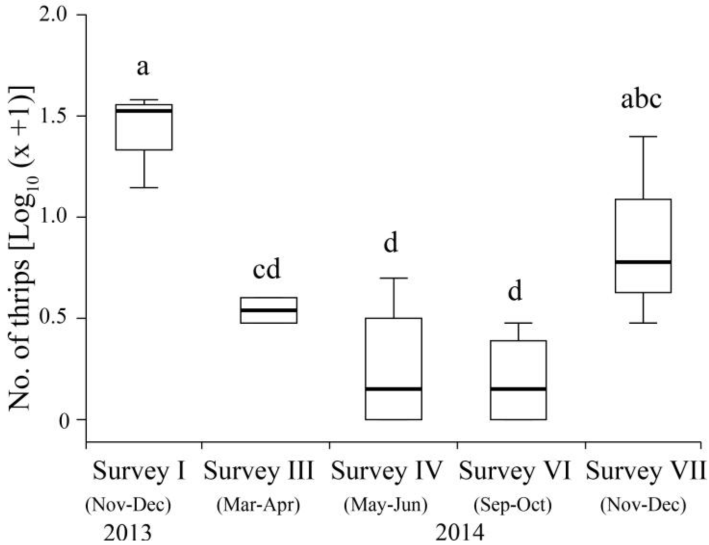

FIGURE 4. Box plots of Tukey's HSD multiple comparisons of the individual number of thrips in the form of logarithm$_{10}$(x+1) between surveys**.** Boxes show the median, 25th and 75th percentiles; whiskers show minimum and maximum observations.

whiteflies, plant bugs, stink bugs, mealybugs, and lace bugs. They were found to feed on the undersides of leaves, on stems, and on buds, and sometimes moved to flowers and feed on flower tissue. These insects spent longer times per visit on flowers/inflorescences when compared to potential pollinator groups (Table 2 and Fig. 2). These results were related to feeding and dwelling behaviors of herbivorous species. They can frequently feed without time limits because their feeding times are equal to the ratio of handling time to digestion time (Jeschke and Tollrian, 2005). In addition, this study also found several families of phytophagous mites, namely Tarsonemidae, Tenuipalpidae, Tetranychidae. Walter (1999) reported more than fifty species of mites that can be found on the leaves and flowers of *L. camara*. These mites could also directly cause severe damage to lantana, as they often do in other plants (White, 1984), Besides, mites, such as flower dwelling mites, could be competitors with pollinator insects by consuming nectar (Watanabe et al., 2007). All phytophagous arthropods reported in this study have potential to be used as biocontrol agents in a *L. camara* management program, in addition to the 41 biological control agents previously reported by Day et al. (2003). However, this study did not find some other important insect groups that have been used in biological control programs, i.e., Coleoptera and Diptera (Day et al., 2003; Napompeth, 2004). This is probably because these insects destroy other parts of lantana plants and do not often have interactions with the flower or inflorescence.

In the present study, ants were sometimes observed biting into the bases of lantana corolla tubes and collecting nectar without direct contact to reproductive organs. Ants are unlikely pollinators and rarely benefit a plant (Beattie et al., 1984). They can disrupt pollination by deterring other flower visitors (Ness, 2006), or by stealing nectar (Wyatt, 1980). This behavior of stealing nectar is called nectar robbing (Inouye, 1980). Nectar robbers can decrease plant reproductive success by reducing the amount of nectar available to other pollinators (Wyatt, 1980), and, in some cases, damaging or completely destroying floral reproductive structures (e.g. Galen and Butchart, 2003).

This study also revealed considerable variation of insect numbers over different seasons. Thrips were found in large numbers on the inflorescence of lantana during Survey I and VII (Nov-Dec 2013, and 2014; Fig. 4), and this was significantly higher than other surveys. The average temperature of November and December in Thailand is relatively low when compared to other months. This result is related to Lee et al. (2001), who suggested that most overwintering thrips usually are not active and do not fly during the winter season. In the present study, the inflorescence extraction data also showed that mites (Trombidiformes) increased in number when the number of thrips decreased (Fig. 3). It is possible that some groups of thrips and mites are antagonists in a predator-prey interaction, as has been reported previously, e.g. predatory mites feed on juveniles thrips (Wiethoff et al., 2004), and *vice versa*, flower thrips feed on spider mite eggs (Trichilo and Leigh, 1986).

In conclusion, a high diversity of flower-visiting arthropods and their activities on *L. camara* in Thailand was found. Several groups of associated animals found here were potential pollinators that may have an important role in the reproductive success of lantana, such as bees, butterflies, and thrips. However, other groups of animals were phytophagous, such as hemipterans and mites, which could be used in biological control program of lantana. Furthermore, florivores, nectarivores, and seed predators, such as ants in this study, need to be focused on in the future in a biological control aspect, since they can damage floral tissue or plant reproduction parts which directly reduce fitness of the plant. This study is the first to reveal the diversity of flower-visiting arthropods on lantana in Thailand. The main finding of this study will shed light on ecological functions of associated arthropods and on temporal changes of community structure in different seasons which could be used in further management programs of lantana.

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