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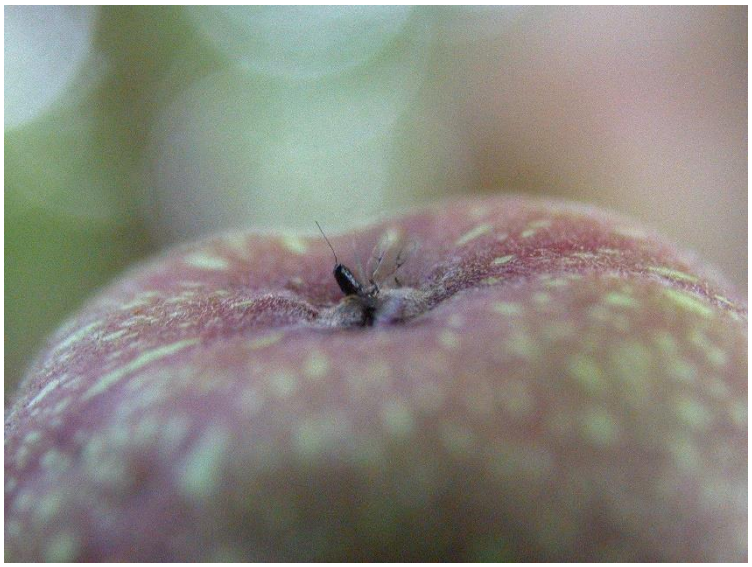
The regional variations of fig and fig-wasp communities in different regions



Khin Me Me Aung, Research Assistant-2

Forest Research Institute

Dr. PENG Yan-Qiong, PI, Professor

Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences

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Table of contents

The regional variations of fig and fig-wasp communities in *Ficus racemosa*

Khin Me Me Aung, Research Assistant-2, Forest Research Institute
Dr. PENG Yan-Qiong, Professor, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences

Abstract

The interaction between *Ficus* species and their pollinating wasps (Agaonidae) is a striking example of mutualism. Seed production by fig trees is dependent on a unique fig-pollinating wasps, and the pollinator's offspring feed only in the ovules. Except for species-specific pollinating fig wasps, each *Ficus* species is also exploited by diverse non-pollinating chalcid wasps, including gallers, inquilines and parasitoids. Multiple species often develop side by side in a single fig, and constitute a multitrophic fig wasp community which represents an interesting model for studies on a community ecology. Fig wasp community can be influenced by regional species pools, biogeographic features, interspecific interactions and so on, but they remain poorly researched. In this study, the monoecious *Ficus racemosa* that is widely distributed in the Indo-China Peninsula, and its fig wasps were selected as the study materials. The study was conducted in Mandalay of Myanmar, Xishuangbanna of China, Luang Namtha of Laos and Udon Thani of Thailand. The main results are as follows: fig sizes of *F. racemosa* were varied and large figs had more female flower resources. The species composition of fig wasp community was same in the Indo-China Peninsula with the same pollinator and five species of non-pollinating fig wasps. However, the wasp body size of each fig wasp species was varied, and nine morphological traits about wasp body size per each species were measured and PCA values showed that wing length was a good morphological trait for representing body size of six wasp species in *F. racemosa*. Pollinator *Ceratosolen* sp. wasp was the dominant species in all four study sites, while the population size was the largest in Luang Namtha and the non-pollinating fig wasps were most abundant in Mandalay. Thus, not only community structure and species abundance differed among four study sites, but the variations in the coexistence networks of fig wasps also existed. Different seasons and geographic regions had various climate conditions so that they could affect fig wasp community. Through comparing multiple climate factors, the monthly minimum temperature (T_{min}) was found to be the most important factor, which was used to analyze the effects on fig wasp community. The results showed a clear separation between Mandalay and other three geographic regions, and the separation was largely determined by the temperature not the geographic distance. Taken together, the results strongly indicate that climate especially temperature plays an important role in shaping fig wasp community.

Keywords: *Ficus*; Fig wasps; Mutualism; Exploitation; Abundance; Community structure; Multitrophic

Ficus racemosa နှင့် ၎င်း၏အင်းဆက် အဖွဲ့အစည်းများကြားရှိ ဒေသတွင်း ကွာခြားချက်များအား လေ့လာခြင်း

ခင်မိမိအောင်၊ သုတေသနလက်ထောက်-၂၊ သစ်တောသုတေသနဌာန
Dr. PENG Yan-Qiong၊ ပါမောက္ခ၊ စစ်ဆောင်ပနား အပူပိုင်းရက္ခဗေဒဥယျာဉ်-
တရုတ်သိပ္ပံအကယ်ဒမီ

Ficus မျိုးစိတ်များနှင့် ၎င်းတို့၏ ဝတ်မှုန်ကူးအင်းဆက်များ (pollinators) အကြားမှ ဆက်နွယ်မှုသည် တစ်ဦးနှင့် တစ်ဦးအပြန်အလှန် အကျိုးပြုသော ဆက်နွယ်မှုတစ်ခုဖြစ်ပါသည်။ *Ficus* မျိုးစိတ်များ၏ မျိုးစေ့ထုတ်လုပ်မှုသည် ၎င်းတို့၏ ဝတ်မှုန်ကူး အင်းဆက်များပေါ်တွင် အဓိက မူတည်နေပြီး ဝတ်မှုန်ကူးအင်းဆက်များ၏ မျိုးပွားမှုသည်လည်း *Ficus* မျိုးစိတ်များပေါ် တွင် မှီခိုနေပါသည်။ ဝတ်မှုန်ကူးသောအင်းဆက်များ (pollinators) အပြင် အခြားဝတ်မှုန်မကူး နိုင်သောအင်းဆက် (non-pollinators) မျိုးစိတ်များသည်လည်း *Ficus* မျိုးစိတ်များအပေါ်တွင် မှီခို လျှက်ရှိပါသည်။ *Ficus* မျိုးစိတ်တစ်ခုခြင်းဆီတွင် အင်းဆက် မျိုးစိတ်များသည် အဖွဲ့အစည်း တစ်ခုအဖြစ် မှီခိုလျှက်ရှိနေကြပြီး ၎င်းတို့ကြားရှိ ဆက်နွယ်မှုသည် ဂေဟဗေဒအင်းဆက်အဖွဲ့ အစည်း လေ့လာခြင်းအတွက် အကောင်းဆုံး လေ့လာခြင်းတစ်ရပ်ဖြစ်ပါသည်။ ယခုသုတေသနသည် မြန်မာနိုင်ငံ၊ တရုတ်နိုင်ငံ၊ ထိုင်းနိုင်ငံနှင့် လာအို နိုင်ငံများတွင် ပေါက်ရောက်သော *Ficus racemosa* မျိုးစိတ် အဓိကလေ့လာ ထားခြင်း ဖြစ်ပြီး ၎င်းမျိုးစိတ်သည်အင်ဒို-ဆြိုင်းနား ကျွန်းဆွယ် အတွင်းအများအပြား ပေါက်ရောက် ပျံ့နှံ့သော မျိုးစိတ်တစ်ခု ဖြစ်ပါသည်။ သုတေသန၏ အဓိကလေ့လာတွေ့ရှိချက်များမှာ *Ficus racemosa* ၏ အသီးအရွယ်အစားသည် ဒေသအလိုက်ကွဲပြားပြီး အသီးအရွယ် အစားကြီးလျှင် ပန်းပွင့်များပိုမိုများပြားစွာ ပါဝင်သည်ကိုတွေ့ရှိ ရပါသည်။ အင်ဒို-ဆြိုင်းနား ကျွန်းဆွယ်ရှိ အင်းဆက်အဖွဲ့အစည်းတွင် ဝတ်မှုန်ကူး အင်းဆက်နှင့် ဝတ်မှုန်မကူး နိုင်သောအင်းဆက် မျိုးစိတ်များသည် (Pollinator and Non-pollinating fig wasps) တူညီ ကြောင်း တွေ့ရှိရပါသည်။ သို့သော်လည်း အင်းဆက်အရွယ်အစားမှာ ကွာခြားပြီး PCA တန်ဖိုးအရ အတောင်ပံ အရွယ်အစားသည် အဓိကအရေးကြီးသော morphological trait တစ်ခု ဖြစ် ကြောင်း တွေ့ရှိရပါသည်။ ဝတ်မှုန်ကူးနိုင်သော အင်းဆက် (pollinator) သည် ယခုလေ့လာခဲ့သော နိုင်ငံလေးနိုင်ငံတွင် အဓိကပေါများသော အင်းဆက်မျိုးစိတ် တစ်ခု

ဖြစ်ပြီး လာအိုနိုင်ငံ၊ လန်နသမ်မြို့တွင် ဝတ်မှုန်ကူးနိုင်သော အင်းဆက် (pollinator) သည် ပိုမိုများပြား၍ မြန်မာနိုင်ငံ၊ မန္တလေးတိုင်းဒေသကြီး၊ ပုသိမ်ကြီးမြို့တွင် ဝတ်မှုန်မကူးနိုင်သော အင်းဆက် (non-pollinator) သည် ပိုမိုများပြားကြောင်း တွေ့ရှိရပါသည်။ ရာသီဥတု သတင်းအချက်အလက်များအား လေ့လာခြင်းအရအနည်းဆုံးအပူချိန် (minimum temperature) သည် အင်းဆက်အဖွဲ့ အစည်းအပေါ်တွင် အဓိကသက်ရောက်မှုရှိကြောင်း တွေ့ရှိ ရပါသည်။ အင်းဆက်အဖွဲ့အစည်းသည် အနည်းဆုံး အပူချိန်ပေါ် မူတည်၍ မြန်မာနိုင်ငံ၊ ပုသိမ်ကြီးမြို့သည် အခြားသော နိုင်ငံသုံးနိုင်ငံများနှင့် ကွဲပြားကြောင်း လေ့လာတွေ့ရှိရပါ သည်။

The regional variations of fig and fig-wasp communities in *Ficus racemosa*

1. Introduction

1.1 A brief introduction to community

An insight into the community structure, which affects by both ecological interaction and evolutionary history, provides the better understanding of the coexistence of species competing for similar resources (Ricklefs and Schluter, 1993; Emerson and Gillespie, 2008). On the one hand, closely related species might have similar functional traits (Faith, 1992), thus, they are restricted by their ability to use resources, so they may choose a similar habitat and use the same resources. On the other hand, interspecific competition can prevent similar species from coexisting within a community (Cody *et al*., 1975). Fig wasp community structure is complex, typically involving the coexistence of multitriophic interactions, which are influenced by ecological and evolutionary factors (Segar *et al*., 2013; Darwell *et al*., 2018).

In insect communities, insect species utilize the similar resources which will have the natural enemies (parasitoids), either competition for space or food resources can also influence community structure (Jones *et al*., 2009). In multitrophic communities, research regarding the species richness of a region is less informative than the one with the consideration of the species abundance (Bailey *et al*., 2009). In accordance with the biodiversity in tropical regions, the relationship between the insect communities and plant species is complex due to the coexistence of many species at the different trophic levels (Cook and Segar, 2010). Moreover, the trophic positions and resources portion are also important factors for the determination of community composition (Naeem and Hawkins, 1994; Vincent *et al*., 1996; Bonsall *et al*., 2002; Giacomini *et al*., 2009).

1.2 Research progress on fig wasp community

Several studies have investigated fig wasp communities from both evolutionary and ecological perspectives (Kerdelhue *et al*., 2000; Jousselin *et al*., 2008; Segar *et al*., 2014). Fig wasp community is the excellent system to study about ecological networks. In a regional community of *Ficus* species, some non-pollinating fig wasps shared one or more *Ficus* host resulting in the high abundance in an individual host, and thus they are not restricted to be specialists (Farache *et al*., 2018). According to the studies of fig wasp community in different geographic areas, the fig wasp community structure and genus level composition are largely conserved (Darwell *et al*. 2018) and the structure of multitrophic communities over three continents is converged (Segar *et al*., 2013). The ecological interactions between species may play a persistent role in shaping these communities, but the variations of fig wasp communities in the underlying ecological networks across biogeographic regions is rarely studied.

In tropical insect community, the ecological importance, the composition and structure of inter-specific interactions has been rarely investigated. The community composition of fig wasp species associated with *F*. *rubiginosa* in Australia highlighted that

the small wasps (pollinators, gallers, and parasitoids) had higher abundance than larger wasps (both gallers and parasitoids) (Segar *et al*., 2014).

The insect species composition and richness are varied with the different elevations but they are also divergent among different taxonomic groups (Manusell *et al*., 2015; McBoy, 1990; Peck *et al*., 2008; Warren *et al*., 1988). However, species abundance of fig wasps is more likely to decrease with raising elevation (Warren *et al*., 1988). In addition, parasitoids and the mutualisms of parasitoids are also complex and they can affect the stability of mutualistic partners directly or indirectly (Bronstein, 2001). Fig wasp can disperse for long distance by using wind flow up to 160 km distance (Ahmed *et al*., 2009). Moreover, non-pollinating larvae can parasitize the pollinator larvae, which can affect the pollinator population and dynamics, and male functions of fig trees (Kerdelhue and Rasplus, 1996; Weiblen, *et al*., 2001; Weiblen, 2002). The fig volume (diameter and length) and total number of pollinating and non-pollinating fig wasps, and seed production can be affected by elevation, however it varied among different fig species (Souto-Vilaró *et al*., 2019). Moreover, seed production has positively correlated with the number of foundress (Corlett *et al*., 1990; Nefdt and Compton, 1996; Moore and Greeff 2003), besides it also can be restricted by the amount of pollen that pollinator carry (Kjellberg *et al*., 2014).

In northern Mexico, the distribution of foundress in monoecious *F. petiolaris* influences the abundance of pollinating and non-pollinating fig wasps, and seed production (Duthie and Nason, 2016). *F. racemosa* has higher abundance of non-pollinating fig wasps in highly fragmented forest (Wang *et al*., 2005). Furthermore, the fig wasp community in *F. racemosa* had more numbers of non-pollinating fig wasps and few pollinating fig wasps in dry season (Wang and Sun, 2009).

1.3 Fig and fig wasp interaction

Fig and fig wasp mutualism is one of the most well-known symbiotic systems and is an ideal system to study the process of coevolution between organisms (Janzen, 1979; Cook and Rasplus, 2003). Moreover, figs and fig wasps constitute an excellent model of insect-plant association access the patterns of species diversity, community structure (Lewinsohn *et al*., 2005), ecology of mutualistic and exploitive communities (Cook and Rasplus, 2003; Herre *et al*., 2008) and the evolution of ecological interactions (Borges *et al*., 2018). *Ficus*, commonly known as figs, belongs to family Moraceae and mainly distributed in the tropics and subtropics. Figs exhibit a wide range of life forms (trees, shrubs, stranglers, vines), and occupy a diversity of habitats (rainforest understories and canopies, savannahs, riversides) (Corner, 1940; Janzen, 1979; Harrison, 2005). *Ficus* is one of the largest woody genera in the tropical regions and plants are well known for their unique urn-shape inflorescence, occupying monoecious and dioecious functions, thus, *Ficus* plants can be divided into two major groups. Approximately, half of the *Ficus* species are monoecious, thus they produce a mixture of seeds and wasps from the same individual fig. The rest of the species are dioecious, they produce seeds and wasps separately that the female fig produce only seeds and male fig produce only wasps (Janzen, 1979; Berg and Corner, 2005).

There are about 800 *Ficus* species distributed worldwide and more than 500 species occur in the Indo-Australasian region (Berg and Corner, 2005). High diversity of *Ficus* species occur in Asia, and 130 occur in Borneo (Berg and Corner, 2005), 101 in China (Wu *et*

al., 2003; Chantarasuwan *et al*., 2014; Liu *et al*., 2015) and 106 in Myanmar (Kurz, 1877; Kress *et al*., 2003). In general, fig trees with larger crops can sustain frugivores through the lean period of low fruit availability as fig trees produce fruits all year round, especially in winter when other trees are lacking of fruits. Therefore, fig trees play the important role in the forest ecosystem so that they are thought to be the keystone species in the rainforest (Shanahan *et al*., 2001; Kumar *et al*., 2011).

Ficus species are, perhaps, best known for their relationship with pollinating wasps (Hymenoptera: Chalcidoides: Agaonidae), which are species-specific with relatively few exceptions (Wiebes, 1979; Cruaud *et al*., 2012; Yang *et al*., 2015; Wang *et al*., 2019). Seed production by fig trees is dependent on a unique fig-pollinating wasp, and the pollinator's offspring feed only in the ovules (Wiebes, 1979; Weiblen, 2002). Fossil evidence shows that the morphology of the pollen and pollinating wasps of *Ficus* has not changed significantly for about 34 million years (Compton *et al*., 2010) and this evidence shows that the stability of the relationship between fig and pollinating fig wasp. Moreover, molecular evidence indicates that this relationship dates back to around 75 million years ago (Cruaud *et al*., 2012). The interaction between *Ficus* species and their pollinating wasps (Agonidae) represents a striking example of a mutualism (Herre *et al*., 2008). Except for species-specific pollinating fig wasps figs are exploited by a large community of chalcidoid wasps belonging to five families (Agaonidae, Pteromalidae, Eurytomidae, Ormyridae, and Torymidae). They accomplish only the development stages within the figs, however, do not transfer pollen (Weiblen, 2002; Zhen *et al*., 2005; Compton *et al*., 2018). About 800 species of fig wasps are described worldwide, of which about 300 species are recorded in the Indo-Australasian region including gallers (gall maker/ primary gallers), parasitoids (parasitoid of primary gallers) and kleptoparasites (parasitoids of gallers but kill the host gallers) (Kerdelhue *et al*., 2000; Chen *et al*., 2013; Borges *et al*., 2018; Compton *et al*., 2018). Multiple species often develop side by side in a single fig; in New World figs, offspring of non-pollinators can be more numerous than the pollinator offspring (Bronstein, 1991).

The fig-fig wasp system is characterized by their mutualistic and antagonistic wasp species, which develop inside the inflorescence called syconium or fig (Cook and Rasplus, 2003; Herre *et al*., 2008). Pollinating fig wasps enter the fig through a hole called ostiole to oviposit and pollinate the female flowers. Pollinators are specifically attracted by volatile organic compounds emitted by figs (Hossaert-McKey *et al*., 1994). Most figs are pollinated by a single or limited number of wasp species and most wasps are specifically related to a single fig species (Cook and Rasplus, 2003; Molbo *et al*., 2003; Cook and Segar, 2010; Cruaud *et al*., 2012; Liu *et al*., 2015). In general, non-pollinating fig wasps use their long ovipositor to deposit eggs through the fig wall, and most species are flower gallers, inquilines, or parasitoids of other fig wasps or of each other (Elias *et al*., 2008; Ghara and Borges, 2010; Compton *et al*., 2018). In addition, they attack the figs at different stages of fruit growth but complete their own development at the same time as pollinating fig wasps, thus forming a multitrophic fig wasp community (Kerdelhue *et al*., 2000; Borges *et al*., 2018). A fig wasp community that associates with a fig species can consist of more than 40 wasp species at different trophic levels (Compton *et al*., 2018). However, the diversity of non-pollinating fig wasps may differ depending on the reproductive systems of plants (Kerdelhue and Rasplus, 1996).

F. racemosa is a monoecious fig species that widely distributed throughout the Indo-Australasian region. The trees grow rapidly, reaching up to 25-40 m in height, and produce 2-7 fig crops per year (Zhang *et al*., 2006; Krishnan *et al*., 2015). According to the genetic structuring of *F. racemosa* and its pollinating wasps, there are strong gene flows in four biogeographical populations, namely India, China to Thailand, Borneo and Australia, which make the population of *F. racemosa* pollinated by a single pollinator species in the Indo-China Peninsula (Bain *et al*., 2016). Geographic isolation results in obvious genetic differentiation between the populations of India and other three biogeographic groups (Kobmoo *et al*., 2010; Bain *et al*., 2016). *F. racemosa* is pollinated by four species of *Ceratosolen* wasps including *Ceratosolen mysorensis*, *Ceratosolen* sp., *Ceratosolen fuscipes* and *Ceratosolen nigriscapus* identified by Jean-Yves Rasplus in the Indo-Australian region. The occurrence of *C. mysorensis* is assessed only in India, *Ceratosolen* sp. in China to Thailand, *C. fuscipes* in Borneo and *C. nigriscapus* in northern Australia, respectively, thus highlighting different evolutionary histories of four *Ceratosolen* pollinators in *F. racemosa* (Figure 1) (Kobmoo *et al*., 2010; Bain *et al*., 2016). In addition, five species of non-pollinating fig wasps coexist with *F. racemosa* figs (Xu *et al*., 2003). In India, *F. racemosa* is pollinated by *C. mysorensis* and exploited by six species of non-pollinating fig wasps, namely *Sycophaga stratheni*, *Sycophaga testacea*, *Sycophaga fusca*, *Sycophaga agraensis*, *Apocrypta westwoodi*, and *Apocrypta* sp. (Ranganathan *et al*., 2010). However, only five species of non-pollinating fig wasps are found in China, thus the occurrence of *S. stratheni* has not uncovered yet (Xu *et al*., 2003; Ranganathan *et al*., 2010). This shows that the fig wasp communities of *F. racemosa* are different between China and India, although some of the non-pollinating fig wasps such as *S. testacea*, *S. agraensis*, *A. westwoodi* and *Apocrypta* sp. share their occurrence between two countries. All fig wasp species of male fig wasps in *F. racemosa* are wingless (Kerdelhue *et al*., 2000). *Ceratosolen* sp., *S. testacea* and *S. mayri* are the gallers (Proffit *et al*., 2007; Wang and Zhang, 2008). *S. agraensis* is a parasitoid or an inquiline and *A. westwoodi* and *Apocrypta* sp. are parasitoids of pollinator or other parasitoids (Proffit *et al*., 2007; Wang and Zhang, 2008). All species of non-pollinating fig wasps in *F. racemosa* are usually oviposit from the outside of the fig wall.

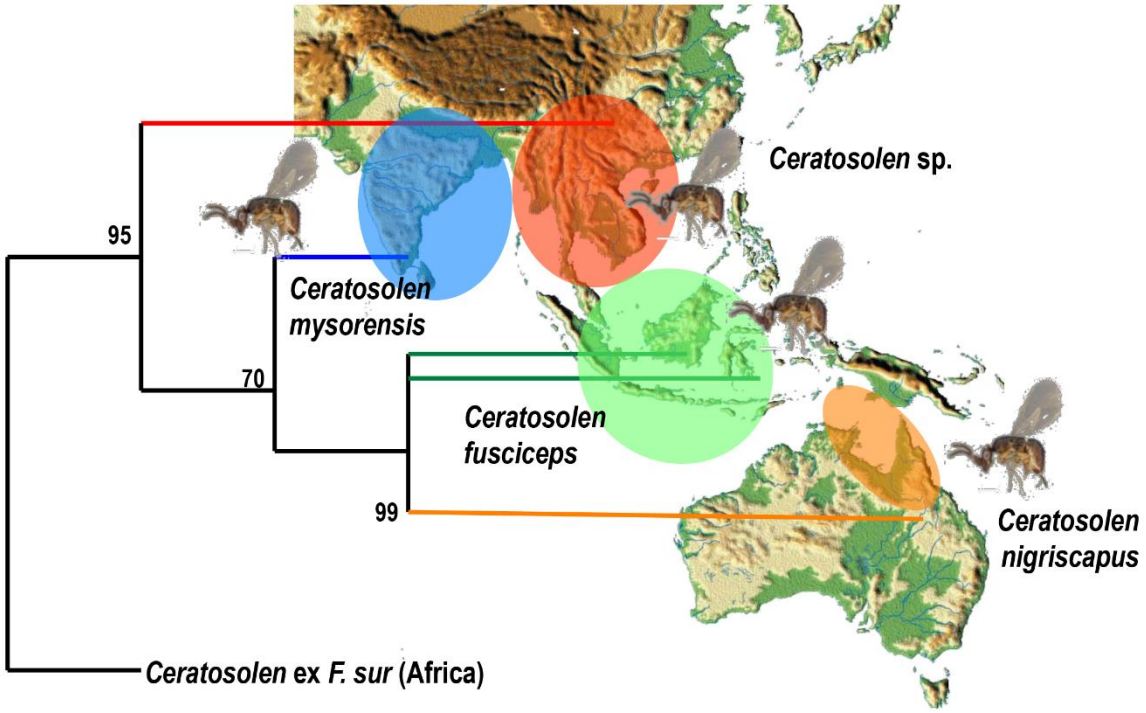

Figure 1. Four pollinator species of *Ficus racemosa* into a monophylogenetic of different geographic regions (The photo is from identification of Jean-Yves Rasplus)

There are five developmental phases in fig phenology of *F. racemosa* (Galil and Eisikowitch, 1968; Rangananthan *et al*., 2010): A phase (pre-female) consisting of immature flower; B phase (receptive or female) consisting of mature female flowers, with pollinators entering figs for pollination and oviposition; C phase (inter-floral) consisting of seed and gall development, with similar developmental time for figs and wasps; D phase (male), where male wasp pollinators exit the galls to mate with female wasps and tunnel through the fig wall. The female wasps escape through the tunnel, and then fly to another host tree to start their new life cycle; E phase (post-floral), during the time of the fig color changes to attract seed dispersers (Borges *et al*., 2008).

Moreover, a comparative investigation from China on *F. racemosa* in southern Xishuangbanna and northern Liuku of Yunnan province reports a higher number of pollinators in Xishuangbanna, however the lower number of non-pollinating fig wasps are reported. In contrast, the fig wasp community was varied even the pollinator and non-pollinating fig wasps were same species in Xishuangbanna and Liuku (Chen *et al*., 2018). In Xishuangbanna, the pollinating fig wasp of *F. racemosa* was initially thought to be *C. fuscipes*. However, recent molecular evidence has shown that there are four species of pollinating fig wasps from India to north Australia, and *F. racemosa* actively pollinated by *Ceratosolen* sp. in the Indo-China Peninsula (Kobmoo *et al*., 2010; Bain *et al*., 2016).

In Myanmar, 106 *Ficus* species have been reported (Kurz, 1877; Kress *et al*., 2003), however, *F. racemosa* is excluded in that checklist. During the investigating species interaction of fig trees and fig wasp in 2016 in Myanmar, *F. racemosa* was recorded in several localities such as Mandalay, Bagan, Yangon, and so on. Therefore, *F. racemosa* is a

newly recorded species for Myanmar based on the published book and checklist (Kurz, 1877; Kress *et al*., 2003). Myanmar is located between China and India where it is the natural distribution range of *F. racemosa*. The recent research confirmed that fig wasp community of *F. racemosa* in Myanmar was same with China (Aung *et al*., 2020). However, species composition and abundance of fig wasp community in *F. racemosa* in these regions were different.

The undescribed species *Ceratosolen* sp. is a species-specific pollinator of *F. racemosa* in China-Thailand (Bain *et al*., 2016; identification of Jean-Yves Rasplus), however, no study has confirmed yet that *F. racemosa* shares same non-pollinating fig wasps or not. Fig wasp community has varied between Xishuangbanna and Liuku (Chen *et al*., 2018) within China, although they shared the same species of non-pollinating fig wasp. It is crucial to study the fig wasp community structure in the broader spatial scale and to have the better understanding of community composition in elevational and latitudinal gradients. This study aims to reveal whether species of non-pollinating fig wasp in *F. racemosa* are same or not in China-Thailand whether the same pollinator are shared. Therefore, we sampled the D-phase figs of *F. racemosa* and their fig wasps in Myanmar, China, Laos and Thailand, and then compare the regional variations of fig wasp community. This result will provide for important evidence how fig wasp community change with latitudes representing temperature changes and reveal the response of fig wasp community to climate change and adaption.

2. Objectives

This study aims to compare the morphological differences of figs and fig wasps in *F. racemosa* in Myanmar, China, Laos and Thailand, to set up the species composition, abundance and coexistence networks of fig wasp communities of *F. racemosa* in Myanmar, China, Laos and Thailand, and to discover the effects of climate factors on the variations of fig wasp communities.

3. Materials and Methods

3.1 Study sites and species

The research was conducted in Patheingyi Township, Mandalay Division, central Myanmar, Xisuangbanna Tropical Botanical Garden, Menglun, Yunnan Province, southwest China, Nateuy Villate, Luang Namtha Province, Laos and in Mueang Udon Thani District, Udon Thani Province, Thailand. Four study sites in detail were shown in Table 1, and also look the distribution map in Figure 2. From September to December 2018, we collected fig wasps in four study sites and at least 10 figs per tree and one tree per site were sampled.

Patheingyi Township is located in the eastern part of Mandalay, Myanmar. The sampling site was along a small stream with secondary forest. The climate presents as dry season from March to April, rainy season from May to October and winter season from November to February. The monthly maximum temperature is 33.21°C and minimum temperature is 24.69°C and total precipitation is 168.91 mm during the study period (Fick and Hijmans 2017).

Xishuangbanna is located in the south of Yunnan Province, the sampling site was in Xishuangbanna Tropical Botanical Garden along Luosuo River. The climate presents as hot-

dry season from March to April, rainy season from May to October and cool-dry season from November to February (Cao *et al*. 2006). The monthly maximum temperature is 25.34°C and minimum temperature is 16.08°C and total precipitation is 140.4 mm during the study period. The climate data of Xishuangbanna was collected from Xishuangbanna Station for Tropical Rainforest Ecosystem studies.

Luang Namtha is located in the northern part of Laos, the sampling sites was along the road and near the river. The climate pronounces as hot dry season from March to April, rainy season from May to October and cool dry season from November to February. The monthly maximum temperature is 29.36°C and minimum temperature is 20.74°C and total precipitation is 149.93 mm during the study period (Fick and Hijmans 2017).

Udon Thani is located in the north of Thailand, the sampling site was in farmland and near villages. The climate represents hot season from March to mid-May, rainy season from mid-May to October, and cool-dry season from November to February. The monthly maximum temperature is 32.37°C and minimum temperature is 22.78°C and total precipitation is 50.67 mm during the study period (Fick and Hijmans 2017).

Table 1. Four study sites in detail and sampling sizes in *Ficus racmeosa*

Population	Longitude (E)	Latitude (N)	Altitude (m)	Sample size (figs/tree)
Mandalay (MMM) Myanmar	96°12′29.34"	21°59′03.18"	169	40/2
Xishuangbanna (XTBG) China	101°15′22.19"	21°56′54.87"	555	58/2
Luang Namtha (LN) Laos	101°38′40.22"	21°3′42.09"	602	17/1
Udon Thani (TMUT) Thailand	102°43′13.37"	17°21′39.75"	191	32/2

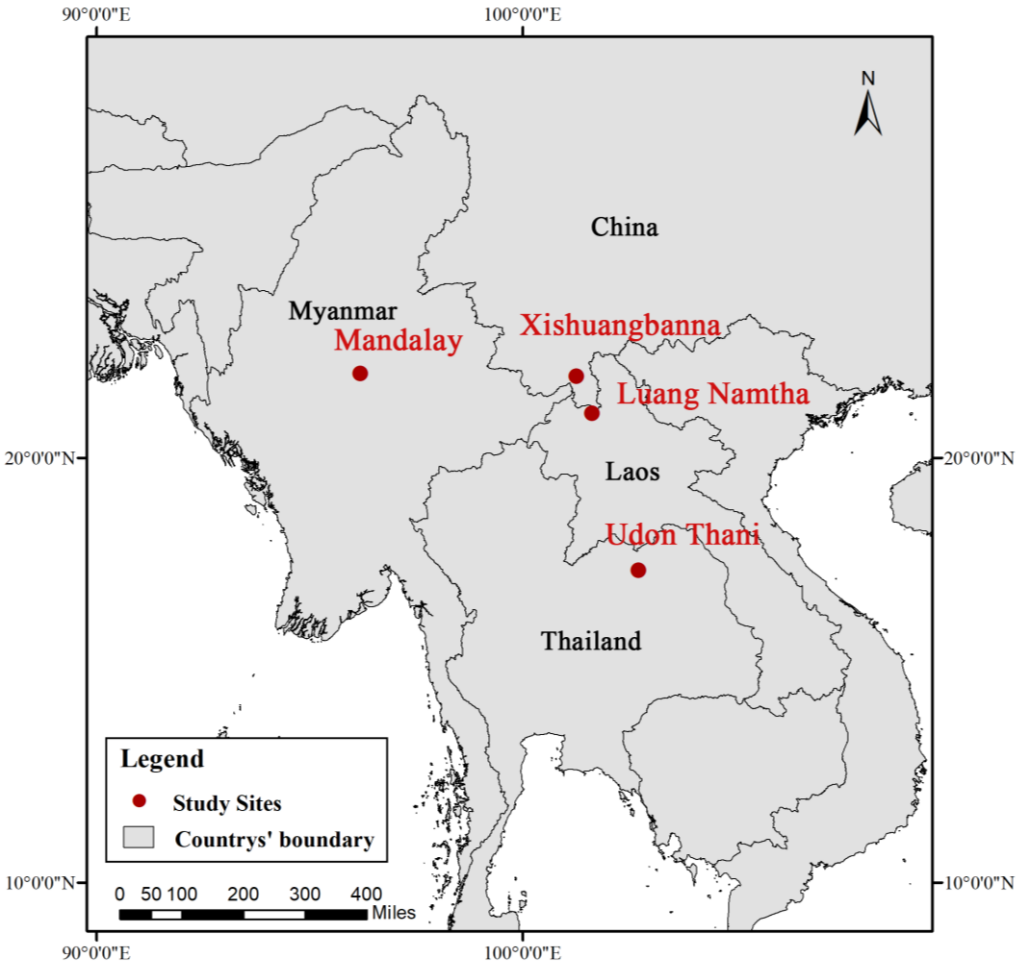

Figure 2. Sample sites located in China, Myanmar, Laos and Thailand

Ficus racemosa is a monoecious *Ficus* species which commonly occurred in Xishuangbanna with a wide distribution from India to Australia (Corner, 1965; Wu, 1995) and were abundant in the moist places and along the rivers. *F. racemosa* figs, which were located on the tree trunk, reached about 55 mm in diameter at maturity, with an average fig wall thickness of 4.97 mm (4.01-5.23 mm) (Zhen *et al*., 2005). Figs were also exploited by the other five species of non-pollinating fig wasps in Xishuangbanna visiting figs and ovipositing at different developmental phases. For example, *S. testacea* and then *Apocrypta* sp. first display oviposition during the A phase; *S. mayri* oviposits from late A, to B and early C phases; the *Ceratosolen* sp. pollinator only visits and oviposits in the B phase; and *S. agraensis* and *A. westwoodi* oviposit in the C phase (Figure 3 and 4). These differences in oviposition time are beneficial for the coexistence of multiple wasp species in a single fig species because of temporal niche differentiation to exploit fig resources.

Figure 3. Monoecious *Ficus racemosa* and its fig wasps

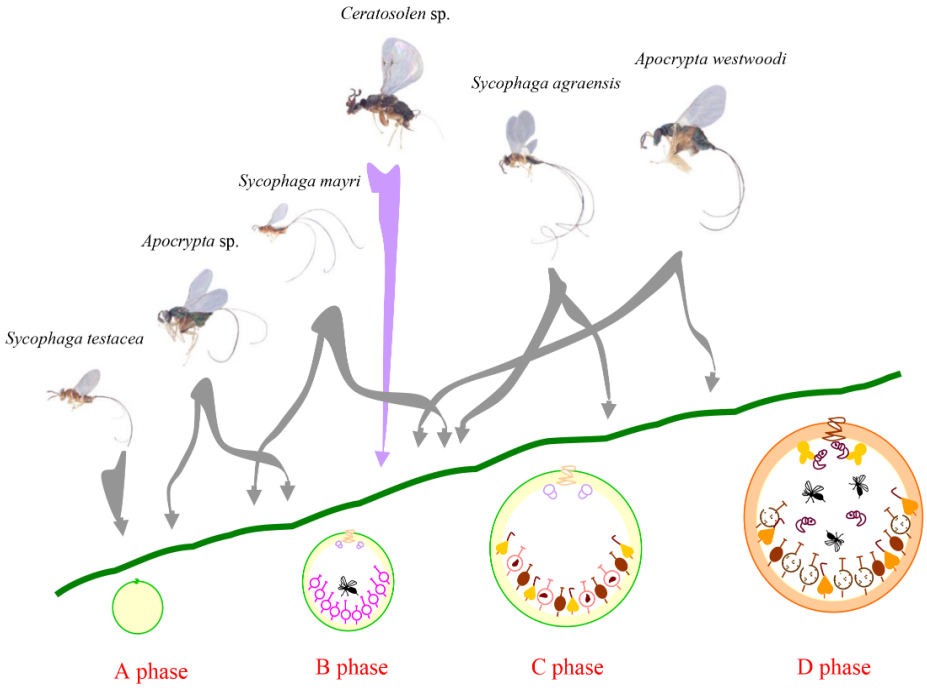

Figure 4. Developmental stages of figs and oviposition times of fig wasps in *Ficus racemosa*

3.2 Collection of D-phase figs of *Ficus racemosa*

From north Mandalay of Myanmar, Luang Namtha of Laos to south Udon Thani of Thailand, the D-phase figs of *F. racemosa* were collected within two weeks, total 40 D-phase

figs were collected from two trees in Mandalay, 17 D-phase figs were collected from one tree in Luang Namtha and 19 D-phase figs were collected from one tree in Udon Thani. More fruiting trees and D-phase figs were relatively hard to find. Fifty-eight D-phase figs were collected from two trees in Xishuangbanna. The length and diameter of each D-phase fig and thickness of fig wall were measured using Vernier caliper to the nearest hundredth of millimeter, and then each fig wasp placed into a nylon bag to allow the wasps to naturally emerge. The figs were preserved in 75% ethanol to count the flowers and seeds. Each fig was dissected into eight parts averagely. One part from them was selected to count the following categories: healthy galls (with exit hole), bladders (galls without hole and empty inside), unparasited flowers, male flowers, and seeds. All the results were multiplied with eight.

3.3 Collecting fig wasp from D-phase figs of *F. racemosa*

Fig wasp species were naturally emerged out per D-phase fig, 40 figs from two *F. racemosa* trees in Mandalay, 58 figs from two *F. racemosa* trees in Xishuangbanna, 17 figs from one *F. racemosa* tree in Luang Namtha, and we collected fig wasps from 32 figs from two *F. racemosa* trees in Udon Thani, but only 19 figs were brought to XTBG. Fig wasps per each fig were collected in time and saved in small tube with 75% ethanol, and then all wasp species were identified under the stereo-microscope (NTX3C-40X) to morphospecies level and counted the numbers of individuals.

3.4 Morphological traits measurement of fig wasps in *F. racemosa*

Thirty female fig wasps per species were sampled to measure the nine morphological traits about wasp body sizes by using stereo-microscope (NTX3C-40X) with a micrometer. Nine morphological traits were measured in this study, including head width (HW), head length (HL), thorax length (TL), wing width (WW), wing length (WL), front femur length (FFL), hind femur length (HFL), abdomen length (AL) and ovipositor length which ovipositor sheath was excluded for ovipositor measurement. The protocol referred to the picture from Liu et al., 2011 (Figure 5). However, both *Apocrypta* sp. and *S. mayri* had only very few individuals in Udon Thani so that the wasp body sizes were not measured.

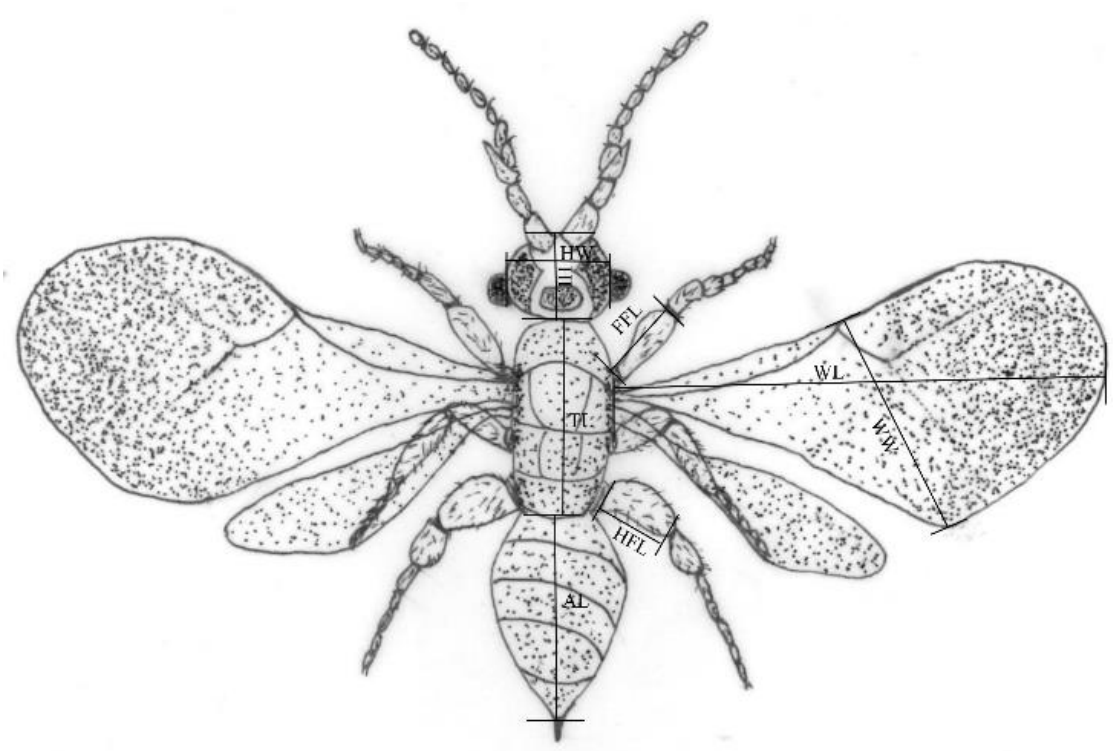

Figure 5. Morphological measurement traits of fig wasps in *Ficus racemosa*. HW: head width; HL: head length; TL: thorax length; WW: wing width; WL: wing length; FFL: front femur length; HFL: hind femur length; AL: abdomen length.

3.5 Collection of climate data

Matching the fig collection periods, the climate data were provided from the Xishuangbanna Station for Tropical Rainforest Ecosystem studies, including monthly average temperature (T_{ave}), monthly minimum temperature (T_{min}), monthly maximum temperature (T_{max}), and monthly total precipitation (P_{total}). Moreover, the same climate data of Mandalay, Luang Namtha and Udon Thani were downloaded from the WorldClim database (Fick and Hijmans 2017). We downloaded the historical monthly weather data of the three study sites from WorldClim database and used the spatial analysis tools to extract data and extract values to decimal using ArcMap in version 10.7.

3.6 Statistical Analysis

The mean values and standard error (Mean ± SE) of diameter, length, and thickness of D-phase figs of F. racemosa were calculated and used the one-way ANOVA to analyze the significant differences in four study sites. Principal component analysis (PCA) was used to reveal which morphological trait was the strongest indicator of wasp body size. One-way ANOVA was applied to test whether the species composition and abundance of fig wasps in *F. racemosa* were varied in different regions. TukeyHSD test analyzed the significant difference within groups. The relationship between fig diameter and total number of female flowers was analyzed using Pearson correlation. Simpson index (D) (Greenberg, 1956), Shannon index (He') (Shannon, 1948) and Pielou evenness index (Pielou, 1966) was used to calculate the species diversity of fig wasp community in four study sites. The Bipartite

package (Dormann *et al*., 2009) was applied to calculate network metrics. All analyses were performed in R version 3.5.3 by using easyGgplot2, ggplot2, dplyr packages.

To examine the extent of change in fig wasp community composition in different climate conditions, we calculated the taxonomic beta diversity (TBD) of all pairwise fig wasp communities using the abundance-based Bray-Curtis dissimilarity index in the R package 'betapart' (Baselga, 2013). To visualize the effect of climate conditions on fig wasp community structure, we performed two-dimensioanl non-parametric multidimensional scaling (NMDS) based on the values of TBD between sites using R package 'vegan' (Oksanen *et al*., 2019).

4 Results

4.1 Fig morphological traits of *F. racemosa* in four study sites

The fig diameter, length and thickness of *F. racemosa* were measured from four study sites. Among them, the largest fig sizes appeared in Xishuangbanna including fig diameter, length and thickness of fig wall followed by Luang Namtha, Mandalay and Udon Thani (Table 2.). The fig sizes varied geographically and Xishuangbanna and Luang Namtha had the larger fig sizes than other two study sites.

Table 2. Fig diameter, length and thickness of *Ficus racemosa* in four study sites (mean ± SE)

Location	Figs/trees	Diameter (mm)	Length (mm)	Thickness (mm)
Mandalay	40/2	33.10 ± 0.85 a	26.33 ± 0.42 a	2.96 ± 0.11 a
Xishuangbanna	58/2	41.10 ± 0.52 b	36.83 ± 0.59 b	5.58 ± 0.14 b
Luang Namtha	17/1	36.47 ± 0.68 c	31.87 ± 0.63 c	4.68 ± 0.15 c
Udon Thani	19/1	29.67 ± 0.53 d	24.26 ± 0.20 a	2.92 ± 0.08 a

Note: same letter represents to have no difference, different letters represent to have significant difference at the 0.05 level.

The numbers of female flowers, galls, seeds, and male flowers were compared. The number of female flowers varied in four study sites, including galls, bladders, unparasited flowers, and seeds. Number of male flowers in Luang Namtha and Udon Thani were higher than those in Xishuangbanna and Mandalay. Galls made by fig wasps and seed production had similar pattern. The larger number of galls appeared in Luang Namtha, and the lowest was in Mandalay. There was no significantly different in number of galls between Xishuangbanna and Udon Thani (Figure 6).

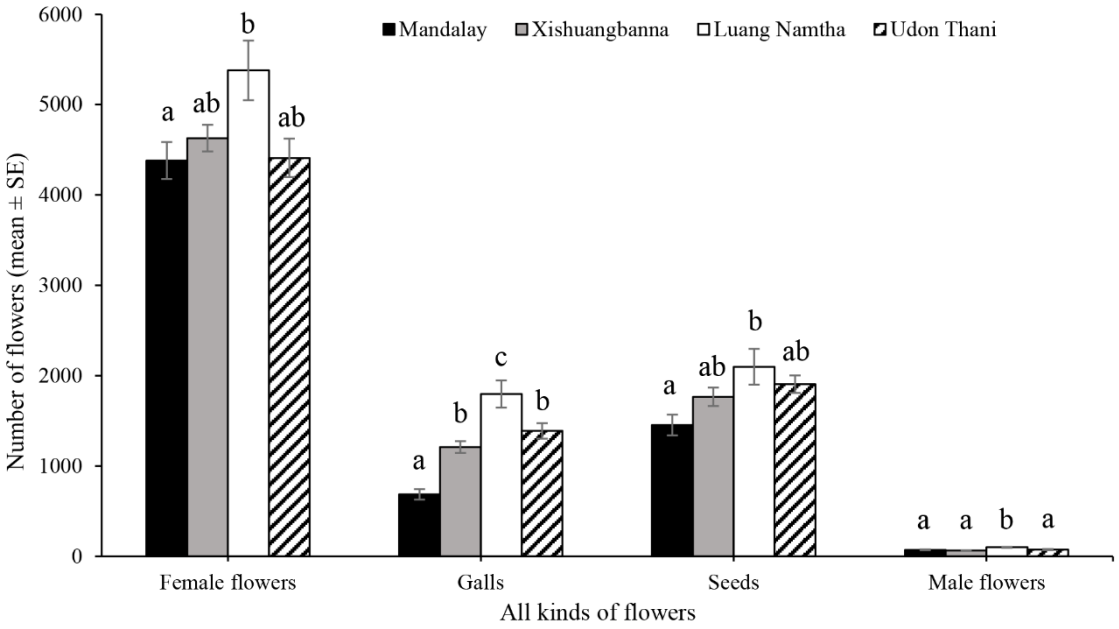

Figure 6. Fig morphology of *Ficus racemosa* in four study sites. Same letter on the bar chart represents to have no difference, different letters represent to have significant difference at the 0.05 level.

4.2 Relationship between fig diameter and female flowers of *F. racemosa* in four study sites

The average of the diameter of fig was 34.76 ± 0.51 (mean ± SE, n = 134) and the average of the total number of female flowers was 4619.76 ± 104.73 (mean ± SE, n = 134). The results from four study sites showed that there was a positive correlation between fig diameter and number of female flowers (Mandalay: $r = 0.76$, $P < 0.001$; Xishuangbanna: $r = 0.59$, $P < 0.001$; Luang Namtha: $r = 0.44$, $P = 0.073$; Udon Thani: $r = 0.83$, $P < 0.001$) (Figure 7). The large fig has more female flower resources.

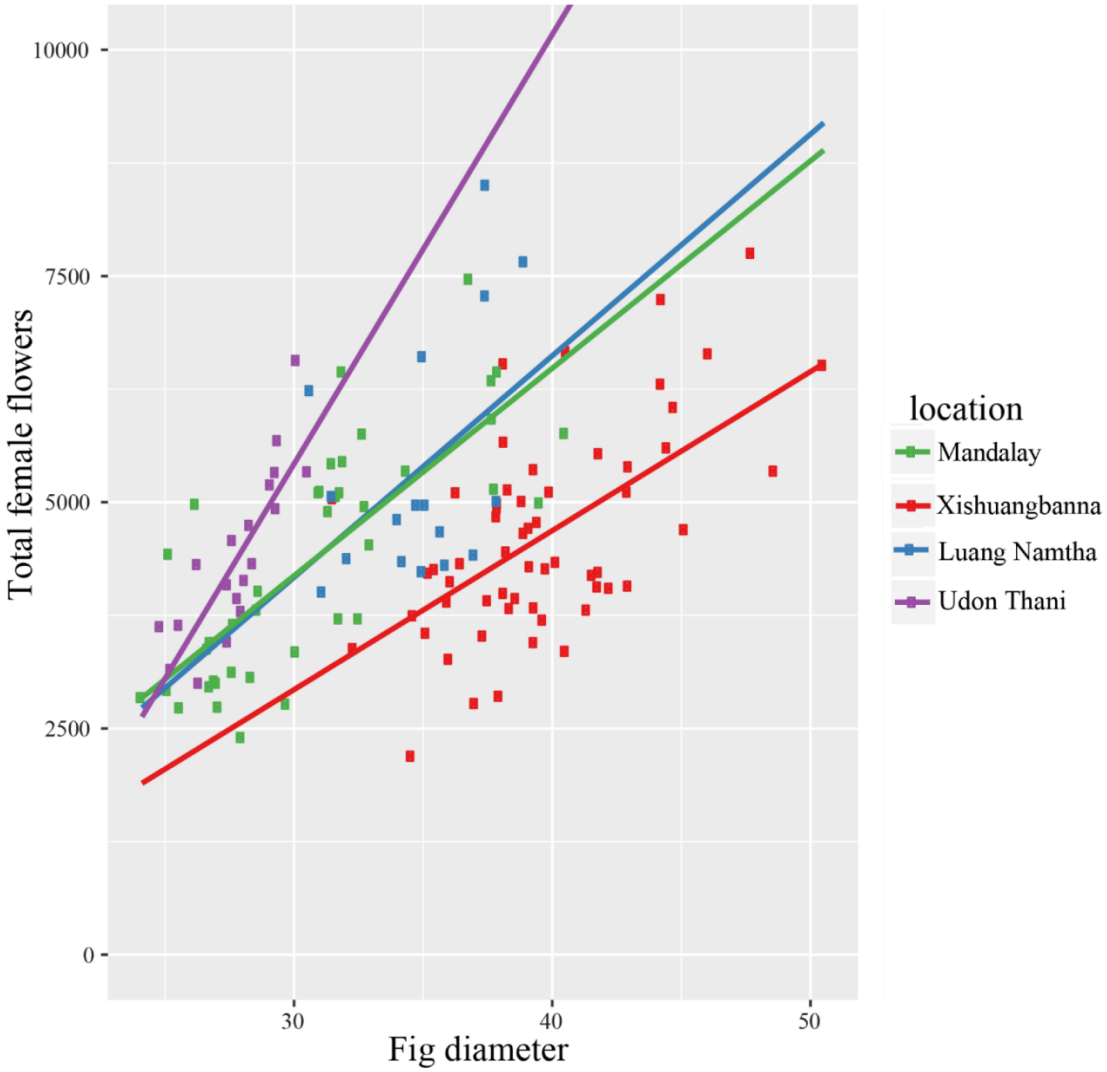

Figure 7. The relationship between fig diameter and number of female flowers in four study sites

4.3 Representative trait of fig wasp body sizes in *F. racemosa*

The same six species of fig wasps were identified in Mandalay, Xishuangbanna, Luang Namtha and Udon Thani, i.e., pollinating wasp *Ceratosolen* sp. and non-pollinating wasps, namely *S. testacea*, *S. mayri*, *S. agraensis*, *A. westwoodi* and *Apocrypta* sp.. The nine morphological body size traits were measured to compare the differences among four study sites. All morphological traits showed significantly different for the six species of fig wasps among four study sites. Principle component analysis of the nine morphological traits showed a mean item complexity of 1, this implied that one component was enough the representative of wasp sizes. The PC1 values for the nine morphological body sizes were shown in Table (3). The wing length trait stably demonstrated the highest values. As such, wing length was used to represent wasp body size for the six fig wasp species found in *F. racemosa*.

Table 3. PC1 values of principle component analysis for nine morphological traits of six fig wasp species in *Ficus racemosa* in four study sites

Trait	*Ceratosolen* sp.	*S. testacea*	*Apocrypta* sp.	*S. mayri*	*S. agraensis*	*A. westwoodi*
Head width	0.32	0.86	0.95	0.92	0.81	0.82
Head length	0.85	0.78	0.94	0.89	0.71	0.85
Thorax length	0.91	0.86	0.91	0.95	0.86	0.90
Wing width	0.86	0.94	0.98	0.95	0.94	0.96
Wing length	0.92	0.97	0.98	0.95	0.94	0.97
Front femur length	0.82	0.79	0.92	0.86	0.69	0.89
Hind femur length	0.84	0.91	0.96	0.83	0.90	0.95
Abdomen length	0.40	0.74	0.58	0.81	0.63	0.55
Ovipositor length	0.87	0.70	0.99	0.89	0.94	0.95

Wing length was regarded as the representative trait of body sizes and used to compare the differences of fig wasps in four study sites. The wing lengths of all six fig wasp species in Xishuangbanna were the largest, and the smallest ones appeared in Mandalay, and then the body sizes of fig wasps were secondary in Luang Namtha, and larger than those in Udon Thani. Moreover, the body sizes of *Ceratosolen* sp., *S. testacea*, *S. mayri* and *S. agraensis* were significant variations in different study sites. However, there was no significant difference in wing length of *Apocrypta* sp. between Xishuangbanna and Luang Namtha, and *A. westwoodi* between Luang Namtha and Udon Thani (Figure 8).

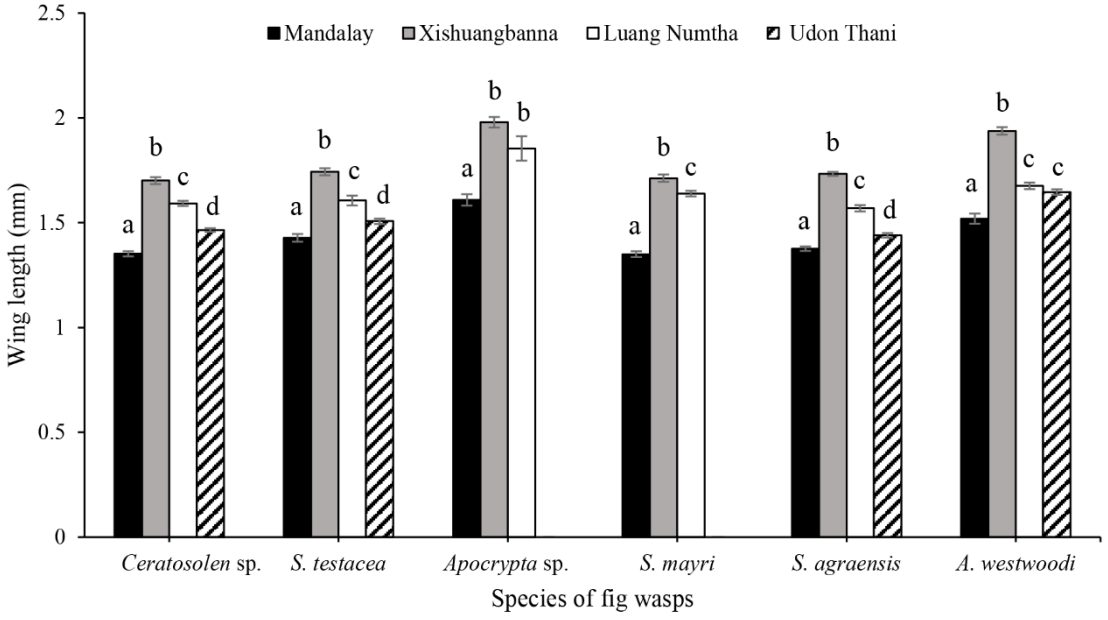

Figure 8. Differences in body sizes of six species of fig wasps in *Ficus racemosa* in four study sites. Same letter on the bar chart represents to have no difference, different letters represent to have significant difference at the 0.05 level.

4.4 Species composition of fig wasp communities in *F. racemosa* in four study sites

In total, 22,712 fig wasps were collected from 40 figs in Mandalay, 56,547 fig wasps were collected from 58 figs in Xishaungbanna, 29,094 fig wasps were collected from 17 figs in Luang Namtha and 35,793 fig wasps were collected from 32 figs in Udon Thani. The community composition differed among four study sites. The pollinator *Ceratosolen* sp. was the dominant fig wasp species and showed highest percentages in all sites, accounting for 44.36% (10,076 wasps) in Mandalay, 76.48% (43,245 wasps) in Xishuangbanna, 89.62% (26,073 wasps) in Luang Namtha, and 94.39% (33,784 wasps) in Udon Thani. Besides, the composition of non-pollinating fig wasps was also different among sites. The percentage of each non-pollinating fig wasps were less than 7% in Xishuangbanna, less than 5 % in Luang Namtha, and less than 4% in Udon Thani, respecitvely. Among them, *S. testacea* showed the largest composition (6.54%), followed by *A. westwoodi* (6.35%), *S. mayri* (6.09%), *S. agraensis* (4.21%) in Xishuangbanna. In Luang Namtha, *A. westwoodi* was the largest composition (4.16%) and followed by *S. testacea* (3.17%), *S. agraensis* (2.24%), and *S. mayri* (0.73%). In Udon Thani, *A. westwoodi* was the highest composition (3.44%) among non-pollinating fig wasps, and then followed by *S. agraensis* (1.35%), *S. testacea* (0.70%), and *S. mayri* (0.11%). The composition of non-pollinating fig wasps in Mandalay showed the highest composition in fig wasp community among four study sites, with *A. westwoodi* showing the highest percentage (24.38%), *S. mayri* (14.04%), *S. agraensis* (11.76%), and *S. testacea* (3.96%). Moreover, *Apocrypta* sp. showed same lowest composition, and all less than 2% in all study sites (Figure 9).

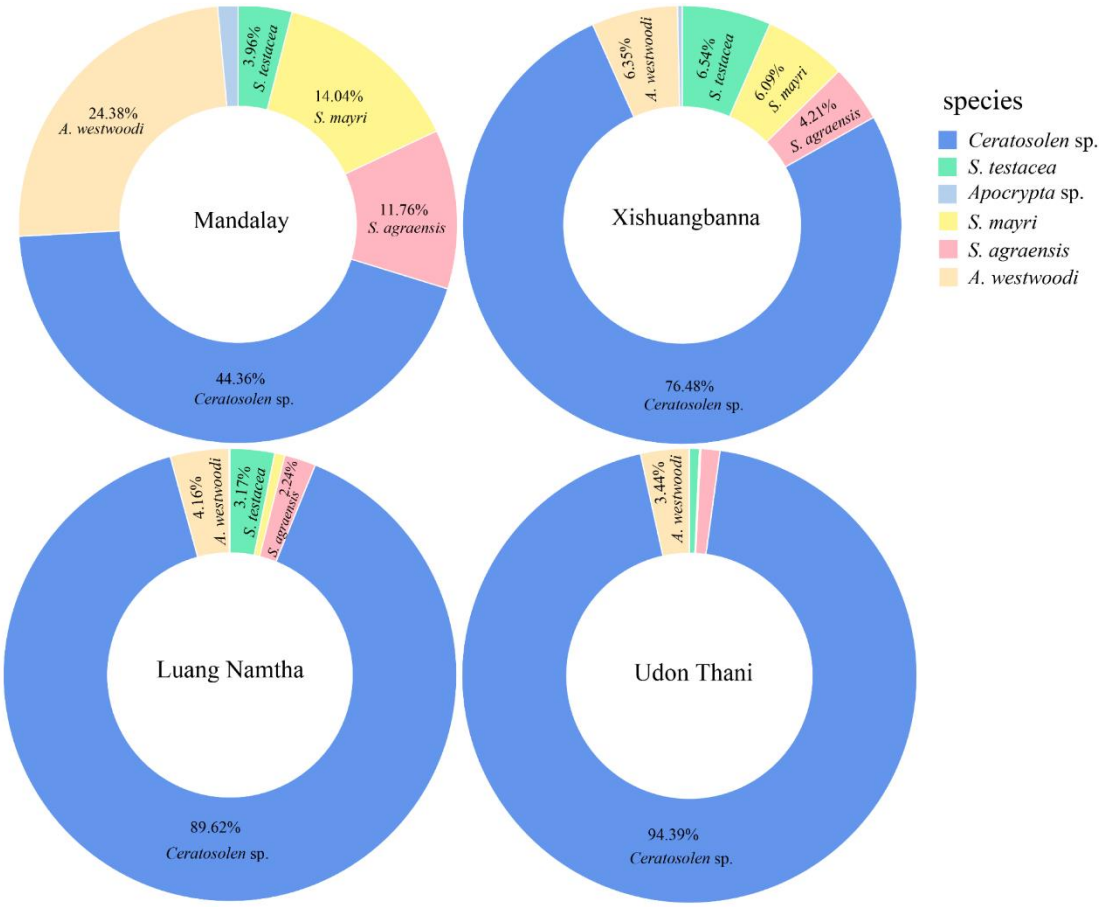

Figure 9. Species composition of fig wasp communities in *Ficus racemosa* in four study sites

4.5 Abundance variations of fig wasp communities in *F. racemosa* in four study sites

In the fig wasp community of *F. racemosa*, *Ceratosolen* sp. was the most abundance, accounting for an average of 251.90 ± 45.75 (SE, n = 40) wasps in Mandalay, 745.60 ± 59.08 (SE, n = 58) wasps in Xishuangbanna, 1533.71 ± 164.06 (SE, n = 17) wasps in Luang Namtha, and 1055.75 ± 74.05 (SE, n = 32) wasps in Udon Thani. The abundances were significantly different in four study sites (F = 40.29, P < 0.001). Non-pollinating fig wasps were also varied among sites. The number of *S. testacea* in Xishuangbanna (63.81 ± 7.35) was significantly higher than other three sites (Mandalay: 22.50 ± 3.16, Luang Namtha: 54.29 ± 24.20, Udon Thani: 7.88 ± 2.17) (F = 10.85, P < 0.001). Besides, *A. westwoodi* was observed with the higher abundance in Mandalay than other three sites (F = 18.96, P < 0.001) (Mandalay: 138.45 ± 10.47, Xishuangbanna: 61.86 ± 8.16, Luang Namtha: 71.18 ± 15.32, Udon Thani: 38.50 ± 8.86). *Apocrypta* sp. showed lower abundance in all study sites (Mandalay: 8.48 ± 1.53, Xishuangbanna: 3.28 ± 0.94, Luang Namtha: 1.41 ± 0.90, Udon Thani: 0.16 ± 0.08). The abundance alone was higher in Mandalay than other three study sites (F = 9.883, P < 0.001) (Figure 10).

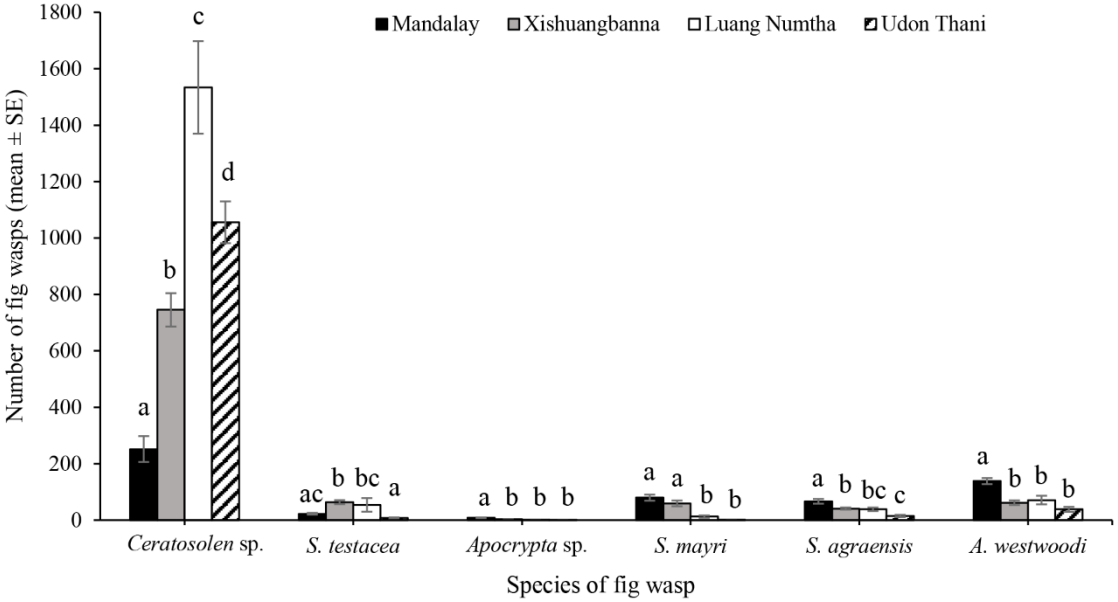

Figure 10. Species abundance of fig wasp communities in *Ficus racemosa* in four study sites. Same letter on the bar chart represents to have no difference, different letters represent to have significant difference at the 0.05 level.

4.6 Species diversity of fig wasp communities in four study sites

The indexes of species diversity were calculated, the results showed that Simpson index (D), Shannon index (H_e') and Pielou evenness index (J_e) were all the highest in Mandalay, followed by Xishuangbanna, Luang Namtha, as well as the lowest indexes appeared in Udon Thani (Table 4). There was a trend that non-pollinating fig wasps increased with latitudes so that species diversity also increased from south to north distribution.

Table 4. Species diversity of fig wasp communities in four study sites

Study sites	Simpson index (D)	Shannon index (H_e')	Pielou evenness index (J_e)
Mandalay	0.708	1.423	0.794
Xishuangbanna	0.401	0.881	0.491
Luang Namtha	0.194	0.467	0.261
Udon Thani	0.108	0.272	0.152

4.7 Coexistence networks of fig wasp communities in *F. racemosa* in four study sites

In *F. racemosa*, six species of fig wasps coexisted and demonstrated the same species composition in Mandalay, Xishuangbanna, Luang Namtha and Udon Thani. However, interspecific interaction was different, resulting in different coexistence networks of fig wasp communities in each study site. The coexistence networks of fig wasp communities in four study sites similarly consisted of six nodes, 15 edges, one connection, one global clustering coefficient, and five node connections. However, the network diameters in Mandalay, Xishuangbanna, Luang Namtha and Udon Thani were 40, 57, 6 and 8, respectively. Each fig wasp species exhibited species interaction. The matrix temperatures of fig wasp communities were 0.29 in Mandalay, 2.22 in Xishuangbanna, 0.72 in Luang Namtha and 5.68 in Udon Thani (Figure 11).

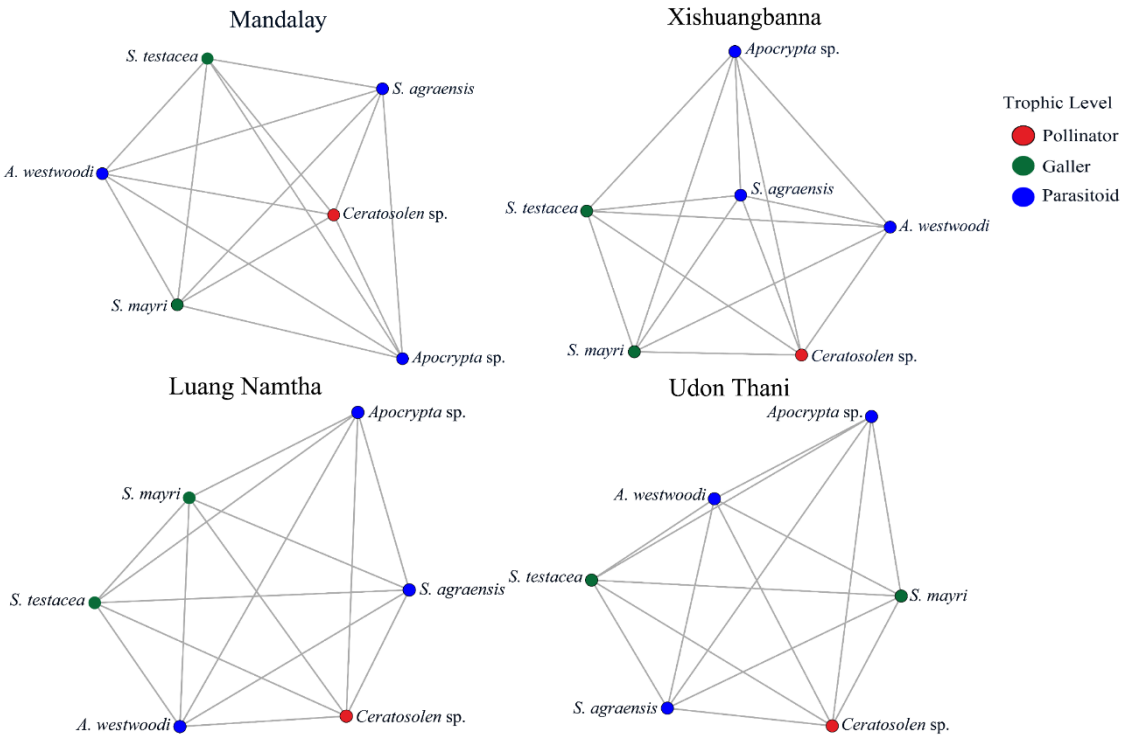

Figure 11. Species interaction networks of fig wasps in *Ficus racemosa* in four study sites

4.8 Fig wasp community structure of *F. racemosa* in four study sites

All the temperature variables are highly correlated with each other (Spearman's correlations between variables and responses |r|>0.8). We selected the variable with the highest explanatory power (T_{min}) to present the temperature. No significant correlation was found between P_{total} and beta diversity (GLM, R2=0.07, P = 0.24). Therefore, we only use T_{min} to represent climate conditions in the following results.

Based on the observation data collected from four study sites in 2018, we examined the fig wasp community structure in different sites. The result showed a clear separation between Mandalay and the rest of the study sites (Figure 12). The separation was largely determined by the temperature not the geographic distance, highlighting the importance role that climate has played to shape the observed fig wasp community structure.

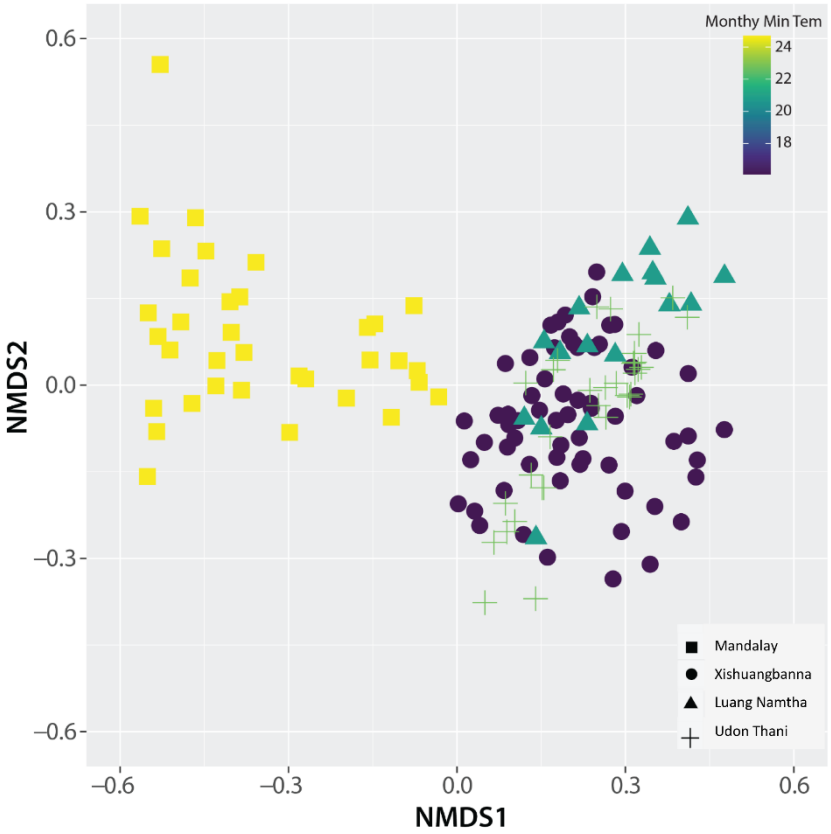

Figure 12. Nonmetric multidimensional scaling (NMDS) ordination of each fig collected from four study sites based on taxonomic beta diversity. Color indicates the minimum temperature of the month when figs were collected.

5. Discussion

In this study, the D-phase figs of *F. racemosa* were collected during the similar period in 2018 from four study sites, including Mandalay in Myanmar, Xishuangbanna in China, Luang Namtha in Laos, and Udon Thani in Thailand, the latitudes range from N 21.59 to N 17.21. The results showed that fig sizes varied in different regions, thus the figs were larger in Xishuangbanna and Luang Namtha than those in Udon Thani and Mandalay. It is known that fig sizes are related to female flower resources. In general, large figs have more female

flowers, and produce more fig wasps and seeds (Peng *et al*., 2010). Our results support this opinion. In four study sites, *F. racemosa* was not only pollinated by the *Ceratosolen* sp., but also exploited same five species of non-pollinating fig wasps in the Indo-China Peninsula, which the species composition of fig wasps was different to Indian continent (Kobmoo *et al*., 2010), also implying that the pollinator and non-pollinators in same *Ficus* species have long-term coevolutionary history in same regions, and different regions could go through different evolutionary routes because of geographic isolation (Bain *et al*., 2016).

In different biogeographic regions, various fig sizes and female flowers could provide different nutrition for fig wasp development. In this study, the results showed that six species of fig wasps in *F. racemosa* had various body sizes, nine morphological traits about wasp body sizes were measured, and firstly confirmed that the wing length was the best trait representing the wasp body size by principle component analysis. In previous studies, head traits were used to represent wasp body sizes because of no wing measurement (Dunn *et al*., 2008, Liu *et al*., 2011, Zhao *et al*., 2014). In *F. racemosa*, six wasp species were all the largest in Xishuangbanna, and the smallest wasps appeared in Mandalay. A recent study reported that the ovipositor of *Philotrypesis* wasps on *F. hirta* is longer in northern Guangdong, Fujian, and southern Jiangxi provinces than those in southern Guangdong, Hainan, and Guangxi provinces in China (Yu *et al*., 2018), suggesting that large fig diameter and fig wall thickness may shape ovipositor length of non-pollinating fig wasps. In this study, we compared the ovipositor lengths of the five non-pollinating fig wasp species in *F. racemosa*. Through small fig sizes in Mandalay were exploited by more non-pollinating fig wasps, but did not get the consistent pattern.

Fig wasp community structure and genus-level composition are largely conserved over a wide geographic range but can show convergent structure of multitrophic communities (Segar *et al*., 2013, Darwell *et al*., 2018). However, the species composition and community structure of fig wasps in *F. racemosa* were confirmed to be the geographic variation in this study, and showed a trend that non-pollinating fig wasps increased with latitudes, which species diversity increased from south to north distribution. Moreover, the coexistence networks of fig wasp communities were also variation, and the matrix temperatures of fig wasp communities were higher in Udon Thani and Xishuangbanna, where both sites indeed had more human activity so that fig wasp communities could encounter more disturbance and were less stable.

The ecological and evolutionary characteristics of competitors in communities are important fundamental factors of resource partitioning (Bonsall *et al*., 2004). For fig wasps, ovipositor morphology is correlated with the thickness of the fig wall and is regarded as an important morphological trait (Ghara *et al*., 2011, Elias *et al*., 2018). Fig size varies with different phases of fig development time. Most non-pollinating fig wasps lay eggs from the outside of the fig, so the length of their ovipositor can differ according to their oviposition time (Kerdelhue and Rasplus, 1996, Darwell *et al*., 2018). Early-arriving gallers have shorter ovipositor length, and lay eggs at the initial stages of fig development, whereas late-arriving parasitoids have longer ovipositors and usually oviposit during late fig development (West *et al*., 1996, Kerdelhue *et al*., 2000). The differentiation in oviposition times allows multiple species of fig wasps to coexist in one fig species. Monoecious *Ficus* species harbor multiple species of non-pollinating fig wasps, with the general pattern to exploit multiple figs but

reproduce few individuals (Kerdelhue *et al*., 2000, Compton *et al*., 2018, Darwell *et al*., 2018). In contrast, the non-pollinating fig wasps of *F. racemosa* have large population sizes and easily coexist together. In additional to temporal heterogeneity of oviposition, the pattern and network of interspecific interaction can also influence the stability of fig wasp communities.

Previous study identified a latitudinal effect on fig wasp communities of *F. racemosa*, with northern communities in Liuku having fewer pollinating fig wasps and more non-pollinating fig wasps per fig than those in southern Xishuangbanna (Chen *et al*., 2018). The altitude of Mandalay is the northest site among four study sites, which the community structure of fig wasps in *F. racemosa* is similar to that in Liuku. Whereas, the altitude of Udon Thani are the southest site, and had more pollinators. Thus, geographic heterogeneity could drive the differences in the structure and species abundance of fig wasp communities of *F. racemosa* among four study sites. The reasons could result from different climate conditions or habitats. Pollinators and gallers compete for the same female flower resources, and the interaction between gallers and parasitoids may prevent the over-utilization of female flowers to maintain stable fig-fig wasp mutualism (Kerdelhue *et al*., 2000, Compton *et al*., 2018). Additionally, more pollinator are found in the sample figs of Xishuangbanna, while more non-pollinators appear in north Liuku, implying that different species of fig wasp could have different ability to adapt environmental change (Chen *et al.*, 2018). In this study, the ecological networks were used to determine differences in fig wasp communities among sites. The results showed some similar traits in four study sites, such as the same numbers of nodes, edges, connection, and global clustering coefficients, suggesting similar species numbers and interspecific interactions of fig wasps on *F. racemosa* at all four study sites. However, the matrix temperatures of fig wasp communities in Udon Thani and Xishuangbanna are higher than those in Mandalay and Luang Namtha, implying that the interspecific interactions resulted in higher disturbance in Xishuangbanna and Udon Thani and greater fig wasp community instability than that found in Mandalay and Luang Namtha.

Fig wasps are very tiny and have the short longevity during adult period, which are more sensitive to climate change. In equatorial tropics, the high temperature is the limited factor, thus an increase of 3°C could markedly decrease active adult lifespan (Jevanandam *et al*., 2013). Moreover, low temperature is a limited factor in the northern edge leading to a slow fig development which could results to few crops in each year, few seed and few pollinator production and more non-pollinators (Chen *et al*., 2018). We compared the climate effects on fig wasp community, including monthly average temperature, monthly minimum temperature, monthly maximum temperature and monthly total precipitation, and found that monthly minimum temperature was the most important factor, which can clearly separate the community structures of fig wasps in *F. racemosa* in different sampling years in Xishuangbanna and four study sites.

In general, increasing temperature affects the physiology of the flowering plants, and evolving the alteration of flower production, nectar and pollen production (Koti *et al*., 2005, Petanidout and Smets, 1996, Saavedra *et al*., 2003). The structure of fig wasp composition also depends on fig volatiles to find the adaptive figs for oviposition, different habitats show various chemical cues, resulted in having different fig wasp communities (Proffit *et al*., 2007). At present, human disturbance and climate change are intensifying. The assessment of 15

years interval, the fig wasp communities in *F. racemosa* showed that the pollinators significantly decreased while non-pollinators increased in same region. Moreover, from south to north study sites, pollinators also decreased and non-pollinators increased. The possible reason is related to the biological difference of fig wasps, which the life span of pollinating fig wasp has only 1-2 days, while non-pollinating fig wasps have more longevity (Peng *et al*., 2005, Dunn *et al*., 2008). This could lead to pollinators and non-pollinators to have different temperature tolerance so that non-pollinators are better adaption to human activity and climate change. Our results strongly indicate that climate especially temperature plays an important role in shaping fig wasp community. These results provide basic information for community stabilization and species conservation; however, the reasons for network differences require further study. Furthermore, it is worth comparing the thermal and cold tolerances among fig wasps, and analyzing the effects of temperature on fig wasp community.

6. Conclusion

F. racemosa is a monoecious fig species which is widely distributed from India to Australia. *F. racemosa* is pollinated by *Ceraotsolen* wasps, and there has four species of *Ceratosolen* wasps which pollinate *F. racemosa* in different geographic regions. In this study, the variation of fig wasp communities of *F. racemosa* were compared the variations of fig wasp communities in Mandalay (Myanmar), Xishuangbanna (China), Luang Namtha (Laos) and Udon Thani (Thailand) during the similar period. The fig diameter, length and fig wall thickness of D-phase figs were measured, and then collected fig wasps per fig to identify and count them. Furthermore, the species composition, abundance, diversity and coexistence networks of fig wasp communities were compared, and analyze the effects of climate factors on fig wasp community. Main conclusion are as follows:

We identified to have one pollinator species and five species of non-pollinating fig wasps to coexist in *F. racemosa* in Mandalay, Xishuangbanna, Luang Namtha and Udon Thani, suggesting that the pollinator and non-pollinators to be long-term coevolution in Indo-China Peninsula so that *F. racemosa* had not only same pollinator, but also shared same species composition of fig wasps. However, the fig sizes and female flower resources were different in four study sites, leading to produce different numbers of fig wasps and wasp body sizes. The nine morphological traits about body sizes of fig wasps were measured, and PCA analysis showed wing length to have the highest values, which can represent wasp body sizes for six wasp species. There were larger wasp body sizes in Xishuangbanna and Luang Namtha than in Mandalay and geographic regions.

In different geographic regions, the species abundance, diversity and coexistence networks of fig wasp communities in *F. racemosa* are varied, which the pollinator *Ceratosolen* sp. was the dominant species in fig wasp communities among four study sites. The composition of non-pollinating fig wasps gradually increased with latitudes so species diversity was the highest in northern Mandalay, and the lowest in southern Udon Thani. Moreover, the coexistence networks of fig wasp communities exhibited similar number of nodes, edges, connections, and global clustering coefficients, but there were the higher matrix temperatures in Udon Thani and Xishuangbanna, where both sites indeed had more human disturbance, and were not advantage to maintain the stabilization of fig wasp community.

Fig wasps are very sensitive to environmental and climate changes. Through comparing climate factors among four study sites, the monthly minimum temperature was confirmed to be the most important factor, which can clearly separate the community structures of fig wasps in *F. racemosa* in different sampling years in Xishuangbanna and four study sites. The pollinator and non-pollinators could have different thermal and cold tolerances, and non-pollinators showed better adaption to human disturbance and climate change.

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Appendix

Table A 1. ANOVA results for fig Morphology of *Ficus racemosa* in four study sites

		Sum of Squares	Df	Mean Square	*F*	*P*
Female flowers	Between Groups	12910263	3	4303421	3.06	<0.05
	Within Groups	182580002	130	1404462		
	Total	195490265	133			
Galls	Between Groups	16990879	3	5663626	26.11	<0.001
	Within Groups	28201814	130	216937		
	Total	45192693	133			
Seeds	Between Groups	6025932	3	2008644	3.81	<0.05
	Within Groups	68531150	130	527163		
	Total	74557082	133			
Male flowers	Between Groups	16945	3	5648	7.69	<0.001
	Within Groups	95501	130	735		
	Total	112446	133			