東海大學生命科學系碩士論文

正榕小蜂間的共存機制

The coexistence mechanisms among fig wasps associated with *Ficus microcarpa.*

研究生：劉佩瑜

Liu, Pei-Yu

指導教授：林宜靜、孫義方

Lin, Yi-Ching、Sun, I-Fang

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摘要

榕果與榕果小蜂系統為榕屬植物與其授粉蜂間的互利共生。除了授粉蜂外，也有許多非授粉蜂利用榕果資源，並和授粉蜂競爭產卵空間。此複雜的系統如何維持平衡一直是研究榕果與榕小蜂系統的核心問題。寄生蜂寄生壓力假說指出授粉蜂為了避免被寄生蜂寄生，產生偏好產卵在內層胚珠的行為，因而不過度剝削榕果。棲位分化假說認為授粉蜂與非授粉蜂會藉由空間或時間上的分化來維持共存。此研究的目的是為了檢驗寄生蜂寄生壓力假說能否解釋種子與授粉蜂間的分層現象，並檢驗授粉蜂與造癭蜂之間是否存在棲位分化的現象。

我的結果發現授粉蜂在內層與外層的寄生率有顯著差別，此結果符合寄生蜂寄生壓力假說。授粉蜂和造癭蜂間在產卵位置上有空間分化的現象，授粉蜂偏好在短花柱雌花、榕果的中間部位產卵;而造癭蜂偏好產卵在長花柱雌花、榕果底部或無偏好。在研究期間，我將文理大道上的正榕族群依照其開花物候分成四個開花季，觀察小蜂族群在四個開花季間的族群動態有無變化。我的結果顯示授粉蜂與造癭蜂的族群動態在不同開花季間上有差異，但還需要更長的研究時間才能證明小蜂間的確存在時間上的分化。

The coexistence mechanisms among fig wasps associated with *Ficus microcarpa*

Abstract

Fig-fig wasp mutualism is a symbiotic interaction between *Ficus* and its pollinating fig wasps. Besides pollinating wasps, many non-pollinating fig wasps also utilize the same figs and compete with pollinating wasps for breeding sites and plant resources. How does this complicated system maintain its stability has intrigued ecologists for a long time. The parasite pressure hypothesis indicates that parasitoids contribute in stabilizing mutualism by forcing pollinators to oviposit in inner ovules and do not over-exploit fig. The niche partitioning hypothesis proposes that parasites and pollinators can coexist through spatial or temporal separation. The aims of my study were to examine whether parasite pressure hypothesis can explain the stratification of seeds and pollinators, and to test if niche partitioning between pollinators and gallers do exist in fig-fig wasps system of *F. microcarpa*.

My results indicated there were significant differences in parasitism between inner and outer ovules, which are consistent with the parasite pressure hypothesis. My results also suggested there was spatial separation in oviposit sites between pollinator and non-pollinator wasps. Pollinators prefer to oviposit in inner ovules and the central region of a fig. In contrast, gallers prefer to oviposit in outer ovules and the basal or randomly in different fig regions. In my investigation period, I defined four crops of *F. microcarpa* in Campus mall according to their flowering phenology, and investigated whether wasps' population dynamics varied between crops. I found population of pollinators and galler *Odontofroggatia* fluctuated between crops. Although abundance of pollinators and gallers differed significantly between crops, the observation period was not long enough to have concrete evidences to support temporal partitioning hypothesis.

Introduction

Mutualism describes the interactions between species that benefit each other and increase fitness of both parties though this relationship. One of these interactions, *Ficus* species and its mutualistic partner, Agaonidae wasps, provides an excellent example of a coevolutionary relationship. Previous studies suggested this mutualistic relationship between figs and pollinating wasps might have originated in the middle of Cretaceous (Lopez-Vaamonde et al. 2009, Machado et al. 2001).

About 750 species of *Ficus* have been described (Berg 1989), with diverse life form such as trees, shrubs, climbers, and vines (Harrison 2005). Fig trees are native to tropical and subtropical forests. Due to its all-year-round fruiting phenology, they often regarded as a keystone species in forests, providing food resources to a large fauna from invertebrates to mammals (Harrison 2005; Shanahan et al. 2001). The mutualism between figs and pollinating wasps bind various animals altogether.

The syconium (also called fig) of *Ficus* species is urn-shape and hollowed, and numerous flowers grow on inside surface of enlarged receptacle. The only opening of fig is the ostiole, and it opens slightly when female flowers mature. According to the length of style, the flowers of figs can usually divided into two types: inner layer ovules (short-styled) and outer layer ovules (long-styled). As female flowers are receptive (female phase), pollen-loaded pollinating wasps enter the fig through the ostiole. This phase usually last only for one to two days, so as the life longevity of pollinating wasps. Therefore, the timing of wasps emergence and female flowers maturation must be matched precisely to ensure the persistence of both populations. As a result, the within-tree synchrony and between-tree asynchrony is the key to maintain fig wasp populations as well as fig tree populations (Corlett 1984, Smith and Bronstein 1996, Spencer et al. 1996).

After enter figs, pollinators insert their ovipositor through style then lay eggs in ovules (Galil and Eisikowitch 1968). During or after oviposition, a pollinator cleans herself and pollen falls from her body, and so pollinates female flowers. In the interfloral phase, figs and wasp larvae both grow for several weeks. Then, when male flowers mature, wasps are also ready to emerge from figs. Apterous male pollinating wasps emerge first, and mate with female wasps while they are still inside galls. After mating with female pollinating wasps, male pollinating wasps chew a way to escape figs. Next, female pollinating wasps emerge from galls and they carry pollen actively or passively. These female pollinating wasps escape from figs with pollen and locate another fig that is in female phase, to start the next life cycle. Most pollinators are host-specific (Ramirez 1970, Rasplus 1996, Wiebes 1979), though there are some exceptions (Kerdelhué et al. 1997, Ware and Compton 1992). In consequence, pollinating wasps depend entirely on figs.

Parasitic wasps are dependent on their host, figs or fig wasps (Bronstein 1991, Bronstein 1999, Compton et al. 1994, Kerdelhué and Rasplus 2000), but show reduced host species-specificity (Weiblen and Bush 2002, Marussich and Machado 2007) than do pollinating wasps. The association between parasitic wasps and their host may be as ancient as the origin of fig and pollinator symbiosis in some lineages, while some species invaded this mutualism more recently (Cook and Segar 2010, Cruaud et al. 2011). The parasitic wasps provide no pollination service for figs (but see Jousselin et al. 2001a); moreover, they lower the fitness of pollinators and figs by decreasing the numbers of pollinators and viable seeds (Kerdelhué and Rasplus 1996, Peng et al. 2010, West and Herre 1994, West et al. 1996). Even though parasitic wasps are ubiquitous in figs and fig wasp systems, these groups received less attention and therefore we have very little knowledge about them. Since parasitic wasps have negative effects on both figs and fig-wasps, the question of why they do not break down this mutualism has puzzled ecologists for a long time (Herre et al 2008).

Despite the fact that figs rely on pollinating wasps to pollinate its flowers, and pollinating wasps rely on figs to provide resources and space for its offspring, there is an apparent conflict between the two partners (Janzen 1979b). In theory, natural selection will favor both figs and pollinators to maximize their individual fitness by produce as many offsprings as possible. However, pollinators produce their offsprings at the cost of seed production. Thus natural selection in wasps for increased fitness could destroy this mutualistic relationship if there was no mechanism to prevent pollinating wasps from over-exploiting figs. Pollinating wasps die soon after laying eggs, so they cannot receive any direct benefit by pollinating figs. In this situation, natural selection would favor pollinating wasps to lay as many eggs as they can to maximize their fitness. On the contrary, selection will favor fig trees to limit the number of ovules being oviposited by pollinating wasps. Field observations indicated the number of wasp offsprings and seeds usually reach a constant ratio in figs (Cook and Power 1996, Dunn et al. 2008, Herre 1989, Herre and West 1997). In addition, seeds and pollinators show stratification in location: offsprings of pollinating wasps are usually located in inner layer ovules while seeds usually located in outer layer ovules (Anstett 2001, Galil and Eisikowitch 1969, Janzen 1979a, Jousselin et al. 2001b). This implies that there must be some mechanisms prohibiting or discouraging pollinating wasps from laying eggs in outer ovules and so preventing wasps from over-exploiting figs.

Several hypotheses have been proposed to explain the stable exploitation of figs by pollinators. The *unbeatable seeds* hypothesis suggests that outer layer ovules are protected by physical or chemical barriers result in pollinating wasps being unable to oviposit in these seeds (Anstett et al. 1996). The *insufficient eggs* hypothesis proposes that fig trees limit the number of foundresses entering figs to avoid over-exploitation by wasps (Nefdt and Compton 1996). The *short ovipositor* hypothesis posits that due to morphological limitation, foundress could not reach outer layer ovules (Ganeshaiah et al. 1995, Nedft and Compton 1996). Yu et al. (2004) proposed the idea of *Optimal foraging strategies* to explain the partitioning of seeds and pollinator offspring. Their model showed that when several biological factors were considered, such as pollinator life longevity and handling time of oviposit in inner and outer ovules into the model, assembling eggs in inner ovules seems to be the most efficient choice for pollinators. Recently, another hypothesis suggested that parasitoid wasps might play an important role in stabilizing fig and fig wasps system. The *parasite pressure* hypothesis states that since parasitoids oviposit from outside of figs, they might parasitize outer layer ovules more easily than those that in inner layer. Accordingly, pollinator offsprings located in outer layers ovules suffer from higher predation risk. Therefore, predation pressure may select pollinators to oviposit in inner layers ovules (Dunn et al. 2008). Both the *unbeatable seed* and *short ovipositor hypotheses* cannot provide a satisfactory explanation for why seeds and pollinating wasp offspring exhibit stratification in some monoecious figs. Although the *Optimal foraging strategies hypothesis* suggested pollinators laid eggs in inner ovules for efficiency, it did not consider the predation pressure from parasitoids. The *parasite pressure hypothesis* provides a new insight into explaining stratification of seeds and pollinators, but so far it has not been tested in many systems (Dunn et al. 2008, Herre et al. 2008).

Non-pollinating wasps are another important group of wasps that are associated with figs. They are distinguished into three groups according to their diet and ecology: parasitoid, inquiline and galler (Weiblen 2002). Parasitoids feed directly on the larvae of host, and consume host tissue to grow. Inquilines feed on plant tissue, but they cannot induce galls, and thus they compete with pollinators or gallers to occupy their galls. Gallers are able to stop abortion of unpollinated figs and induce continuous development of those figs; thus they are independent from the pollinator wasps and can occupy figs alone. Since the resources of figs are limited, gallers who utilize the same fig as pollinating wasps do will reduce the fitness of both plants and pollinating wasps, although the impact varies among species (West and Herre 1994, West et al. 1996, Pereira et al. 2007, Yang et al. 2005). In addition, galler wasps are larger than pollinator wasps, therefore they may require more resources to develop than pollinators do. From these aspects of their ecology, gallers are considered predominately as competitors to pollinators, and directly impact the fitness of both figs and pollinating wasps. Therefore, one intriguing questions about gallers is why gallers would not out compete pollinators and destroy this mutualistic relationship.

Previous studies indicated that by utilizing different oviposition locations or temporal partitioning in timing of oviposition, pollinators and gallers could coexist in the same fig (Cook and Power 1996, Kerdelhué and Rasplus 1996, Proffit et al. 2007, Wang and Sun 2009, Sun et al. 2008). Pollinators oviposit from inside of fig whereas gallers insert their ovipositors from fig surface. Therefore, pollinators should use more inner layer ovules and gallers should prefer outer layer ovules. The differentiation in ovipositing locations may decrease interspecific competition between gallers and pollinators thus facilitating their coexistence. If this hypothesis is supported, we should expect to see clear separation in oviposition sites in which pollinators will be found in short-styled flowers and gallers will be found in long-styled flowers.

Zavodna et al. (2005) suggested foundresses would place their low mobility sons at the sites close to his sisters in order to increase its mating efficiency. Their results showed pollinator offsprings clustered in the central part of a fig. However, male gallers seem to have higher mobility compared to male pollinators, and winged male gallers could mate after they escape from figs. Consequently, gallers do not need to oviposit in clusters or use certain locations in the fig. If this hypothesis is supported, we expect to see niche partitioning in oviposition location between pollinating wasps and gallers, in which pollinator foundresses will cluster her offsprings at certain locations whereas gallers will not favor any specific location and oviposit randomly inside the figs.

In subtropical area, the highly seasonal environment could be a strong select pressure to fig wasps. Several studies showed that fig trees produced fewer figs and decreased flowering frequency in dry and cold season (Hill 1967, Janzen 1979, Compton 1993, Yang 2011), and this may decrease the pollination success rate. Cold weather may also increase mortality of minute fig wasps. Differential tolerance to environmental conditions in competing species may be one way to partition resources. For instance, if different wasp species have differential survival rates and reproductive success in different season, their population abundance will differ between seasons. This way, species that can tolerate certain environmental conditions, such as cold temperature will be favored at winter and other species that cannot tolerate cold temperature will have low abundance. However, very few studies focus on this subject (Wang et al. 2005, Peng et al. 2010). By monitoring population dynamics of fig wasps between crops, we can infer life history strategies of different fig wasps species, and further understand if temporal partitioning promotes coexistence between competing wasp species.

Here, we used *Ficus microcarpa* and its associated wasps as the study system. I tested the parasite pressure hypothesis to determine if parasites promote the stratification of seeds and pollinator offsprings, and contributed to the maintenance of mutualism. In *F. microcarpa*, galler species in the genus of *Odontofroggatia* were very common and their population sizes are second only to that of pollinator wasps. What the effect of *Odontofroggatia* spp. is on the pollinator wasp-fig mutalism and how they coexist with pollinators remain unclear. Thus, I examined the effect of galler

Odontofroggatia on number of seeds and pollinators. I further examined niche partitioning between galler *Odontofroggatia* and pollinator from spatial and temporal aspect, by measuring offspring locality within fig and monitoring population size among crops of gallers and pollinators. In this study, I focus on two main questions: 1) how is the stability of fig and pollinating wasps is maintained? 2) what mechanisms maintain the coexistence between mutualist and parasite? I specifically address the following questions: (1) Does the parasitism rate on pollinators differ between inner and outer layer ovules? (2) Does the presence of galler *Odontofroggatia* affect production of seed and pollinator? (3) Do pollinators and galler *Odontofroggatia* show spatial (oviposition preference) or temporal partitioning (different population dynamics between crops)?

Material and methods

Study species

Ficus microcarpa, a monoecious ficus species, is widely distributed in tropical and subtropical forests. This species can grow up to 20 meters tall, and have extended aerial root systems. They produced three to four crops a year, and the fig size is about 0.5-1.2 centimeters in diameter. The pollinator of *F. microcarpa* is *Eupristina verticillata*, which use figs as nursing ground for offspring but also help to pollinate figs. There are about 19 non-pollinating fig wasps species that have been reported to exploit *Ficus microcarpa* (Chen et al. 1999). The common species include gallers (genus *Odontofroggatia* and genus *Walkerella*), parasitoids (*Sycoscapter gajimaru*, *Sycoryctes moneres*, *Philotrypesis taiwanensis* and genus *Sycophila*) and inquilines (genus *Philotrypesis*).

Study site and data collection

This study was carried out on the campus of Tunghai University, Taichung, Taiwan (Fig 1). I used two populations of *F. microcarpa* in this study, one from Campus Mall and another from Tunghai Lake. I sampled 76 and 28 individuals in Campus Mall and Tunghai Lake, respectively.

I monitored phenology of *F. microcarpa* on a weekly basis from February 2010 to September 2011, and collected figs from November 2010 to November 2011. During each survey, I split about 10 figs of each tree to observe and determine the growing phase (pre-female, female, interfloral or male phase) of that tree, followed the method developed by Galil and Eisikowitch (1968). Meanwhile, I collected 15-30 figs from trees with male phase figs, and stored them in the refrigerator to kill all wasps before they hatched. These collected figs were usually from the outer branches that were less than four meter in height. I measured the size of figs before dissection. Figs were divided into three sections: ostiole, central and basal part. I carefully dissected the figs and recorded style length (long or short style), location (ostiole, central or basal) and fate (developed into seed, fig wasps or undeveloped) of each ovule. Furthermore, I took every wasp from its gall and identified it to species. In so doing, I could identify which species of wasps was associated with which gall.

Parasitism ratio of inner and outer layer ovule

To calculate the parasitic ratio of parasitoid, I first counted the number of pollinators found in outer and inner layer ovules, and calculated its ratio (e.g. if number of pollinator is 500 in outer ovules and 600 in inner ovules, the ratio was 1: 1.2). Then I counted the number of parasitoids found in the inner/outer ovules. If parasitoid showed no preference in choosing outer or inner ovules, one should expect to find the numbers of parasitoids found in the outer and inner ovules are proportional to the outer/inner pollinator ratio. Therefore, if parasitism ratio in outer/inner ovules is not proportional to pollinators’ expected ratio, it suggests parasitoids have oviposition preference.

The effect of gallers on pollinator offspring and seed numbers

If gallers compete with pollinators and seeds for the same plant resources, they should exert strong effect on seeds and pollinators production. Therefore, one should expect to see a negative relationship between number of gallers and number of seeds and pollinators found within the same fig. In addition, figs without gallers should have higher number of seeds and pollinators.

Niche partitioning: oviposition site preference

If pollinators and gallers oviposit randomly inside the fig, the number of pollinator or galler found in the long styled and short styled flowers should be proportional to the ratio between long styled/short styled flowers. To see if niche partitioning occurred between pollinators and gallers, I counted the total number of long and short styled flowers, and calculated the ratio of gallers and pollinators found in each type of flowers.

Following the same reasoning, I calculated the observed and expected ratio of flowers in three sections (ostiole, central and basal). If *Odontofroggatia* and pollinators have no preference in oviposit location, there should be no difference between observed and expected ratio in each section. Again, I used figs emerged with pollinator alone, galler alone and pollinators coexist with galler to see if they have different preferences in oviposition sites under different situations.

Temporal partitioning: population dynamics between crops

I defined four crops of *F. microcarpa* from November 2010 to November 2011 based on phenology survey of all trees on Campus mall. Trees were considered in the same crop if their figs overlapped in sexual phases during the survey period. For example, trees with female phase and/or trees with male phase figs occurred during the same period will be considered as in the same crop. In addition, most fig trees enter a temporal break (with no figs produced) between crops. Thus, when trees start flowering after the break, I defined it as the beginning of each crop, and as trees enter the temporal break, I defined it as the end of each crop.

I estimated wasp population size based on wasps emergence data collected from Campus mall, and then compared wasp population size between crops to determine whether pollinators and *Odontofroggatia* populations exhibited temporal separation.

Data analysis

I used the chi-square test for independence to compare if the parasitism ratio between inner and outer layer ovules were the same. Negative binomial regressions were used to examine effects of gallers on pollinators and seed production (Ripley et al. 2002). In the first negative binomial regression, number of seeds was included as the dependent variables. The number of two species of gallers (*Odontofroggatia* and *Walkerella*), number of pollinators and total number of female flowers were treated as independent variables. The second regression had similar independent variables, but the number of pollinators was used as the dependent variable instead of an independent variable.

To examine whether niche partitioning among wasps existed, I used chi-square tests (goodness-of-fit tests) to examine if the observed ratio between inner/outer flowers and among three sections (ostiole/central/basal) deviated from the expected values. In addition, oviposition preference was compared among three types of figs: figs with pollinators alone, figs with gallers alone, and figs with both pollinators and gallers. Finally, I used the chi-squared test for independence to examine if population sizes of gallers and pollinators differed among four crops.

The statistical analyses were carried out by R 2.14.1 (R Core Team 2011).

Result

Summary of the wasp fauna in *F. microcarpa*

I collected 465 and 170 figs from the Campus mall and Tunghai Lake, respectively. In total, I found 11 genera of wasp species. Wasps from six genera were identified to species but wasps from the other five genera: *Odontofroggatia*, *Walkerella*, *Sycophila*, *Ormyrus* and *Conidarnes* were identified to genus only (Table 1). Some wasps emerged before figs were dissected, so their gall position could not be identified. *Eufroggattisca okinavensis* and *Meselatus bicolor* were recorded before study begins (captured in adhesive traps), so I did not have information of their gall position and population sizes. The following analyses did not include *E. okinavensis*, *M. bicolor*, and species from genus of *Ormyrus* and *Conidarnes* because few specimens were collected from them, plus they were too few to identify their ecological groups (gallers, inquilines or parasitoids).

Due to the diet of larva are usually the same in the same genus, I lumped the species from the same genus together to perform the analyses except for *P. taiwanensis*. The galler included species in genus *Odontofroggatia* and *Walkerella*. The parasitoids of pollinators are *Sycoscapter gajimaru*, *Sycoryctes moneres* and *P. taiwanensis*. The inquilines species are *P. okinavensis* and *P. emeryi*. They were suggested to compete with pollinator and occupied galls formed by pollinators. *Sycophila* species are parasitoids of *Odontofroggatia* species, but whether they are host specific is unclear because both species were identified to genus only.

In average, a syconium contains 140 to 160 flowers (Table 2), fewer than those that found in previous study (about 200-250 flowers per fig) in Taipei (Chen 1994). The population of pollinator showed dramatic fluctuation among crops (Table 2). Compared to pollinators, other wasps group (gallers, inquilines, parasitoids) showed less fluctuation in their population abundance.

The fig trees produced almost no seeds in the second crop, the reason may be due to few foundresses successfully entered figs and low pollination rate. I collected 166 figs from the second crop, and pollinators were only presented in 58 of them. Moreover, the average number of pollinator was 3.7 per fig for this crop, and the average number of seed was 1. In addition, almost 60% of figs (95/166 figs) collected in this crop was occupied by gallers alone (Table 3).

In the third and fourth crops, although pollinators were in greater numbers, the production of seed remained low. The number of pollinators per fig increased to 17.48, and the number of seeds per fig increased too (average number of seeds was 6.4). In these two crops, I collected 96 figs with pollinators but only 50 of them produced seeds. This low seed set even though pollinators were present indicated that foundresses entered the figs and laid eggs but did not pollinate the flowers.

Parasitism ratio of inner and outer layer ovules

The results of chi-square test for independence showed that the ratio of parasitism was significantly higher in the outer layers than that in the inner layers. Although more *S. gajimaru* were found in the inner ovules than the outer ovules, the parasitism ratio was higher in outer ovules (Table 1, Table 4).

The effect of galler on pollinator offspring and seed productions

Since there were several wasps combinations occurred in a fig, I classified these figs into four groups based on its wasps combination, and used negative binomial regression to examine the effect of gallers on fig-wasps system. The first group was figs contained pollinator alone (n=53), the second group was figs contained pollinators and *Odontofroggatia* (n=37), the third group was figs contained pollinators, *Odontofroggatia* and *Walkerella* (n=7), and the last group was figs contained *Walkerella* and pollinators. I did not include figs received *Walkerella* alone because they were too few to analyze (n=2).

The presences of gallers have negative effects on production of seed and pollinator (Fig 2). The production of seeds and pollinator were both affected by the total number of flowers, and seed production was significant influenced by the number of pollinators (Table 5). The presence of *Odontofroggatia* has negative effects both on seeds (P=0.021) and pollinator production (P=0.0013). *Walkerella* also showed significant negative effects on production of seeds (P=0.0001) and pollinators (P=0.0013) (Table 6). However, *Walkerella* seems to have stronger negative effects than *Odontofroggatia* on production of seeds and pollinators (Table 5 and 6).

Niche partitioning: oviposition site preference

Chi-square tests showed that pollinators were more abundant in short styled flowers no matter whether they appeared alone or coexisted with gallers (alone: Chi-squared = 74.4303, $P < 0.0001$; coexist: Chi-squared = 163.9712, $P < 0.0001$). However, the galler *Odontofroggatia* was more abundant in long styled flowers (alone: Chi-squared = 56.9186, P<0.0001; coexist: Chi-squared = 101.7382, P<0.0001).

Pollinators were most abundant in the central part of a fig and the least in the ostiole part when they appeared alone (Chi-squared = 15.8568, P= 0.0003); *Odontofroggatia* showed no preference in three sections when they colonized figs alone (Chi-squared = 1.1588, P = 0.5602). When coexisted, pollinators still clustered in central part (Chi-squared = 44.5895, P<0.0001), while *Odontofroggatia* assembled in the basal part of figs, and the ostiole part received the fewest galls (Chi-squared = 10.1026, P = 0.0064).

Temporal partitioning: population dynamics between crops

The first crop was from November 8, 2010 to January 25, 2011; the second crop was from January 26, 2011 to May 16, 2011; the third crop was from May 17, 2011 to July 18, 2011; the last crop was from July 19, 2011 to November 5, 2011 (Fig 3, Table 7). Pollinators were abundant in the first crop, and rapidly declined in the next crop. In the third and fourth crops, populations of pollinators recovered slowly (Table 2). *Odontofroggatia* were abundant from November 2010 to May 2011, but declined in the next two crops. I compared the frequency of pollinator and *Odontofroggatia* presence (the number of figs with wasps presence divided by total number of figs) with their relative abundance (abundance of pollinator and *Odontofroggatia* to total wasps abundance) to further investigated their population dynamics between crops (Fig 4). In crop 1, pollinators were high in both relative abundance and frequency of presence, while *Odontofroggatia* were in low relative abundance but in high frequency of presence. In crop 2, pollinator dropped to the lowest presence and abundance, but both relative abundance and frequency of presence of *Odontofroggatia* species increased to its high. In the third crop, relative abundance of pollinator increased to about 0.35, but their frequency of presence remained low. Meanwhile, relative abundance of *Odontofroggatia* dropped to about 0.1, and the frequency of presence were slightly decreased. In crop 4, the relative abundance and frequency of presence of pollinator reached the highest peak, while *Odontofroggatia* were in opposite situation. The populations of pollinators and *Odontofroggatia* showed significant difference between the four crops (Chi-squared = 2463.51, $P <$ 0.0001).

Discussion

Parasite pressure hypothesis

My results showed that the rate of parasitism was higher in outer layers than in inner layers, supporting the parasite pressure hypothesis. Pollinating wasps may suffer lower mortality by ovipositing in inner ovules, because their offspring located in inner ovules were less susceptible to parasitoids. However, among the three parasitoids, *S. gajimaru* has a very long ovipositor (Chen 2001), and they were able to reach inner ovules. In fact, I found more *S. gajimaru* in inner ovules than in outer ovules, in contrast to the other two parasitoids (Table 1). The other two parasitoids, *P. taiwanensis* and *S. moneres*, were found mostly in outer ovules.

The insufficient eggs hypotheses suggested that foundresses carry limited number of eggs and therefore are unable to oviposit in all ovules. According to previous studies, an *E. verticillata* foundress carries about 80 eggs in average (Chen 1994). Thus two to three foundresses are expected to be able to oviposit all ovules. In this study, the foundress number was not recorded, but a previous study (Yang 2011) showed the most syconia contained one to two foundresses, and my results showed the average number of flowers was about 140-160. Therefore, two foundresses could oviposit in almost all flowers in a fig. From this aspect, the insufficient eggs hypothesis cannot explain the stratification of seeds and pollinators.

In my study, I found many *E. verticillata* and parasitoids wasps developed in the outer ovules, this indicated that *E. verticillata* could reach outer ovules. In fact, their ovipositors were long enough to reach outer ovules (Chen 1999), therefore outer ovules were not “unbeatable ” to pollinators. This seems to indicate that the short ovipositor and unbeatable seeds hypotheses could not give a satisfactory explanation for why all eggs are not exploited. Although the optimal foraging strategies hypothesis (Yu et al. 2004) suggested that ephemeral pollinators prefer short-styled flowers to oviposit in because of increased efficiency, this hypothesis cannot explain why many pollinators were found in outer ovules when inner ovules were still available. Although pollinators in inner ovules could not avoid been attacked by *S. gajimaru*, my data showed that pollinators located in inner layers were less likely to be parasitized than those that in outer layers. Hence, the parasite pressure hypothesis might be one possible mechanism that drives pollinators to oviposit in certain region and caused spatial partitioning in oviposition site. The selected pressure from predators may have contributed to the stability of this mutualism.

The effects of gallers

Odontofroggatia were the common gallers found in this system, and they often appeared with pollinators in the same figs. *Walkerella* were less common in this system, and half of sampled specimen were from occupied figs alone or coexist with inquilines. *Walkerella* oviposit in pre-female phase, and *Odontofroggatia* colonized figs from pre-female phase to early interfloral phase (Chen 1994; personal observation).

Previous study suggested early colonizing gallers influenced pollinator production more while late colonizing gallers influenced seed production more (Xu et al. 2007) However, in this study, *Walkerella* (an early colonizer) seemed to have more negative effects both on production of seeds and on pollinators than *Odontofroggatia* (an early to late colonizer) does. One possible explanation is that *Walkerella* occupied immature and un-pollinated flowers, and so decreased the number of flowers available for pollinator to oviposit. These pre-empted figs might become unable to use for pollinator (The fact that half sampled *Walkerella* were from occupied figs alone might have some implication in this.), and thus decreased production of seeds and pollinator offsprings. Another possibility is that when pollinators enter pre-empted figs to pollinate, the large galls of gallers may hinder pollen from attaching to the stigma of the outer layer ovules, and thus reduced seed production. In this study, early colonizers (*Walkerella spp.*) showed more detrimental effect on the production of seeds and pollinators than late colonizers (*Odontofroggatia spp.*) do.

Spatial partitioning

The pollinators showed strong preferences for inner layer ovules and *Odontofroggatia* preferred outer layer ovules no matter they existed alone or coexisted together, implied that their oviposition preference resulted from long-term evolution. My results indicated that the oviposition preference of pollinator might be caused by parasite pressure, which forced pollinators to oviposit in inner layer ovules. For gallers, the strong preference in outer layer ovules was probably due to short ovipositor lengths, which prevent it from reaching inner layer ovules. Through using different layer of flowers and so partitioning different flower resources, pollinators and gallers could occupy the same fig and coexist.

Another result indicated that pollinators preferred clustering their offspring in the central cavity of a fig. Interestingly, galler *Odontofroggatia* tended to oviposit randomly when pollinators were absent, but clustered their offspring in the basal region of the fig when pollinators were present. This fact suggested the presence of pollinator in a fig forced gallers to change its oviposit preference. This may be due to pollinators occupying the central part earlier than gallers, so that gallers could only oviposit in vacant parts of a fig. The reason why ostiole region received the least number of galls might be due to the fact that ostiole part is lined with scales that hinder wasps from ovipositing.

My findings seemed to support the hypothesis proposed by Zavodna (Zavodna et al. 2005) who suggested that pollinators cluster their offspring in central cavity for mating efficiency. On the contrary, male *Odontofroggatia* have high mobility and their mother would not need to put them near to galls of female offsprings. Hence, the factor that determined the oviposition sites of galler may be simply the accessibility of ovules.

These partitioning of oviposition sites (preference in different layer of ovule and section of a fig) could decrease the competition between pollinators and gallers, thus further promote the coexistence between them.

Population dynamics between crops

The pollinator population reached their peak in the first crop, then dropped to the lowest population size in the next crop. After that, the population recovered slowly in the successive crops. However, the pollinator was abundant in the previous summer, before this study begun. In theory, the pollinator population should recover rapidly after harsh season (Chen 1999, Chen 2001), but in our investigating period, the pollinator population showed a slowly recovery rate. The cause of pollinator population decline in summer 2011 was unclear, and a long-term survey is needed to provide more reliable information.

The *Odontofroggatia* showed the largest population size in the first two crops, and then declined in the next two crops. This indicated that the pollinator and galler populations might separate temporally, and this partitioning may be a mechanism to maintain their coexistence. However, this study last for one year only, to obtain a more reliable result, long-term investigation is needed.

The presence and abundance of pollinator and *Odontofroggatia* often showed contrary situation (Fig 4). It inferred that they used different strategies between crops. Pollinators were usually more abundant than *Odontofroggatia*, whereas

Odontofroggatia were usually in high presence rate. This may due to the higher fecundity of pollinator and higher dispersal ability of *Odontofroggatia*, and the population fluctuation could result from the different fecundity and dispersal ability of wasps between crops. Previous studies observed different population sizes of pollinator and non-pollinators among seasons (Wang and Sun 2009, Wang et al. 2009, Yang 2011, Chen 1994, Chen 2001), which implies the pollinator and non-pollinators have different tolerance under different environmental conditions. Further, some studies showed wasps live longer in certain season (Wang et al. 2005, Zhang et al 2009). The wasps could lay more eggs when their longevity become longer, and thus their population size may increase in certain season. Thus, the variation in fitness between seasons could be a mechanism to promote temporal partitioning in fig wasps.

Comparison with previous studies in Taipei

Previous study (Chen 2001) reported 20 species of wasps associated with *F. microcarpa*, but in my study, I did not found *Acophila microcarpa*, *Bruchophagus sensoriae* and *Micranisa degastris*. Whether it was because they were too few to discover or their distributions were restricted in north Taiwan is unclear. During my study, I collected five winged male of *P. okinavensis*, which was not recorded in Taiwan before. Moreover, I discovered a new wasp species associated with *F. microcarpa*. This new species belongs to a new genus *Conidarnes*, which was published recently (Cruaud et al. 2011).

Chen (2001) suggested *P*. *okinavensis* and *P*. *emeryi* are inquilines of pollinator, however, I found several inquilines lived in galls which apparently belonged to *Walkerella* species. In addition, their body size was bigger than those of inquilines found in pollinators’ galls. We need more evidence to understand if these inquilines also compete with *Walkerella* species.

In my observation, the flowering cycle of *F. microcarpa* were longer in winter and spring (November to April) and shorter in summer (May to September). The trees produced abundant figs from November to January and from May to November, which were different from the Taipei studies (Chen et al. 2004, Yang 2010). Chen and Yang both found that the major production of *F. microcarpa* occurred from March to June and July to November, and nearly no production in December and January. The reason may be the regional difference in climatic conditions. Taichung is warmer than Taipei, which may cause trees to produce figs in winter. Moreover, Chen suggested there were fig gaps (no figs produced period) during her study (Chen et al. 2004), which was absent in my study, and it may due to the warmer climate or the warmer winter in 2009 in my study site.

Conclusion

This study showed the predation pressure from parasitoids contributed to stabilizing the fig and pollinating wasp system by driving pollinators to oviposit in short-styled flowers and leaded to spatial partitioning between pollinator and galler. The gallers have negative effects on production of pollinator and seed, suggested that the influences of gallers do not disappear even though there is spatial partitioning between gallers and pollinators. Although they are located in different layers, the gallers can use the resources for pollinator developing. Inconsistence with previous studies in Taipei (Chen 1994, Chen 2001, Yang 2011), the population of pollinator in this study was highest in winter instead of summer.

According to these results, I suggested the pollinator and galler of *F. microcarpa* coexist through niche partitioning (spatial and temporal). There were few studies examined the coexistence mechanisms between pollinating and non-pollinating wasps, my study provided some insights for this issue. However, the interaction of figs and fig wasps in *F. microcarpa* is very complicated, one need to conduct study which combine phenology of fig trees, wasp population dynamics, life history of wasps, genetic analyses on degree of outcross in fig seed among seasons to understand the whole picture of their relationships.

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Table index 35

Table 1. Number of wasp species and sampled population sizes. This table shows the wasp species collected in this study. The ecological biology role means the ecological group of these species (galler, inquiline, parasitoid). The gall position indicates the number of each species found in inner or outer layer ovules. The total numbers of wasp individuals were listed here.

Species	**Ecological biology role**	**Gall position (inner layer)**	**Gall position (outer layer)**	**Total**	**Note**
Eupristina verticillata	Pollinator	7506	8778	17259	
Odontofroggatia spp.	Galler	478	2001	2636	
Walkerella spp.	Galler	87	362	476	
Sycoscapter gajimaru	Parasitoid of pollinator	579	454	1086	
Sycoryctes moneres	Parasitoid of pollinator	84	488	606	
Philotrypesis taiwanensis	Parasitoid of pollinator	26	174	208	
Philotrypesis okinavensis	Inquilines	67	260	353	Winged males recorded
Philotrypesis emeryi	Inquilines	37	78	120	
Sycophila spp.	Parasitoid of *Odontofroggatia*	120	916	1096	
Ormyrus sp.	?	0	7	7	
Conidarnes sp.	?	-	-	3	New species
Eufroggattisca okinavensis	Galler?	-	-	-	Observed before data collecting period
Meselatus bicolor	Galler?	-	-	-	

Table 2. Mean number of each wasp group, and mean number of seed, undeveloped ovules and total flowers per fig in four crops in Campus mall (464 figs). Galler included *Odontofroggatia* and *Walkerella*; Parasitoid included *P. taiwanensis, S. gajimaru* and *S. moneres*; Inquilines are *P. okinavensis* and *P. emeryi. Sycophila* are parasitoid of *Odontofroggatia.* The wasp populations varied between crops, and the population of pollinator correlated with seed production. The populations of parasitoid and inquiline varied with their host (pollinators or gallers).

Crop	Pollinator	Galler	Parasitoid	*Sycophila*	Inquiline	Seed	Undeveloped ovules	Total flowers	Number of fig
					Mean±SD				
10/11/8- 11/1/25	41.85± 35.85	5.70± 8.58	2.17± 5.8	0.23± 1.10	0.45± 2.18	24.34± 28.28	76.81± 57.66	157.71± 47.46	136
11/1/26- 11/5/16	1.31± 3.26	4.96± 4.24	1.4± 3.19	3.39± 4.13	0.81± 1.96	0.51± 1.57	123.54± 60.69	139.65± 65.21	166
11/5/17- 11/7/18	9.63± 18.59	4.99± 4.83	4.85± 11.6	2.05± 3.23	1.01± 1.95	4.38± 15.96	111.24± 41.22	139.46± 42.36	110
11/7/19- 11/11/5	17.79± 19.77	2.33± 4.23	3.77± 10.58	0.17± 0.88	1.54± 3.06	4.19± 8.00	105.21± 51.71	140.9± 55.25	52

Table 3. The combination of wasps species found in each fig in the two study sites. The abbreviation of P stands for pollinator; G for gallers; Para for parasitoids; I for inquilines.

Wasp combination	**P**	**G**	**P+G**	**P+G+I**	**G+I**	**P+G+I+Para**	**P+G+Para**	**P+I+Para**	**P+Para**	**I**	**P+I**
						(number of fig)					
Campus Mall crop 1	37	38	19	2	2	5	22	6	8	0	0
Campus Mall crop 2	0	95	4	4	14	22	24	2	3	1	0
Campus Mall crop 3	2	64	12	6	1	9	5	1	2	1	0
Campus Mall crop 4	13	7	10	2	0	7	2	10	3	0	0
Tunghai Lake	36	45	43	3	3	5	11	9	9	3	3

Table 4. Tests of independence of parasitoid in inner and outer ovules. The expected value of parasitoid is based on ratio of pollinators in outer/inner ovules.

	Observed		Expected	
	Outer ovules	Inner ovules	Outer ovules	Inner ovules
Pollinator	8778	7506	-	-
Parasitoids	1116	689	984.5	820.5
Chi-squared value	19.3898, $P < 0.0001$			

Table 5. Results of negative binomial regressions of galler effects on seed production. The *z* value was used to test against null hypothesis (coefficient = 0). Both species of gallers have significant negative effects on seed production, and number of pollinators and flowers were positively correlated with seed production.

Factor	N	Estimate	z value	*P* value
Pollinator	174	0.005132	+2.056	0.0397 *
Odontofroggatia		-0.031013	-2.308	0.0210 *
Walkerella		-0.326897	-3.859	0.0001*
Flowers		0.010863	+8.797	< 0.0001*

*: $P < 0.05$

Table 6. Results of negative binomial regression analysis of galler effects on production of pollinators. The *z* values were used to test against null hypothesis (coefficient = 0). Both species of gallers have significant negative effect on production of pollinators, and number of flowers was positively correlated with the fecundity of pollinator wasps.

Factor	N	Estimate	z value	*P* value
Odontofroggatia	174	-0.0307714	-3.202	0.00147 **
Walkerella		-0.1759946	-3.203	0.0014 **
Flowers		0.0028658	+3.264	0.0011 **

*: $P < 0.05$

Table 7. The number of pollinators and *Odontofroggatia* collected among four crops in Campus mall.

Species	11/8/10-1/25/11	1/26/11-5/16/11	5/17/11-7/18/11	7/19/11-11/5/11
Pollinator	5683	217	1175	925
Odontofroggatia	702	760	446	110
Number of figs	139	169	103	54

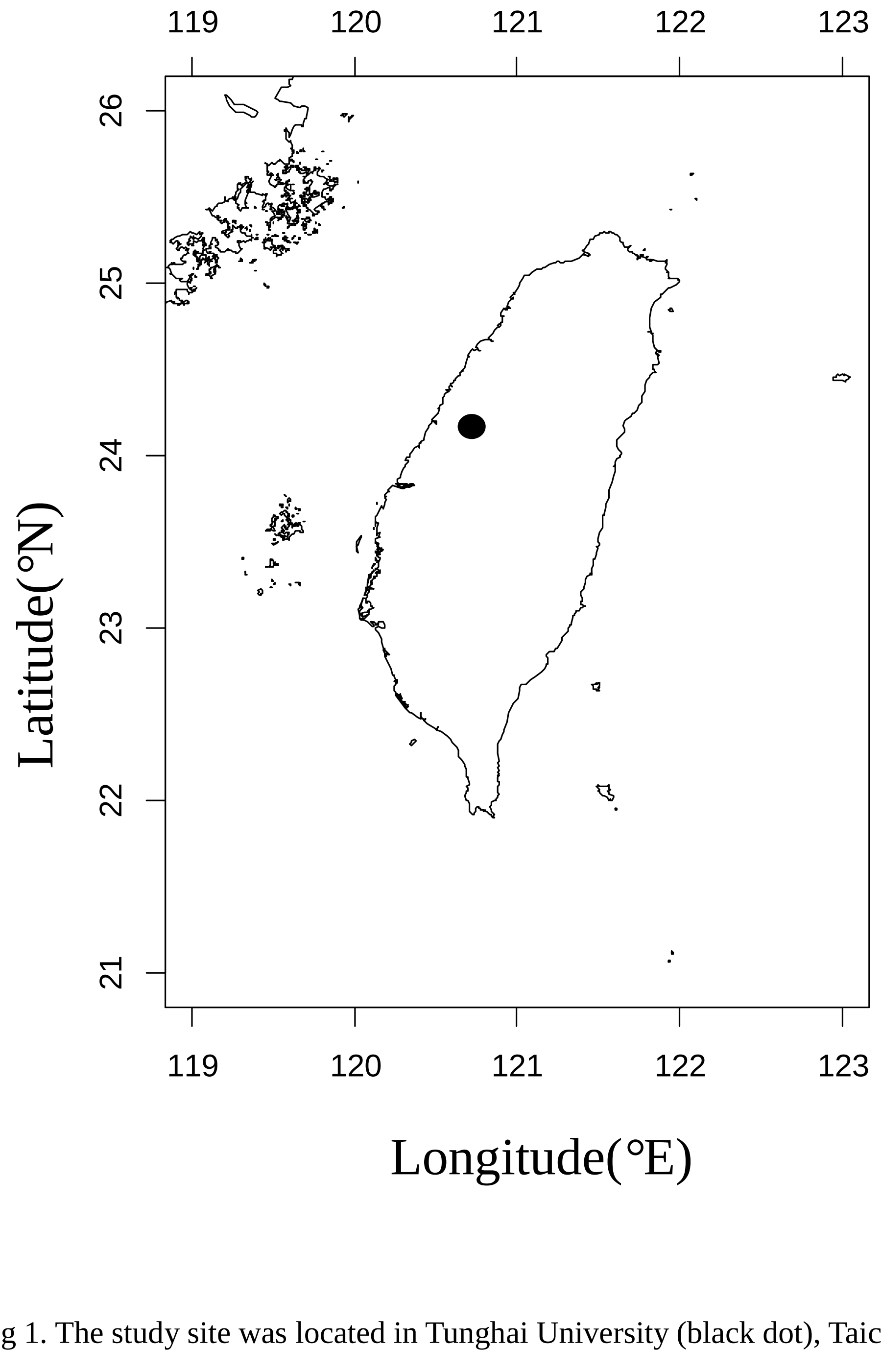

Fig 1. The study site was located in Tunghai University (black dot), Taichung, Taiwan.

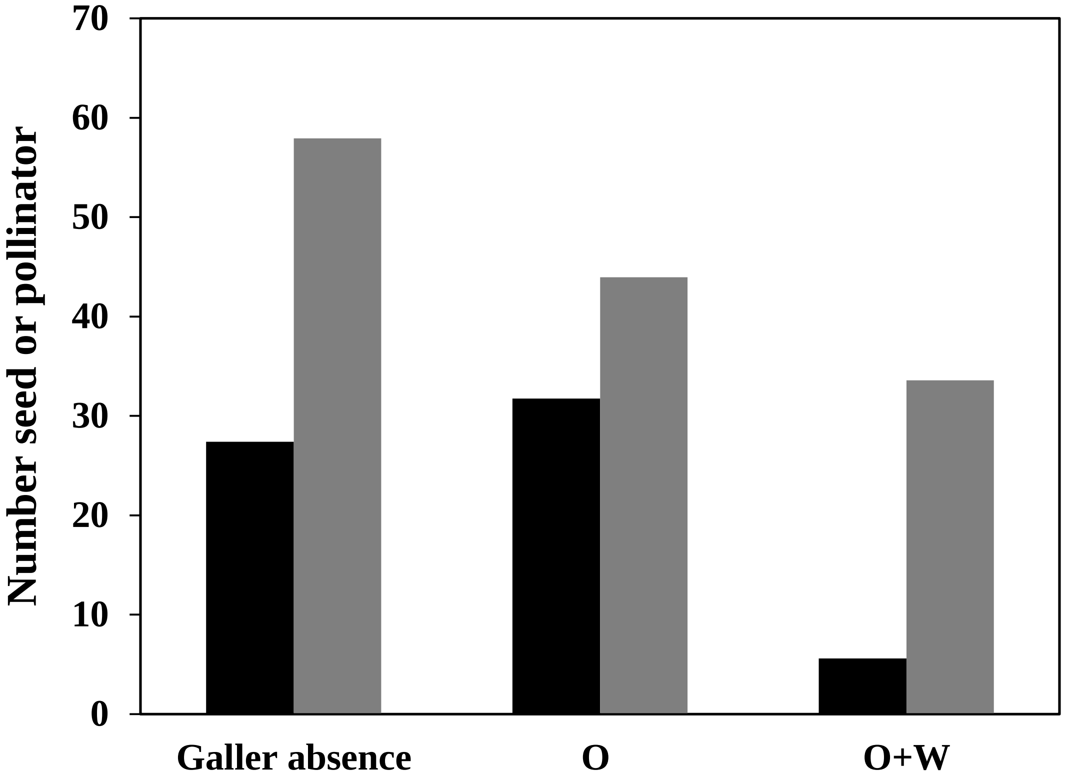

Fig 2. The number of pollinators and seeds in three types of figs. The black bars represent average number of seeds, and the gray bars represent average number of pollinators. O means *Odontofroggatia*, W means *Walkerella*.

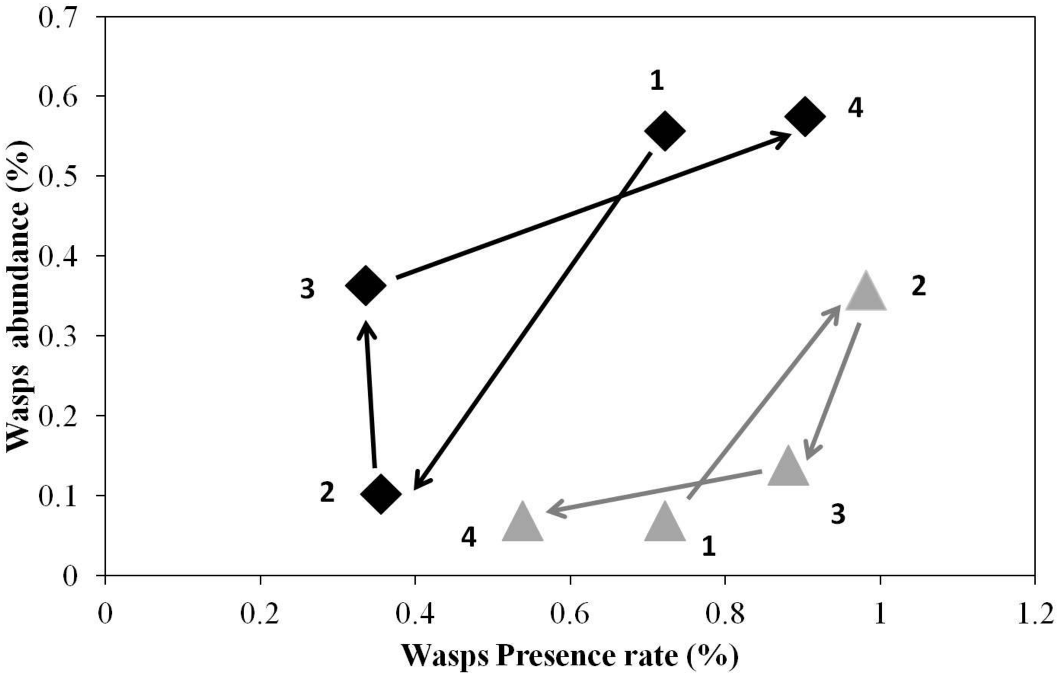

Fig 4. The abundance and presence rate of pollinators (◆) and *Odontofroggatia* (▲). The number beside the symbol and the arrow means the crop sequence. The wasp abundance was the number of pollinators (or *Odontofroggatia*) divided by the total wasps in each crop, and the wasp presence rate was the number of figs which contain pollinator (or *Odontofroggatia*) divided by the total figs in each crop.

個人資料

劉佩瑜　Liu, Pei-Yu

crazycathy915@gmail.com

學歷

2008.9-2012.8 東海大學生命科學系 生態暨生物多樣性研究所 碩士班

2004.9-2008.6 東海大學生命科學系 生態暨生物多樣性研究所 學士班

經歷

97 學年度 普通生物學實驗 小助教

99 學年度 生命科學概論 小助教

2012.3 ~ 臺北市立動物園保育研究中心 研究助理

得獎經歷

97 學年度 碩士班新生入學第一名獎學金

97 學年度 上學期 陳賢芳教授紀念獎學金

2012 年動物行為、生態與全球變遷研討會 壁報展示 優秀獎