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Female figs as traps: their impact on the dynamics of an experimental fig tree-pollinator-parasitoid community

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Abstract

Interactions between fig trees (*Ficus*) and their pollinating fig wasps (Agaonidae) result in both a highly species-specific nursery mutualism and mutual exploitation. Around half of the 800 or so fig tree species are functionally dioecious. Figs on male plants produce pollen and wasp offspring, whereas figs on female plants produce only seeds. Figs on female plants are traps for pollinators. The fig wasps enter the female figs to oviposit, but lose their wings on entry and are then prevented from oviposition by the long styles that characterise the flowers in female figs. Continuation of the mutualism depends on the pollinators' failure to distinguish between male and female figs before entry. Female plants may also have a negative impact on the parasitoid fig wasps that feed on pollinators, if they are also attracted to female figs. We used glasshouse populations of figs (with and without female plants), pollinators and parasitoids to infer the impact of female figs on fig wasp dynamics. Female plants may dampen the amplitudes of pollinator population cycles, and parasitoid populations may be less tightly coupled with host populations, but the presence of female figs did not reduce parasitism rates, nor parasitoid and pollinator densities, only parasitoid sex ratios were affected. Our glasshouse experimental design was likely to favour the impact of female figs on the wasp populations, which suggests that female plants in the field are unlikely to have a major negative impact on their pollinators, despite being a major mortality factor.

Keywords: dioecy; *Ficus*; intersexual mimicry; fig wasp; population dynamics; parasitism; sex ratio.

Introduction

Mutualistic interactions involving figs (*Ficus* spp., Moraceae) and their pollinating wasps (Hymenoptera, Agaonidae) represent a classic case of species-specific obligate mutualism and co-evolution (Compton 1993; Compton et al. 1996; Dunn et al. 2008; Herre et al. 2008). Mated adult female wasps are attracted to the volatile blends produced by young receptive figs (Proffit et al. 2009)In monoecious figs, when seeds and the next generation of wasps mature, adult females exit through a hole constructed by males and transport the pollen of their natal plant. In dioecious figs, where male and female functions are performed by separate plants, female wasps are only able to reproduce within male figs, while wasps entering female figs only pollinate and die without reproducing. On female plants, longer styles of female flowers prevent oviposition and as a result only seeds are produced by pollinated figs (Raja et al. 2008b). The pollination system of dioecious fig species is therefore an example of pollination by deceit (*sensu* Dafni 1984). Female figs in dioecious figs are therefore a dead end for wasp reproduction. There has been much debate on the conflicts involved between the two mutualists, especially in dioecious figs, where the pollinator wasps entering female figs ensure pollination of the plant, but fail to reproduce (Patel et al. 1995).

In some dioecious fig species, wasps that live only few hours, enter the female figs because they have no other choice available, as most male trees are receptive well before or after the receptivity of female figs (for example *Ficus carica*, Kjellberg et al. 1987 and Soler et al. 2012). In *Ficus montana*, like some other dioecious figs (*F. hispida*, Patel et al. 1995; and *F. fistulosa,* Corlett 1987) male and female figs are receptive simultaneously (Suleman et al. 2011a) and thus selection should favour wasps

71 that avoid female figs (Anstett et al. 1998), although this could lead eventually to the
72 potential extinction of both the plant and the pollinator wasps. However, this selection
73 pressure also favours female plants that mimic males so as to deceive wasps into
74 pollinating them (Suleman et al. 2011b). Males similarly need to mimic females to
75 ensure that the next generation of wasps bearing their pollen enter female figs ('vicarious
76 selection', Grafen and Godfray 1991; Soler et al. 2012). Such female mimicry has been
77 described in many other plant species (Agren et al. 1986; Aronne et al. 1993; Dufaÿ and
78 Anstett 2004). The inability of fig wasps to differentiate between male and female figs
79 means that female fig plants act as an additional mortality factor that will reduce the
80 pollinator numbers.

81 *Kradibia (=Liporrhopalum) tentacularis* foundresses, the pollinators of *F.*
82 *montana,* under natural and experimental conditions, typically contribute unequally to
83 shared broods, producing smaller and less female-biased clutches in multi-foundress figs
84 than they would have produced when ovipositing alone (Zavodna, 2004). This increase
85 in *K. tentacularis* brood sex ratios (proportion males) with increasing foundress density is
86 similar to that seen in many other studies conducted on fig wasps, and has generally been
87 attributed to sex ratio adjustments in response to local mate competition (LMC) and
88 inbreeding (Hamilton 1967; Frank 1985; Herre 1985; Pereira and Prado 2006; Greeff and
89 Newman 2011). However, it should be noted that realized sex ratios (based on numbers
90 of adult male and female offspring) in *K. tentacularis* do not necessarily reflect primary
91 sex ratios in this species, because larval mortalities are sometimes high and may not
92 necessarily be similar among male and female offspring (Ghana et al. 2012). Sex ratio
93 adjustment by foundresses entering their second figs (wingless foundresses) was found to

be different to that shown by winged foundresses entering their first figs, probably because of clutch size differences (Raja et al. 2008a; Suleman et al. 2013c).

Each species of fig tree has figs that are attacked by a number of non-pollinating fig wasps (up to 29 species were recorded from one tree species by Compton and Hawkins 1992). Non-pollinators include some species that oviposit externally and some that enter the figs like pollinators. Regardless of their oviposition time, all fig wasp species usually emerge from figs at the same time as the pollinators, which means there must be varying larval growth rates between species (Bronstein 1991; Kerdelhue and Rasplus 1996). *Sycoscapter,* a non-pollinator genus, belongs to the subfamily Sycoryctinae. *Sycoscapter* species have long ovipositors and lay their eggs from the outside of the fig, through the wall. They often are believed to be parasitoids or inquilines, mostly of the pollinators (Galil and Eisikowitch 1968, Compton and van Noort 1992). They oviposit a few hours to several days after pollinators enter the figs, depending on the species (Kerdelhue and Rasplus 1996). They oviposit in figs of a large range of diameters (Kerdelhue and Rasplus 1996; Kerdelhue et al. 2000). Four *Sycoscapter* species were studied by Kerdelhue et al. (2000); one associated with *F. sagittifolia* and three others on *F. ovata*. The four species appeared to have varying relationships with the pollinators; having negative, positive or no correlation with the numbers of pollinator larvae inside the figs.

Female fig plants of dioecious species are not only a dead end for pollinators, they also potentially act as ecological sinks for non-pollinating wasps that do not avoid female figs when searching for oviposition sites, which may explain why dioecious figs to generally have a lower incidence of parasitism (and fewer non-pollinator species) than

117 monoecious species and why pollinator production is often higher (Weiblen et al. 2001).
118 Also, in *F. montana*, female figs if unpollinated, tend to stay longer on female plants and
119 prolong their attractiveness (Suleman et al. 2011a) but there are no other phenological
120 differences between sexes as far as fig initiation and fig composition are concerned
121 (Suleman et al. 2011b). Here for the first time we test the impact of female plants of a
122 dioecious fig on its pollinator and an associated parasitoid. We look at population trends
123 of the pollinator and parasitoid in the presence or absence of female plants. As the
124 female plants act as a drain on pollinators there should be fewer foundresses available to
125 enter male figs when this sex is present. This in turn may result in more female-biased
126 sex ratios, as reduced competition for oviposition sites should allow larger clutches to be
127 laid by individual females. Also, if the parasitoids are distracted by the female figs, then
128 higher rates of parasitism might be expected in the absence of female plants, especially as
129 pollinator larval densities are expected to be higher (Weiblen et al. 2001).

130

131 **Study site and species**

132 The study was conducted using glasshouse populations of a dioecious fig tree *Ficus*
133 *montana* Blume, its pollinator *Kradibia* (= *Liporhoppalum*) *tentacularis* Grandi and the
134 parasitoid *Sycoscapter* sp., originating from the Centre for International Forestry
135 Research (CIFOR) plantation, West Java, Indonesia and from Rakata (Krakatau),
136 Indonesia. These populations had been maintained continuously at the Experimental
137 Gardens, University of Leeds, UK since 1995 (Moore 2001). In *F. montana*, significant
138 variation in flower number among figs has been observed by different individual trees
139 growing under uniform conditions (Suleman et al. 2013a). Pollinating females of *K.*

tentacularis seek out the figs at the receptive stage, enter, oviposit, pollinate and then either die or sometimes leave the fig in an attempt to oviposit in another fig (Suleman 2007). Wingless foundresses (passing through the ostiole physically removes the wings of female fig wasps) are able to locate and enter figs up to 60 cm from the first fig they enter (Suleman et al. 2013c). The non-pollinating wasps (*Sycoscapter* sp.) need figs that have already been pollinated (Raja 2007). It oviposits from the outside of the figs. The larvae develop into adults inside the ovules of the fig. Male are apterous and mating occur inside the female galls. Both species complete their development at the same time, hatch and mate. *Sycoscapter* sp. can significantly reduce the numbers of pollinators emerging from the figs, although the host sex ratios remain undistorted (Suleman et al. 2013b). Also the males of this species are able to construct exit holes for females as male pollinators (Suleman et al. 2012).

Methods

We monitored changes in the numbers of figs and their developmental stages and estimated the population sizes of the pollinator and its parasitoid based on counts made at 14 days intervals for a period of 15 months from November 2002 to February 2004. This period covered two winter and one summer seasons. Fig plants of similar size (small shrubs) were divided into two largely independent, but adjacent, populations separated by a physical barrier (a door) and a buffer zone of other *Ficus* species. Only premature figs (A phase) were left on plants. All others were removed at the beginning of the experiment. The door was kept closed except during brief transits by staff. One glasshouse contained exclusively male plants and the other had male and female plants

arranged together in lines with one male plant followed by one female plant and then one male followed by two female plants throughout. In this way a ratio of 2:3 was maintained, with 80 male and 120 female plants. The male only population consisted of 80 plants. All plants had individual pots placed close together. Daylight, watering, and soil nutrition were similar in the two glasshouses, as was the spacing between plants.

Minimum day lengths were maintained as 16L: 8D by providing artificial lights during periods when natural daylight hours were lower. The minimum temperature was maintained at 15 ^{o}C. Overall temperatures during the 15 month monitoring period were similar in the adjacent glasshouses with mean monthly minimum temperatures varying between 17.9 ^{o}C to 21.8 ^{o}C (mixed glasshouse) and 17.6 ^{o}C to 21.7 ^{o}C (male plants-only glasshouse), and mean monthly maximum temperatures ranging from 22.1 ^{o}C to 32.4 ^{o}C (mixed glasshouse) and 20.4 ^{o}C to 30.3 ^{o}C (male plants-only glasshouse).

Fig numbers and population trends

The numbers of figs on 20 randomly selected female plants and 20 randomly-selected male plants in each glasshouse were counted after 14 days interval. Developmental stages of the figs were recorded as described by Galil and Eisikowitch (1968) and Valdeyron and Lloyd (1979). Phase B figs are receptive and attract adult female wasps (loaded with pollen) to enter them. *K. tentacularis* routinely re-emerges from figs and so can pollinate and lay eggs in several figs. Phase C female figs contain developing seeds, whereas Phase C male figs contain wasp larvae developing in galled ovules. *Sycoscapter* sp. females lay their eggs from the outside of male figs, a few weeks after pollination. Male figs at D

185 phase release the next generation of fig wasps, with female pollinators then flying away
186 in search of B phase figs to enter. Female figs have an extended post receptive phase,
187 which ends when the figs are soft and fleshy and attractive to seed dispersers (E phase).

188 The contents of the male figs were assessed on the basis of samples of ten D
189 phase figs taken at random 10 different trees from both populations each fortnight. The
190 figs were left within fine mesh-covered plastic containers for 24 hours to allow the wasps
191 to emerge. The figs were then split open and all the wasps were identified, sexed and
192 counted. Male flowers, female flowers and their contents were also recorded (as un-
193 utilised, wasp-producing or failed empty galls ('bladders').

194 Variables were log transformed for time series analysis. Parasitism rates and sex
195 ratios were arcsine transformed for all analyses. One and two way analysis of variance
196 (ANOVA) for normal and Kruskal-Walis tests for non-normal data were used.

197

198 ## Results

199 **Fig numbers**

200 During the 15 month sampling period the number of figs on male plants in the males-only
201 population was 63.9 $\pm$ 3.5 (mean $\pm$ SE), compared with 54.5 $\pm$ 2.7 on male plants in the
202 mixed population was and 50.7 $\pm$ 3.0 figs on the female plants. There was strong
203 seasonal variation in the numbers of figs present on the plants (Fig. 1), with both sexes
204 having far more figs during the summer months (May-July) (Kruskal-Wallis test, $X^2_{[29]} =$
205 268.17, $P < 0.001$ for male and $X^2_{[29]} = 285.78$, $P < 0.001$ for female plants in the mixed
206 population and $X^2_{[29]} = 269.54$, $P < 0.001$ for male plants in the males-only population).

Approximately equal numbers of figs were present on the male and female plants in the mixed population (overall ratio = 1: 0.93, during spring and summer (April-September) = 1: 0.91 and autumn and winter (October-March) 1: 0.98). The abundance of male and female figs in the mixed population and of male figs in the two populations did not differ significantly (Kruskal-Wallis test, $X^2_{[2]} = 3.14$, $P = 0.21$, Fig 1 and 2).

Fig wasp population changes

The summer peak in the abundance of figs was not reflected in clear seasonal changes in the mean abundance of pollinators or parasitoids per fig, though wasp numbers varied significantly between sample dates (Table 1 and 2, Fig. 3). No differences in abundance were detected between the populations with and without female figs (Table 3) though the numbers of pollinators and of all wasps combined approached being significantly higher in the glasshouse where no female figs were present (Table 3). Interactions between glasshouses and sampling dates were generally significant, showing that wasp population densities in the two populations were not well synchronised.

The numbers of pollinators and parasitoids in the figs showed a pattern of alternating peaks and troughs in densities over time in both glasshouses (Fig. 4). The peaks appear to have greater amplitude in the males-only population, but the difference was not significant (Table 3). Despite clear cyclical dynamics in both species for both treatments, autocorrelation function analysis (ACF), which detects significant periods or frequencies of cycles in census data (Chatfield 1996), did not reveal strong evidence for consistent cycle periods for pollinator and parasitoids (Fig. 4). This may reflect the relatively short time series, which make detection of significant periods more difficult.

A tight coupling between pollinator and parasitoid numbers in the male-only glasshouse is revealed by cross correlation function analysis (CCF, Fig. 5a), which detects significant lags between the two populations (whether or not their respective peaks or troughs are in phase with each other, Chatfield 1996). However, there was no significant correlation between pollinators and parasitoids in the mixed population (Fig. 5b), which suggests that the tight coupling between pollinators and parasitoids is weakened by the presence of the female figs.

Parasitism rates differed among sampling dates (ANOVA, $F_{(29, 599)} = 3.40$, $P < 0.001$) but were not significantly different in the two glasshouses (29.63% $\pm$ 1.38 in the mixed population and 30.01% $\pm$ 1.51 in the males-only populations; ANOVA, $F_{(1, 599)} = 0.02$, $P = 0.88$). There was a significant interaction between glasshouses populations and sampling dates, showing that on dates when parasitism rates were high in one population they were not necessarily high in the other (ANOVA, $F_{(29, 599)} = 1.63$, $P = 0.02$).

The pollinators had highly female biased sex ratios that did not differ between the two glasshouse populations (Table 4), nor between sampling dates (ANOVA, $F_{(29, 596)} = 1.01$, $P = 0.46$), with a non-significant interaction between populations and sampling dates (ANOVA, $F_{(29, 596)} = 0.69$, $P = 0.88$). In contrast, the parasitoid had less female-biased sex ratios overall, that also varied between glasshouses, with a higher proportion of males present in the population where no female figs were present (Table 4). Parasitoid sex ratios also showed significant variation between sampling periods (ANOVA, $F_{(29, 494)} = 1.88$, $P = 0.004$), with a non significant interaction between populations and sampling dates (ANOVA, $F_{(29, 494)} = 1.37$, $P = 0.09$).

Discussion

The fifteen-month duration of the experiment covered two winter periods and one summer period. Despite artificial heating and lighting, the fig trees responded to the seasonal changes, producing many more figs during the summer period (probably due to increased day length and temperature). This increase in fig production during the summer was seen in both sexes of fig trees, so the proportion of male and female figs available to the pollinators did not vary between them dramatically. Despite the higher numbers of figs in the summer, the densities of wasps inside the figs did not display any seasonal effect. This suggests that there may have been a super-abundance of pollinators throughout the study period. Another study also reported that in *F. montana*, fig composition stays unaffected from seasonal effects (Suleman et al. 2011b).

Our results showed that pollinator and parasitoid populations exhibited remarkably similar discrete cyclic fluctuations in the male-plants-only glasshouse, but in the presence of female plants the amplitude of the cycles seemed to be reduced and peaks and troughs were less evident but with almost no effect on the parasitoids in both populations. It is difficult to detect strong signals of cyclicity or density-dependence in short time series, so we could not get significant patterns for the 15 months of data.

Predators are known to be able to reduce the amplitude of cyclic oscillations (Turchin et al. 1999). Female fig plants in effect act in a similar way to predators in the sense that they drain out foundresses from the system by trapping them without allowing them to reproduce. The parasitoids in both glasshouses did not seem to have any dramatic negative impact on the plant-pollinator mutualism as their numbers most of the

time were lower than those of pollinators. Pollinator progeny numbers were almost always higher than those of parasitoids. Though it has been suggested earlier that distraction by the presence of female plants might lower parasitism rates in male figs as compared to monoecious species (Weiblen et al. 2001), our results did not show any significant variation in parasitism rates in the presence or absence of female plants.

The densities of female figs were very similar to those of male figs in the two populations. If equal numbers of foundresses are being attracted by female figs and, thus, being lost from the mixed population, then the population densities of pollinators might be expected to be reduced. However, our results indicated that although the female plants were clearly removing foundresses from the system, they had no effect on progeny densities, perhaps due to a super abundance of pollinator females as mentioned above. If the female plants were reducing the numbers of foundresses entering figs and ovipositing in the mixed population, then the progeny sex ratio was expected to be more female biased, but again this was not observed, suggesting that the number of foundresses laying in each fig was not altered. Larger pollinator clutches contain a higher proportion of females (Moore et al. 2005). In *K. tentacularis*, brood sex ratios (percentage of males) increase with increasing foundress densities (Moore et al. 2002). This is in agreement with many other studies conducted on fig wasps (Hamilton 1967; Frank 1985; Herre 1985; Pereira and Prado 2006). However, it is worth mentioning that realized sex ratios (based on numbers of adult male and female offspring) in *K. tentacularis* do not necessarily reflect primary sex ratios in this species, because larval mortalities are sometimes high and may not necessarily be similar among male and female offspring (Ghana et al. 2012). *K. tentacularis* foundresses have also been shown often to

298 contribute unequally to two foundress broods and also to adjust their sex ratios according
299 to the size of clutch they lay (Moore et al. 2005). Foundresses of this species adjust the
300 proportion of males in their clutches by laying mostly males eggs first (Raja et al. 2008a).
301 The same study revealed that *K. tentacularis* foundresses lay different brood sizes when
302 they are allowed to oviposit for different lengths of time. In addition, the foundresses of
303 this species often re-emerge and are capable of ovipositing in as many as four figs on the
304 same tress (Suleman et al. 2013c). In the second and subsequent figs, the foundresses
305 show similar sex ratio adjustment behaviour to that in the first, but lay fewer eggs (Moore
306 2001; Zavonda 2004; Raja et al. 2008a) so are less likely to be limited by oviposition
307 sites, and therefore to respond to competition with other foundresses. Pollinator sex
308 ratios in this species are therefore controlled by many factors. The sex ratios of the
309 pollinators were similar in the two populations. More female biased sex ratios might
310 have been expected if female figs had killed substantial numbers of foundresses, because
311 fewer foundresses would have entered each fig, allowing each foundress to lay more male
312 eggs.

313 The proportion of males of the parasitoid *Sycoscapter* sp. was higher in the
314 population where no female plants were present. Little is known about the sex ratios of
315 non-pollinating fig wasps (Patel 1998), though they are often closer to 50:50 than those
316 seen in pollinator species, reflecting the more out-bred population structure exhibited by
317 species which oviposit from the outside of the figs. As *Sycoscapter* oviposits externally,
318 through the fig wall, they can spread their offspring across several figs; hence sex ratio
319 adjustments in these wasps do not fulfil the requirements for LMC. If, like the
320 pollinators, *Sycoscapter* females adjust their sex ratios in response to the number of

progeny laid by other female parasitoids, then higher sex ratios in the males-only population may reflect various possibilities. Either there were higher densities of adult female parasitoids, or there are fewer adult females present, but they are revisiting the same figs to oviposit and are not able to distinguish between the figs that had been visited by them previously. This might end up in a less female biased sex ratio. In the mixed population, more female biased sex ratios might be attributable to the distraction and wastage of time due to the presence of female figs, but there was no other evidence to suggest this.

This study for the first time throws some light on the impact of female plants on plant-pollinator-parasitoid relationships in dioecious fig species, but perhaps because the wasp species were always present in abundance, we could not get remarkably different scenarios with the presence or absence of female figs. Also, for the time series analysis 15-month period turned out to be too short to assess the population dynamics of the wasps. Further work will be needed to fully depict the extent of the variation we observed and its implications for both figs and wasps.

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454 **Table 1 (Variation in numbers of male and female pollinators; male and female**
455 **parasitoids and the total wasps in male figs only and the male and female mixed**
456 **populations (N= 300 figs from each population)**

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Factors tested	**Male figs only Population**			**Male and female figs Population**		
	Mean	**SE**	**Range**	**Mean**	**SE**	**Range**
Female pollinators	22.17	1.13	0-139	20.52	0.98	0-122
Male pollinators	5.49	0.53	0-78	4.41	0.39	0-55
Total pollinators	27.65	1.29	0-165	24.93	1.07	0-136
Female parasitoids	5.54	0.48	0-71	7.80	0.54	0-49
Male parasitoids	5.71	0.44	0-45	3.04	0.21	0-30
Total parasitoids	11.25	0.76	0-94	10.84	0.70	0-79
Total wasps	38.88	1.45	3-166	35.77	1.24	3-148

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Table 2. Two-way ANOVA comparing numbers of pollinators and their parasitoid per fig over a period of fifteen months. One glasshouse contained only male figs, the other a mixed population of male and female plants.

Factors tested	Glasshouse populations			Sampling dates			Glasshouses * sampling dates		
	F	df	P	F	df	P	F	df	P
Female pollinators	1.92	1	0.16	4.17	29	< 0.001	1.66	29	0.120
Male pollinators	2.31	1	0.13	1.92	29	0.003	1.12	29	0.300
Total pollinators	3.06	1	0.08	3.69	29	< 0.001	1.78	29	0.008
Female parasitoids	0.53	1	0.46	3.23	29	< 0.001	2.07	29	0.001
Male parasitoids	0.95	1	0.33	2.51	29	< 0.001	2.01	29	0.002
Total parasitoids	0.002	1	0.96	3.01	29	< 0.001	2.06	29	0.001
Total wasps	2.74	1	0.09	3.77	29	< 0.001	2.15	29	0.001

480 **Table 3. Variations in densities per fig of fig wasps in fig tree populations with and**
481 **without female plants. Coefficients of variation (CV) are from Verrill, 2006).**

Factors tested	**CV2**	**CV1**
	Male figs only Popn.	**Male and female figs Popn.**
Female pollinators	88.46%	82.53%
Male Pollinators	167.35%	153.79%
Pollinators	81.09%	74.42%
Female Parasitoids	130.14%	120.32%
Male Parasitoids	122.04%	111.02%
Parasitoids	117.75%	112.39%
Total wasps	64.64%	60.14%

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493 **Table 4. Sex ratios (proportion males) of pollinators and parasitoids in fig tree**

494 **populations with and without female plants.**

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Factors tested	**Male figs only Popn.**		**Male and female figs Popn.**		**F (df)**	**P**
	Mean	SE	Mean	SE		
Pollinators	0.19	0.01	0.18	0.01	$0.88_{(1, 596)}$	0.35
Parasitoids	0.39	0.02	0.33	0.02	$9.89_{(1, 494)}$	0.002

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Figure Legends:

Fig. 1 Total figs produced by female plants (a) and male plants (b) in the mixed population and male plants (c) in the males only population over a period of fifteen months.

Fig. 2 Mean numbers of different phases of figs on female (a) and male plants (b) in the mixed population and on male plants (c) in the males only population over a period of fifteen months.

Fig. 3 Population trends of pollinators and parasitoids in (a) the mixed population of male and female figs and (b) the male figs-only glasshouse over a period of fifteen months.

Fig. 4 Autocorrelation function analyses (ACF) of mean pollinator and parasitoid numbers per fig in (a) the males-only population and (b) the mixed population. The solid lines represent the correlation coefficients, and the sloping lines represent the confidence intervals of two standard errors that identify significant lags and their periods in fortnights ($p < 0.05$).

Fig. 5 Cross correlation function analysis (CCF) of mean pollinator and parasitoid numbers per fig in (a) the males-only population and (b) the mixed population.

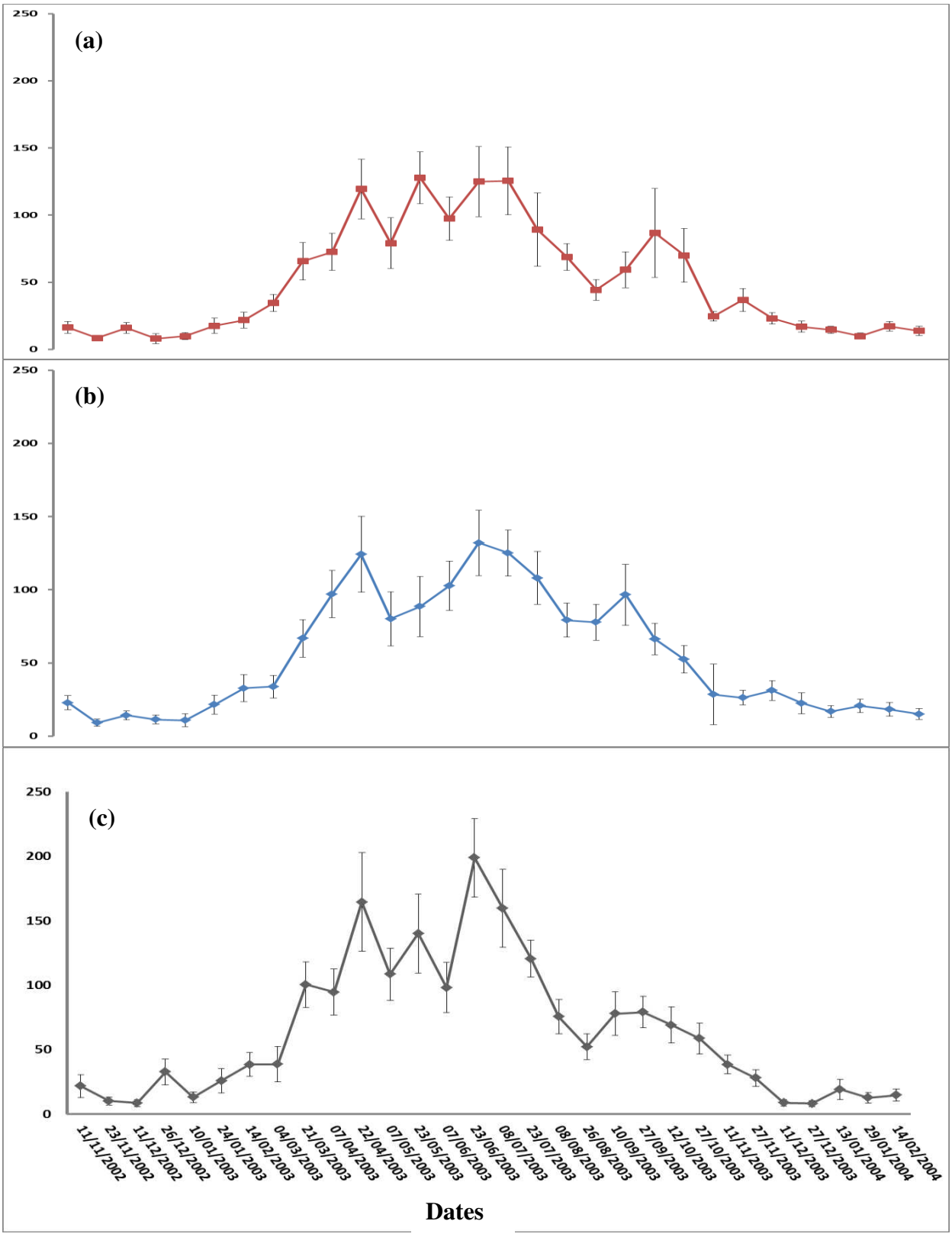
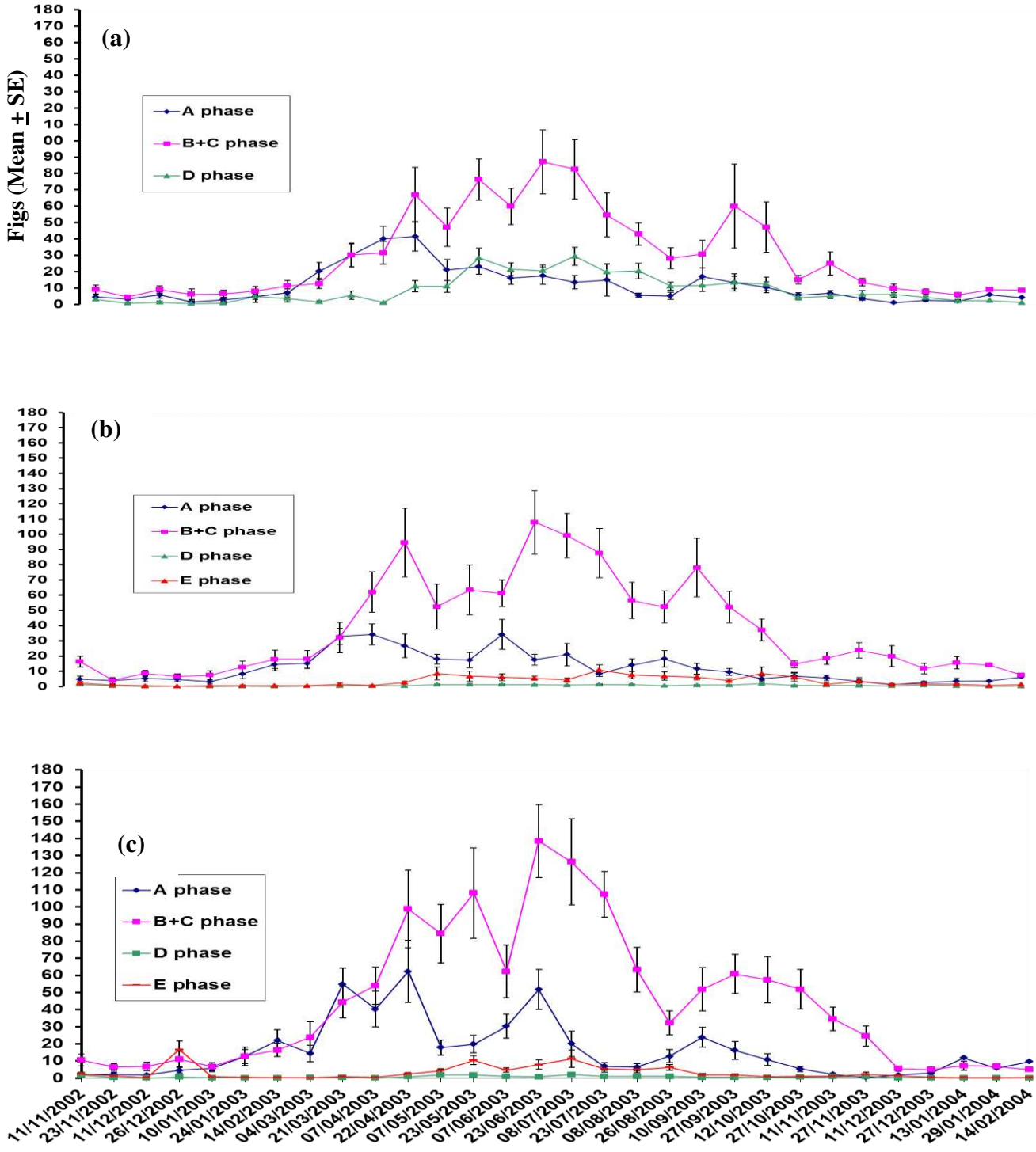

(a)
(b)
(c)
Figs (Mean ± SE
250
200
150
100
50
0
11/11/2002
23/11/2002
11/12/2002
26/12/2002
10/01/2003
24/01/2003
14/02/2003
04/03/2003
21/03/2003
07/04/2003
22/04/2003
07/05/2003
23/05/2003
07/06/2003
23/06/2003
08/07/2003
23/07/2003
08/08/2003
26/08/2003
10/09/2003
27/09/2003
12/10/2003
27/10/2003
11/11/2003
27/11/2003
11/12/2003
27/12/2003
13/01/2004
29/01/2004
14/02/2004
Dates

Fig. 1


(a)
A phase
B+C phase
D phase
Figs (Mean ± SE)
(b)
A phase
B+C phase
D phase
E phase
(c)
A phase
B+C phase
D phase
E phase
11/11/2002
23/11/2002
11/12/2002
26/12/2002
10/01/2003
24/01/2003
14/02/2003
04/03/2003
21/03/2003
07/04/2003
22/04/2003
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23/05/2003
07/06/2003
23/06/2003
08/07/2003
23/07/2003
08/08/2003
26/08/2003
10/09/2003
27/09/2003
12/10/2003
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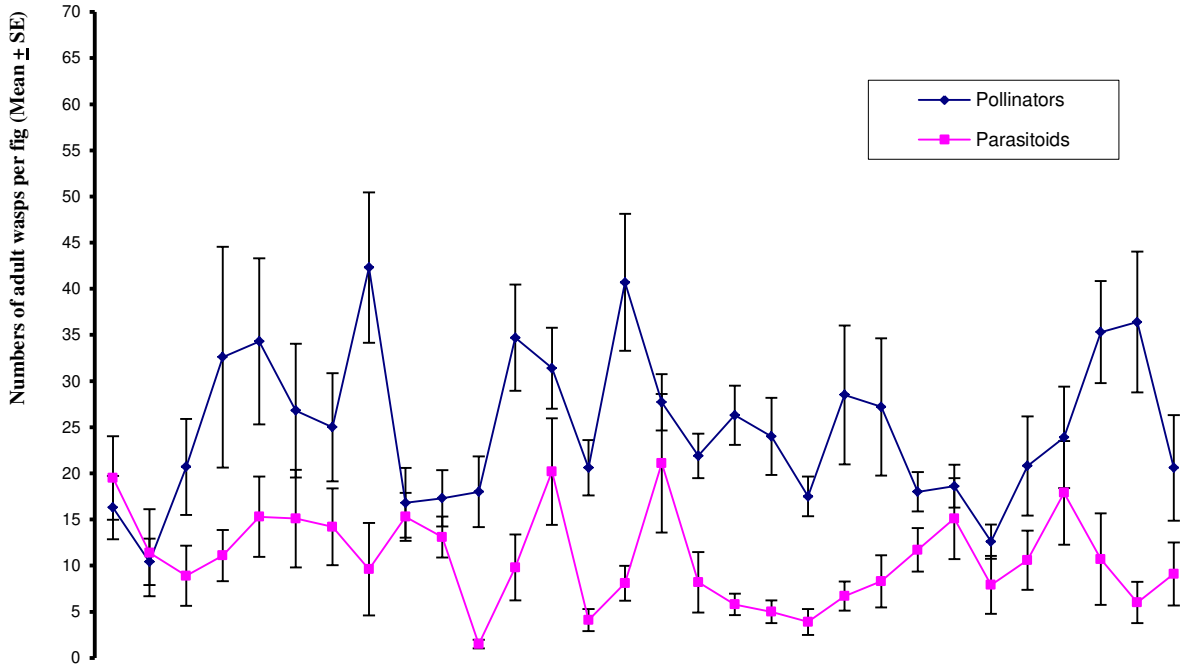
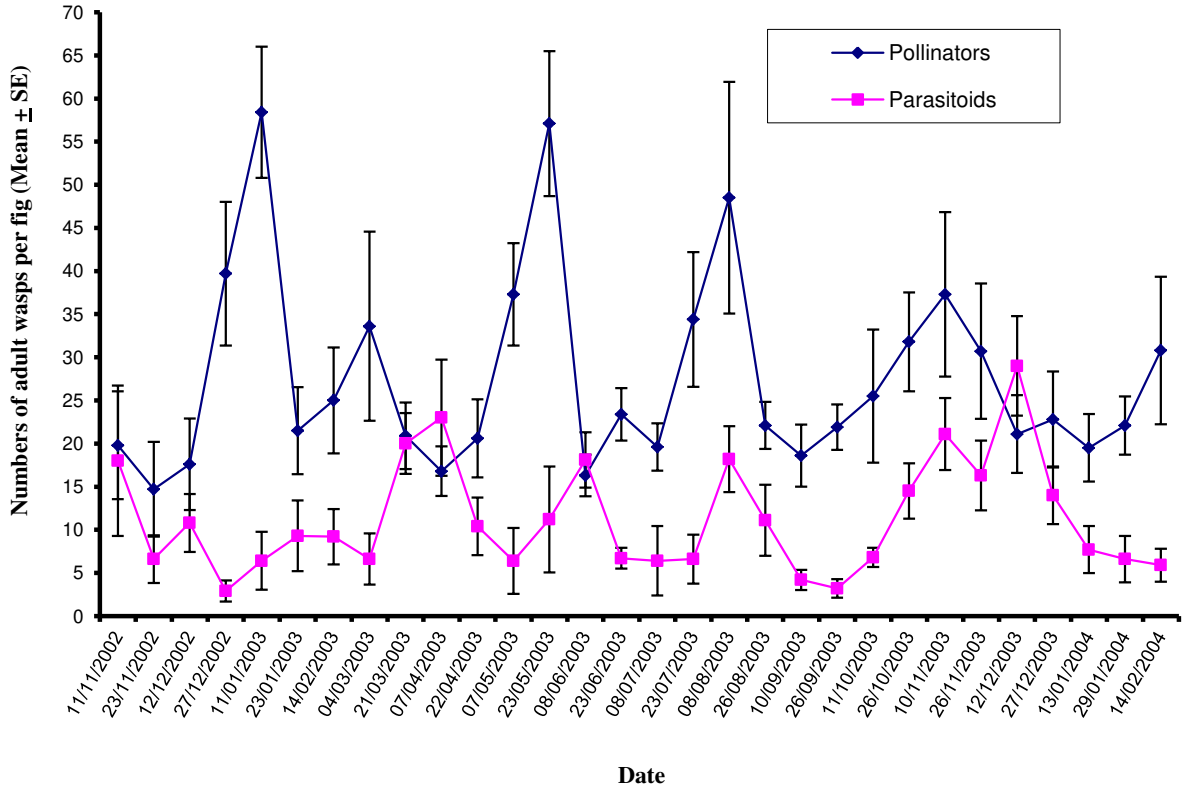
11/11/2003
27/11/2003
11/12/2003
27/12/2003
13/01/2004
29/01/2004
14/02/2004
Dates

Fig. 2

(a)

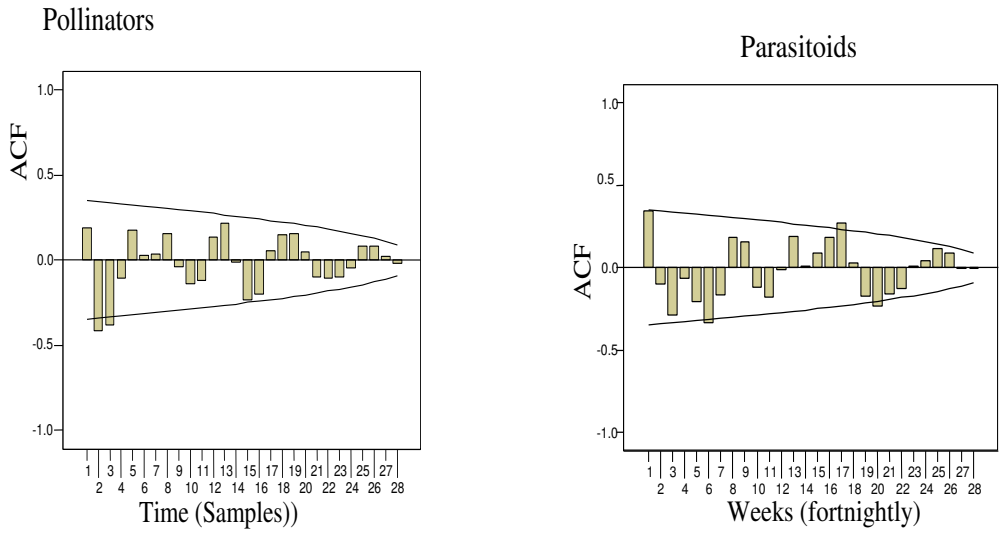

Numbers of adult wasps per fig (Mean ± SE)
Pollinators
Parasitoids

(b)


Numbers of adult wasps per fig (Mean ± SE)
Pollinators
Parasitoids
11/11/2002
23/11/2002
12/12/2002
27/12/2002
11/01/2003
23/01/2003
14/02/2003
04/03/2003
21/03/2003
07/04/2003
22/04/2003
07/05/2003
23/05/2003
08/06/2003
23/06/2003
08/07/2003
23/07/2003
08/08/2003
26/08/2003
10/09/2003
26/09/2003
11/10/2003
26/10/2003
10/11/2003
26/11/2003
12/12/2003
27/12/2003
13/01/2004
29/01/2004
14/02/2004
Date

Fig, 3

(a)


Pollinators
ACF
1.0
0.5
0.0
-0.5
-1.0
1 3 5 7 9 11 13 15 17 19 21 23 25 27
2 4 6 8 10 12 14 16 18 20 22 24 26 28
Time (Samples))
Parasitoids
ACF
1.0
0.5
0.0
-0.5
-1.0
1 3 5 7 9 11 13 15 17 19 21 23 25 27
2 4 6 8 10 12 14 16 18 20 22 24 26 28
Weeks (fortnightly)

(b)

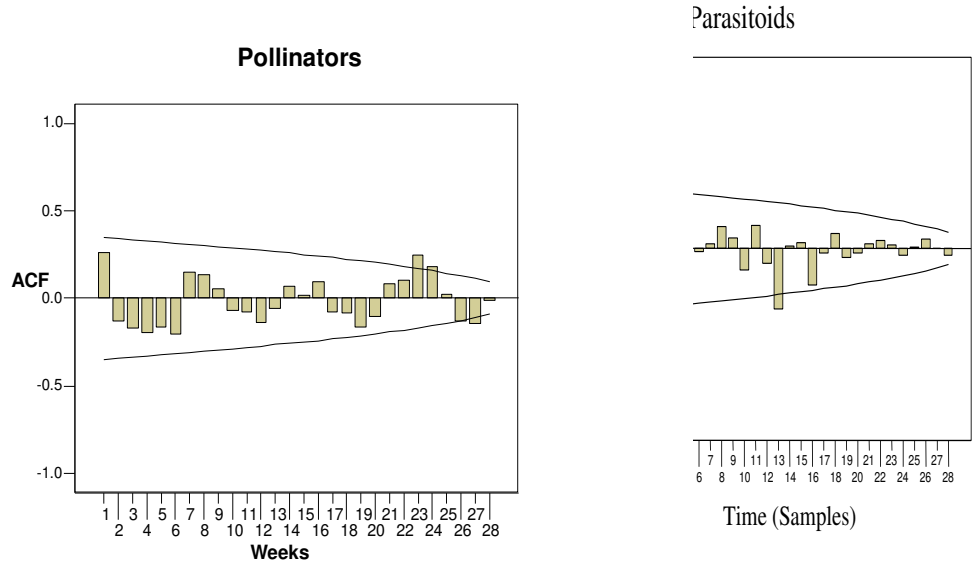
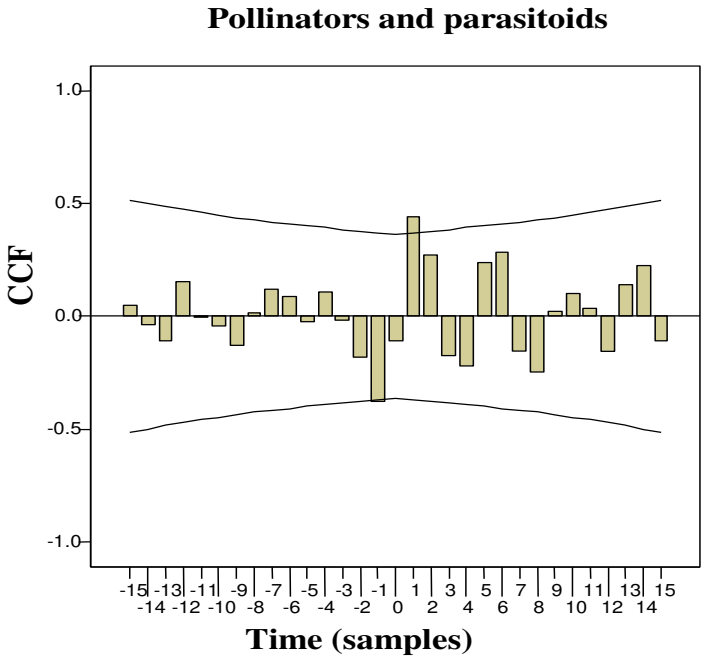

Pollinators
ACF
1.0
0.5
0.0
-0.5
-1.0
1 3 5 7 9 11 13 15 17 19 21 23 25 27
2 4 6 8 10 12 14 16 18 20 22 24 26 28
Weeks
Parasitoids
7 9 11 13 15 17 19 21 23 25 27
6 8 10 12 14 16 18 20 22 24 26 28
Time (Samples)

Fig.4

(a)



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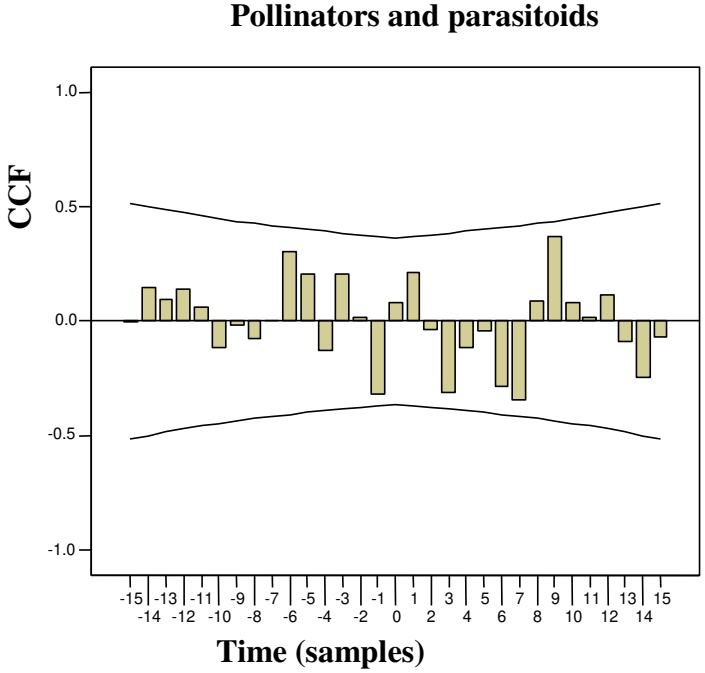
(b)



573
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577 Fig. 5
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